

**Biodiversity climate change impacts
report card technical paper**

Freshwaters, climate change and UK conservation

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Summary of main trends

Abbreviations for confidence levels: L, M, and H for Low, Medium and High agreement on a result or trend among the freshwater scientific community: Li, Me, Ro for Limited, Medium and Robust quantity and quality of evidence. Designations apply to all previous sentences after an earlier designation.

1. Freshwaters form a connected system (Section 1.1) that links rain, standing and flowing waters, the land and the ocean. The basic ecological unit is the catchment [H,Ro]. From it come ions that influence community composition, key nutrients that determine production, and combined energy in the form of organic matter that is the main energy source for pristine streams and a major source for lakes and lowland rivers [H,Ro]. Climate influences all these deliveries through temperature effects on mineralisation, amounts of runoff water and residence times of the water.

Temperature, through effects on metabolism and growth rates, and chemical reactivity, influences virtually every aspect of freshwater ecosystem function. [H,Ro]. Climate change also affects the atmosphere (through storminess for example) and thence the chemical composition of rain (which bears sea spray) and the delivery of air-borne pollutants such as sulphur and nitrogen compounds [H,Ro].

2. Climate change is superimposed on existing large human-made impacts, which make separation of its effects particularly difficult (Section 1.2). These influences include drainage engineering, damming, acidification and eutrophication [H,Ro], and considerable interference with fish communities by both legal and illegal stocking [H,Ro]. There are notable effects of introduced species (Section 3.8), with a few (for example common carp, Canada geese, mink) being particularly widespread and strong [M,Me]. The freshwater biota of Britain and Ireland is not rich compared with mainland Europe because of isolation by the sea since 7000 BCE [H,Ro] and so niches are broad (Section 1.3) and new species have often been accommodated without major problems [L,Lo]. There is no room for complacency because the advance of a new introduced species is difficult to predict [H,Me], but hysteria is also inappropriate.

3. Research in freshwaters has concentrated on processes and predominant species (Section 2) and there is less emphasis on individual charismatic species than in terrestrial systems [L,Li]. This approach lends itself to space-for-time studies on climate effects. There has been a modest amount of experimentation, largely in standing water mesocosms, and analysis of long-term biological data sets, the most extensive from lakes [H,Ro]. Flowing waters offer more long-term hydrological data, but less targeted ecological information [M,Me]. There is high sophistication in creating predictive hydrological models for flowing waters but linking these to ecological consequences is yet at an early stage [H,Me]. A large literature on future climate effects on fish depends extensively on extrapolation of their temperature characteristics to future climate scenarios (Section 5.5). The most detailed information on ecological effects comes from lake plankton (Section 5.1) [M,Me].

4. Freshwaters are inevitably disturbed systems because water readily freezes and evaporates, and wind mixing and stream flow are energetic in changing habitat structure (Section 1.3). Their organisms have evolved considerable adaptation to disturbance [H, Me]. Except in wetlands where plants dominate, primary production is based mainly on microorganisms (a bacterial/protozoan system processing incoming organic matter, and many planktonic and bottom-living photosynthetic algae). Such highly diverse systems are capable, through species substitution and genetic adjustment, of withstanding most conceivable changes [H,Ro]. There is

evidence (Section 1.3), where it has been sought, primarily among the zooplankton, of rapid microevolutionary adjustment to temperature change [H, Li]. Many invertebrates are resilient to disturbance, some with resting stages, in contrast to a near complete absence of these in marine species. Freshwater organisms are more easily distributed the smaller they are. Many can fly as adults and birds redistribute others. Fish face more difficult barriers and in contrast to a largely bottom-up view (determination through physico-chemical processes acting on primary productivity) of how freshwater systems functioned in the past, top-down processes acting from the upper parts of the food web, through predation by fish on zooplankton, and zooplankton grazing on algae, are now known to be very significant (Sections 5.1, 5.2) [H,Ro]. These characteristics are likely to aid accommodation of freshwater processes even to severe climate change, but with changes in diversity that will be greater the larger the organisms [M, Li].

5. It is not yet possible to attribute any loss of species in Britain and Ireland specifically to climate change in the face of the considerable damage [H,Ro] from pressures such as eutrophication, infilling of ponds, and river engineering in particular (Section 1.2). Much of this damage results from downgrading of habitat, but some of it from loss, when wetlands are drained [H,Ro].

6. There is good evidence of raised air and lake temperatures and reduced ice cover in more northerly lakes [H,Ro] and in increased winter rainfall and reduced summer rainfall [H,Me] in the past 150 years, but annual variations are considerable and trends only show over long periods (Sections 3.1-3.3). Increased temperature leads to stronger and lengthier thermal stratification of deeper lakes, increased periods of hypolimnion or surface sediment deoxygenation, and greater release of phosphate, a key limiting nutrient [H,Me]. Much of this understanding comes from analysis of long-term data sets with inherent annual variation, and extrapolation to future scenarios. There is increasing acknowledgement, following severe flooding in 2014, of a greater frequency of heavy rainfall events and implications for sediment and nutrient loadings on lakes and rivers. The bulk of such loads comes from peak flows [H,Me]. There is a strong link, because of the continuity of the system (Section 1.1), between upstream damage, such as loss of wetlands, and damaging consequences for downstream freshwater communities [H,Ro]. A prominent current trend of increasing concentrations of dissolved organic matter in stream waters (browning) [H,Ro] may be linked with warming [L,Lo] and has implications for light absorption and production in lakes (Section 3.4). Climate change, through increased flooding and increased drought, may have positive effects in maintaining pond diversity but equally, permanent ponds may become temporary and land use change may decrease water quality [H,Ro]. Ponds contain a great deal of British freshwater diversity [H,Ro].

7. Coastal lakes behind beach barriers are very vulnerable to rising sea levels (Section 3.5). There is high risk of loss of them as freshwater systems [H,Me]. Estuarine grazing marshes are also vulnerable. Such sites will become brackish or marine [H,Me]. Rural industries, like reed and sedge cutting, providing conservation management in such areas, may decline [M, Me].

8. There is good evidence (Section 3.6) of changed phenology of freshwater organisms and of northward movement of some freshwater invertebrates with winged adult stages [H,Ro], but none that this has yet created significant problems for conservation [L,Li]. The pattern of phenological change differs among terrestrial, marine and freshwater habitats and among plants, invertebrates and vertebrates [M,Me] and there is no underlying hypothesis to explain the differences. Responses of individual species are highly idiosyncratic and patterns are appearing mostly in overall processes [H,Ro].

9. Lake plankton (Section 5.1) has provided the best examples of climate change effects because it is easily investigated and long-term data sets have been maintained. Behaviour of the lake plankton provides analogies for effects that may be occurring in less well investigated aspects of freshwater systems [H,Li]. There is good evidence of direct and indirect (through changes in hydrology) effects on seasonality, community composition, parasitisation, grazing and production, with effects occurring at different rates among physical factors, phytoplankton, zooplankton and zooplanktivorous fish. These are causing somewhat individualistic changes in the seasonal patterns of each component and the implications of these are not yet clear [H,Ro].

Space-for-time studies at different latitudes suggest that warming will likely lead to greater incidence of cyanobacteria in the plankton (Sections 5.1.2, 5.1.4), that the incidence of surface blooms will increase, and that perhaps toxicity will be affected [H,Li]. Such effects have not yet been systematically recorded but one tropical cyanobacterium has invaded northwards and has reached northern Germany. In rivers, plankton is significant only in the lower reaches but it has not yet been possible to disentangle climate effects [H] from the many other impacts on such large rivers [H,Ro].

10. Aquatic plant communities are influenced by warming, with a tendency for floating species and introduced species to become more prominent [M,Me] (Section 5.2). A few introduced garden floating plants of warm temperate origin that currently do not survive the winter, may eventually persist (as likely as not) and become problems on their inevitable escape into the system [L,Li]. Most introduced species come from warmer, more continental, sources and it is likely that, with warming, introduced species may establish more readily than at present [L,Li]. Moreover, since the main pathways for introduction are through the lowest quality waters (lowland rivers and reservoirs and canals), there may (likely) be selection for particularly competitive species [L,Li] (Section 3.8). Climate change increases the symptoms of eutrophication in both plankton and littoral plant communities [H,Me] (Section 4). Warming will mean that attempts to restore freshwaters from eutrophication (generally the most severe pressure on sites of conservation importance) will be hampered (virtually certain). Wetland plant communities may benefit from climate change if engineered floodplains are restored for flood control, but may otherwise suffer in extent and biodiversity from summer drought [H,Me].

11. There has been an increase in biodiversity of macroinvertebrates (Section 5.4) in headwater streams and middle reach rivers in the UK in the last few decades, largely because of improvements in wastewater treatment [H,Ro]. There is evidence of some reduction in biodiversity with warming in some previously acidified but now recovering upland streams [H,Li]. Further warming will have effects (very likely) if summer flows are significantly reduced. Nutrient loads, not least of nitrate, are likely to increase with increased winter rainfall; high nitrate levels are associated, at least in lakes, with reduced plant diversity. Levels, however are already widely above the critical band for reduction of diversity. Chalk streams may dry out for longer periods [H,Me].

12. Dragonflies and damselflies, being charismatic, have been particularly well investigated (Section 5.3). Most species have shown changes in range and there is experimental evidence that they may benefit from warming. The group is of tropical origin. Both nymphs and adults are important predators with potential effects on other invertebrate populations, both aquatic and aerial [H,Me].

13. Cold-water fish communities are changing greatly as a result of climate change [H,Me] (Section 5.5). Arctic charr is becoming scarcer in the Britain as waters warm,

and it competes less well with the more thermally tolerant brown trout. In Britain, the status of coregonid fish, whose distribution in fewer than ten lakes is at the southernmost part of their subarctic ranges, is very likely to become increasingly threatened [H,Me]. Models predict changes in fish communities with warming on continuous landmasses but our island status makes future changes less predictable. However, we may expect (very likely) declines in the lowlands of cold-water salmonids and increases in warm-water cyprinids, with earlier reproduction (Section 5.5.1). There may be declines in oxygen-demanding predators such as pike and perch [H, Me] and consequent higher survival of more small fish that are intensely zooplanktivorous. The effects of these will be (very likely) to damage the conservation interests of plant-dominated shallow lakes by removing zooplankton grazers and allowing development of greater phytoplankton crops that will shade out submerged plants [H,Ro] (Sections 4.3, 5.2.1 and 5.5.1) .

Atlantic salmon is generally declining for many reasons and warming will further threaten it. Carp, an extremely damaging fish to conservation interests, is virtually certain to expand its range northwards and breed more effectively, but increased spread will occur anyway because of its popularity among anglers [H,Me]. There may (likely) be changes in the incidence of fish diseases [M,Li]. Parasites are common and normal components of freshwater systems and may have subtle but not easily predictable effects as temperatures increase. An extreme scenario with a 4°C increase in water temperature could deprive southern and central England of almost all native fish bar tench, with an emerging dominance of common carp (as likely as not) [L,Li] (Section 5.5.1).

14. Amphibians (Section 5.6) are generally declining in the UK, as elsewhere, and summer drought is one of the underlying reasons in warmer countries [H,Li]. In the UK there is evidence of earlier breeding with warming and natterjack toads, at the northern end of their range in Northern Ireland may be favoured (as likely as not) by increased temperatures but not further south [L,Li]. Fish-free ponds favour tadpole survival, and drier summers may increase the numbers of these through occasional complete drying out, which fish communities will not survive [L,Li].

15. The distribution of wetland birds has been affected by warming (Section 5.7), with significant movements of at least some ducks and waders eastwards or north-eastwards [M,Me]. There have been overall declines in many species at particular southern British sites These may be due to birds not now needing to migrate so far southwards to obtain food [L,Li]. There may be greater risks (as likely as not) of bird botulism in the future because of increased amounts of windrowed algae rotting along lake margins [L,Li]. Birds have significant effects on freshwater systems but there is not enough information to assess the top down impacts of changing bird communities on lakes and wetlands [H,Li].

16. The effects of climate change on regulatory ecosystem services (which depend mostly on microorganisms and dominant plants) are likely to be more important than those on the biodiversity of charismatic species [M,Li] (Section 6). Experiments have shown that the ratio of respiration to gross photosynthesis increases quite significantly with rising temperature and pristine freshwater systems are often, perhaps overall, net heterotrophic systems, fuelled by organic matter coming from the land. This material is respired in freshwaters or passed on to the ocean, and freshwaters focus much of the return of carbon dioxide to the atmosphere from net production on the land. They are also major sources of methane. Carbon processing in freshwaters has been under-researched [M,Me].

17. Climate effects acting to change nutrient flows (increased rainfall, greater mineralisation on land) and therefore increasing the severity of eutrophication are

virtually certain to be more important than direct temperature effects on freshwater systems unless the temperature change is large, when changes in fish communities will become very important [H,Ro] (Sections 5.5.1 and 7). Increased rainfall and flood problems may (as likely as not) result in restoration of wetland systems and biodiversity in presently drained lowland valleys [L,Li]. It may (as likely as not) also lead to increased pressure for river engineering and consequent damage to major rivers that are already severely impacted and to which restoration of species diversity is proving difficult despite restoration of habitat features [H,Me]. Many techniques exist for ameliorating the effects of human impacts on freshwaters (Section 7), and the scope for adapting to climate change effects rests indirectly on these. Re-establishment of shade trees overhanging headwater streams and relocation of coldwater coregonids to a greater range of lakes at higher altitudes are possible. Otherwise strategies for adaptation are largely to reduce the impacts of other factors, like acidification, eutrophication, water abstraction and river engineering whose symptoms may be made worse by climate change [H,Ro]. Data on the key role of freshwaters in the global carbon budget (Section 6), however, carry implications that much more radical thinking may be needed (Section 7).

1. Introduction

1.1 Ways of viewing freshwater systems determine how climate change effects are seen

Freshwaters lend themselves to metaphors. Lakes have been described as sentinels, integrators and regulators for climate change (Williamson et al., 2009; Schindler, 2009)). Water bodies are sensitive to climate because the span from melting to boiling points of water largely overlaps the envelope of temperature on Earth, so that freezing, evaporation and condensation are prominent in the water cycle, and changes in these processes are quickly reflected (sentinels) in the state of large water masses. Lake sediments and wetland peats record changes in past climates, and analysis of them contributes to understanding long-term changes (integrators); and significant amounts of carbon delivered in run-off from the land are stored, respired and exported from lakes and wetlands, which are key points in the carbon cycle (regulators).

A less grandiloquent alternative is to see the water cycle as a bloodstream for Earth. Such an analogy accounts for a two way-movement of materials and energy between the waters and the land, manifested in the modern concept of the catchment area (watershed or river basin in American or European terminology) as the fundamental unit of ecology. From it, water, minerals, inorganic nutrients, and energy in the form of particulate and dissolved organic matter, reach rivers, lakes and wetlands. The atmosphere is also part of the system, bringing substances to the catchment in rain, often from large distances well outside the watershed.

Return movements of substances and energy from water to atmosphere and land complete the bloodstream analogy. In North America and eastern Russia, Pacific salmon migrate from river headwaters to the deep ocean, and return with stocks of nutrients in their bodies that fertilise surrounding forest trees through feeding on

them, then excretion and defaecation, by bears and other mammals and birds (Naiman et al. 2002; Helfield & Naiman, 2006). Likewise, moose in Canada import significant quantities of nitrogen to the land following their feeding on submerged plants in lakes and rivers (Bump et al., 2009). In many regions, riparian spiders, bats, birds and lizards depend on the emergence of adult insects from larvae that have spent most of their existence underwater (Baxter et al., 2005). Everywhere, freshwaters are focal points for return of carbon dioxide, fixed on land, to the atmosphere (Cole et al., 2007; Cole, 2013). The implications are that climate change effects on freshwaters are intimately linked with climate change effects on land and in the atmosphere. Many of them may be hidden in a nexus of complex processes and very difficult to disentangle. Moreover there are already many severe human influences on freshwaters, also manifested through activities on land, which further obscure effects of climate change.

1.2 Other impacts on freshwaters complicate detection of climate change effects

British and Irish catchments are *never* unimpacted (National Ecosystem Assessment, Maltby et al. 2011). Deforestation since the Neolithic has altered the relationship between land and water by increasing nutrient leakage and soil erosion; modern farming and forestry can deliver at least an order of magnitude higher loads of nitrogen and phosphorus per hectare than intact forest (Smith et al., 2003). Urbanisation and industry contribute large amounts of nutrients plus a panoply of miscellaneous pollutants both directly to the rivers and through the atmosphere as acidifying gases of sulphur and nitrogen. The large land animals that make connections between the forests and freshwaters in less disturbed landscapes have been extinct for centuries; likewise, migratory fish have severely declined in numbers through modification of river systems by drainage, water storage and power generation, water pollution and overfishing.

The relative youth of British and Irish landscapes, emerging from the ice only ten to fifteen thousand years ago, and soon isolated as islands, has curtailed the natural return of many species and given us an impoverished biota with generally broad niches. It is therefore vulnerable to invasion by exotic species, helped by the predilections of past estate owners, trade in aquarium fish, water gardening and aquaculture, the popularity of angling and the discharge of ballast water from ships in estuarine ports. We have also created freshwater habitats as ponds and reservoirs, scrapes and artificial wetlands for many purposes; we have moved native species, particularly fish, outside their former ranges within Britain and Ireland, potentially threatening genetically complex populations where species like trout and charr are differentiating into new species (Jonsson & Jonsson, 2001; Ferguson, 2004; Adams & Maitland, 2007; McKeown et al., 2010); and we have altered the patterns of water availability and organism distribution through canal building, regulation of rivers, abstraction from surface and ground waters for irrigation, and by water transfers among formerly separated catchments.

The freshwater system, inevitably at the bottom of catchments of altered land, provides apparently inexpensive natural pipes for waste disposal; and freshwaters, being essential to all societies, are the most impacted of all natural systems (Millennium Ecosystem Assessment, 2005). This makes a clear separation of the effects of climate change from the accumulation of other past and continuing changes very difficult. See Bennion et al. (2012) for a partly successful palaeoecological attempt to do this using diatom communities in sediment cores from Loch Leven, Dong et al. (2012) for a lesser success in Esthwaite Water, and Battarbee et al. (2012) for a near admission of defeat.

1.3 Freshwaters are naturally disturbed systems and this may help accommodation of climate change effects

All freshwater systems are naturally disturbed because they are subject to freezing, to infinitely changing water flows that give varying retention times even in large lakes, to stratification caused by surface warming, and mixing by wind, to changes in water level and sometimes to drought, and, in small water bodies, to complete drying out. Fish are often vulnerable but other groups are resilient to such changes. For example, many freshwater invertebrates have resting or diapausal stages (Pennak, 1985); planktonic organisms are essentially r-selected; dispersal of many benthic insects is helped by life histories that include aerial stages; reproduction in many submerged plants is vegetative and turions are common; and many of the animals are essentially omnivorous with flexible diets rather than strict specialisation. There has been frequent selection for strategies to cope with change. Microevolutionary processes are also at work (Bradshaw & Holzapfel (2006), and rapid genetic adjustments to warming have been shown in zooplankton (Hairston et al., 1999; Van Doorslaer, 2007, 2009, 2010) and fish (Hendry et al., 2000; Jonsson & Jonsson, 2001) and are undoubtedly occurring in other invertebrates and certainly in microorganisms.

The rapid replacement of water (retention times from days to months in Britain and Ireland) means that pollutants are rapidly diluted and recovery can be quick, provided the source has been removed. The physical structure of the habitat, particularly in engineered river systems, may be expensive to replace, and changes in the catchment are even more difficult to remedy, but rehabilitation of a functioning freshwater system is, in theory, comparatively easy, provided particular stipulations are not made for the occurrence of particular species, rather than of biodiversity in general. The implications of this are that changes induced by climate are likely to be coped with more easily than in steady, predictable systems like old forests or the deep ocean.

2. Scope and limitations of the review

The literature on climate change is now very large. The 'Web of Science', with largely peer-reviewed papers, has been used as the main basis for this survey. There have been two substantial recent books on climate effects in freshwaters (George, 2010; Kernan et al., 2010) and Moss (2012) recently reviewed major aspects of climate change on the chemistry of lakes. This review is not exhaustive on a world scale but is representative and attempts fuller coverage for Britain. Most processes in freshwaters are influenced by temperature and water flow, and there is a substantial literature attempting to predict future changes in these, though with considerable uncertainties owing to the imprecise nature of future climate change and much greater problems in linking ecological effects. Chaining of such models from the climatic to the hydrological to the biological is nonetheless being attempted, but Prudhomme et al. (2003) cast a cautionary note. They calculated uncertainties in effects of climate change for five British catchments from a set of 25,000 climate scenarios randomly generated by a Monte Carlo simulation, using several Global Climate Models (GCM), emission scenarios and climate sensitivities. Future flood scenarios were compared with current conditions. Most scenarios showed an increase in both the magnitude and the frequency of flood events, but the greatest uncertainty was from the type of GCM used, with predicted changes varying by a factor of up to 9 in Northern England and Scotland. The significance of predictive modelling will increase when better estimates of future changes can be made, but for the moment I have taken a conservative view in assessing its results.

Freshwater research has concentrated on environmental drivers, like water flow and retention, processes such as productivity, mineralisation, nitrogen fixation, respiration, and phenomena such as seasonality, disturbance, food web structure and trophic cascades rather than on individual species responses. This contrasts with terrestrial ecology, where there is a strong tradition of population studies on individual species. Important processes in freshwaters are strongly microorganism - based, because of the importance of bacteria in degrading organic matter derived from both land and water, and algae in the plankton and littoral as the major photosynthesisers. There are strong linkages with an extensive invertebrate community, but conservation assessments tend to concentrate on larger organisms, particularly aquatic plants, adult odonates and fish. Vertebrates, particularly top predators, have key roles (Estes et al. 2011) but the relevant macrofauna of the UK has largely been destroyed. We are thus, in Britain and Ireland, always looking at already severely altered systems, and climate change effects must be seen in this context.

Most freshwater in Britain and Ireland is in Scotland, then Ireland and Wales, and in general its value for nature conservation is in the uplands of the north and west, where agriculture is less intense and human populations and their impacts are smaller. In contrast, England has more varied water chemistry owing to a greater variety of rocks, the greatest pressures on its water resources and the more severe problems for freshwater conservation. This review will consider the whole system but there is much more climate-related information on lakes, rivers, and catchment – linked effects than on other habitats, and for some components, like springs, many wetlands, temporary ponds and cave systems, all that is available is speculation. For convenience, but at the risk of creating a misleading emphasis, biological groups for which there is adequate information (plankton, river benthic invertebrates, aquatic plants, odonates, fish, amphibians and wetland birds) will be reviewed as categories.

Warren (2006) reviewed (though with little attention to freshwaters) current and projected effects of increasing temperature and sea level rise on natural systems, in a book (Schnellhuber et al. (2006) that discusses the implications of dangerous climate change, currently still nominally set at a threshold of a 2 °C increase in global mean temperature over the long-term average. Recent reports of the Intergovernmental Panel on Climate Change (2014) confirm Warren's list. There is much evidence that current mean global change (0.6-0.7 °C) has measurable effects and increasing concerns that temperature will rise by much more than 2 °C by the end of this century (Anderson & Bows, 2008; Jordan et al., 2013; IPCC 2013). The relevance of threshold numbers, however, is increasingly questioned for there is a continuum of projected effects as temperatures increase, and temperature is only one aspect of climate change and not necessarily the most important for aquatic systems. In considering the future in this review, no assumptions are made as to what is 'safe' or indeed as to what is acceptable.

The nature of the information on freshwaters is varied. First there are long-term temperature and biological records for several past decades, and less precise but much longer (millennial) records from lake sediments (Battarbee 2000; Catalan et al. 2013); secondly there are space-for-time studies in which changes along existing climate gradients are used to project possible future status based on predicted climate scenarios. Thirdly there are experimental studies. Temperature has long been examined in the laboratory as an important physical variable affecting freshwater animals, particularly through its many physiological effects and its determination of saturation oxygen concentrations, but what is important for conservation is more the behaviour of the organism in its ecosystem, and so whole-system experiments are emphasised here.

Experiments have been made in replicated mesocosms in shallow lakes across natural climate gradients from the Boreal zone to the Mediterranean (Moss et al., 2004) and in controlled and replicated warmed mesocosms, the first of them in England (reviewed in Stewart et al., 2013) that give explicit information on temperature effects, though there are yet too few experiments to carry out meta-analyses that can eliminate the judgements inherent in the determination of initial conditions. However, phenomena can be isolated in mesocosms that are masked in less controllable whole lake systems (Graham & Vinebrooke 2009) and thus mechanisms can be more easily revealed. One system, in Denmark, is able also to reproduce effects of changing hydrology, an equally important climatic effect to temperature, but hitherto that has not been widely investigated. Mesocosm experiments on climate change in streams are very few (Ledger et al. 2013a,b) and have yet only examined the effects of drought, but not of warming *per se*.

3. Existing general effects of climate change on freshwaters in the UK

The latest reports of the Intergovernmental Panel on Climate Change (2013, 2014) confirm and strengthen previous findings. The expectations for western Europe are of continuing warming, greater total rainfall, more rain in winter and less in summer and a greater frequency of extreme events (torrential downpours, major floods, heat waves, droughts). A general summary of climate change in Europe is given by the European Environment Agency (2012) and there are three convenient summaries by the Department of Energy and Climate Change (2013, a,b,c) for the UK. There is ample evidence of an increasing trend in UK air temperatures with the increase a little greater than the global average (Perry 2006), though much lower than in the Boreal and Arctic. Long-term data series from freshwaters show clear evidence for warming in streams and lake surface waters (Livingstone, 2003; Granskog et al., 2006 (in the freshwater sections of the Baltic sea); Austin & Colman, 2007; Adrian et al. 2009 (for lakes); Shimoda et al. 2011; Orr et al 2014 (for UK streams), and for hypolimnetic warming in large lakes (Dokulil et al., 2006, 2013), and decreasing ice cover in northern and high-altitude lakes (Magnusson et al., 2000; Granskog et al., 2006).

Air temperature in central England has increased by about 1 °C since 1980 and there is a general correspondence between air and water temperatures where both are available, with deviations where other factors like change in land use or damming have come into play (Orr et al., 2010). The most complete data sets for water temperature in lakes are from the English Lake District where records date back to the 1940s. In Esthwaite Water, there was a slight fall from 1940 until 1980 but then a greater rise until the present day, giving a net increase of about 0.6 °C over the period, which is matched by the change in air temperature (Dong et al 2012). Air temperatures increased from 1910 until the 1940s, then fell a little until 1980 before increasing again at many stations in the UK.

The state of the winter North Atlantic Oscillation index (NAOI; milder when positive) has been shown widely to influence temperature in lakes (Blenckner & Hillebrand 2002), not least in Esthwaite Water and in inshore mean water temperature in Windermere with a mean of 10.4 °C between 1961 to 1990 but then a significant rise to a mean of 11.5 °C between 1991 and 2005 (Winfield et al., 2008). There are more long-term data for rivers (Hammond & Pryce, 2007; Orr et al., 2010, Orr et al., 2014). The River Thames at Oxford has increased in temperature by 1.25 °C since 1882 (Worrall et al., 2012); streams around Lyn Brianne increased in temperature between 1981 and 2005 (Durance & Ormerod (2007). Stream temperatures may be influenced by other factors than climate change, such as variations in reservoir

discharges and changes in the North Atlantic Oscillation Index but the Llyn Brianne streams were above the reservoir and the effects of the NAOI were corrected for, still leaving an increase in forest streams of 1.4 °C and in moorland streams of 1.7 °C. Air temperatures in the surrounding Severn uplands increased by 1.7 °C between 1977 and 2005 (Biggs and Atkinson, 2011).

3.1 Ice cover

In colder countries there is extensive evidence of later freezing and earlier melting of the ice on lakes (Fig. 1). Such records have generally been kept where ice impedes access to ports and harbours and the effect is pan-global, not local (Magnusson, 2010). There are daily records of ice-cover for Loch Leven (Kinross) from 1968 to 1995 and Lake Windermere (Cumbria) from 1936 to the present (D.G. George, Environmental Change Network Web site, indicator 34, <http://www.ecn.ac.uk/iccuk/>). Loch Leven, a relatively shallow lake, may still be completely covered with ice during part of the winter, but the thickness has become reduced and unreliable so that the former annual curling competition is no longer held (May & Spears, 2012). Lake Windermere is rarely completely covered with ice, but sheltered bays usually freeze for several days every winter. There is a strong negative relationship between the number of days of ice-cover during January-March on Lake Windermere and the average air temperature for the first ten weeks of the year. This is influenced by the magnitude of the NAOI. In recent years, high values of the NAOI have been associated with mild winters that have been reflected in few days with ice cover on Lake Windermere. There has been a sequence of years when the lake has not frozen at all.

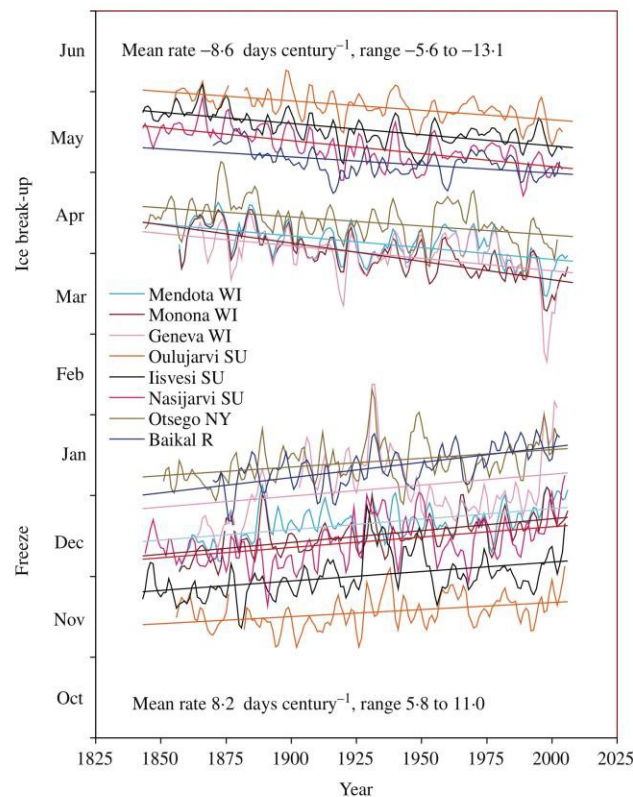


Fig.1. Long-term data on the dates of freezing (lower) and melting (upper) of ice on lakes in the USA (Wisconsin, WI and New York State, NY), Finland (SU) and Russia (Lake Baikal). From Magnuson (2010).

Ice cover may lead to inverse stratification and sometimes deoxygenation in shallow lakes, especially where the ice is covered with snow, which prevents any light penetration. The deoxygenation can lead to fish kills, but there are no published records for the UK. Reductions in ice cover are likely to continue in future but are unlikely to be of great consequence in Britain.

3.2 Summer stratification

Higher summer temperatures mean stronger and more stable direct thermal stratification (George 2007), especially in lakes with continental climates. British lakes deeper than a few metres do stratify in summer, but the thermocline is often mixed downwards and may be destroyed in windy periods, to re-form when the weather calms. Long-term, relatively stable, stratification is a feature of bigger lakes and reservoirs and, especially where the lake is eutrophicated, may lead to increased deoxygenation of the hypolimnion. This may lead to important chemical changes (release of phosphate from the sediments, accumulation of ammonium, soluble manganese and iron, and hydrogen sulphide). When the thermocline is temporarily deepened by wind, some of these substances may enter the epilimnion. This is minor however during the summer, and when overturn occurs in autumn, these substances are re-precipitated or reoxidised. There is little consequence for the lake ecosystem. In shallow lakes, the sediment surface may undergo severe deoxygenation, leading to iron sulphide formation (the black colour) as temperatures rise. Phosphate is not then re-precipitated and may be enriched in the surface waters. This may increase productivity in the plankton and have deleterious consequences, particularly where nitrate concentrations are high from agricultural fertilisation.

There is yet no direct evidence of an increase in these processes with warming in British lakes, though sediment or hypolimnion deoxygenation, linked with increased eutrophication, is common in areas like the Norfolk Broads and North West Midland meres and indicated by a prominent rise in phosphate in summer (Hameed et al., 1999; Kilinc & Moss, 2002). It is likely that summer processes have changed as expected with temperature rise, but have simply not been monitored. Climate-related physical effects on winter and early spring conditions have been detected in Esthwaite Water, Blelham Tarn and Windermere (George, Maberly & Hewitt, 2004; McGowan et al., 2012) and in Loch Leven (Carvalho & Kirika, 2003). Lake surface and bottom temperatures were strongly positively correlated with the NAOI, with the highest correlations being recorded in the shallower lakes. The NAOI is controlled partly by Rossby Waves, which are movements of air masses associated with the jet stream and whose behaviour has been shown to influence surface temperatures of the Lake District lakes throughout the year (Strong & Maberly, 2011), as opposed to the NAO influence mainly in winter. Warmer winters led to lower nitrate concentrations probably because of greater uptake by plants in the catchment. Dissolved phosphate increased in warm winters in the shallower lakes, but not in the deeper. This was attributed to heavier rainfall, which also reduced retention times and reduced phytoplankton development through wash-out.

In rivers, increased temperatures theoretically should lead to reduced oxygen concentrations at saturation, with potential consequences for coldwater fish like the salmonids. Hitherto, however, there is no evidence of reduced oxygen concentrations that can be traced to warming in the face of a range of circumstances that lead to deoxygenation through other means (largely organic pollution, but also eutrophication and increased respiration overnight from algal and plant growth). What may be more important than actual temperature is number of days with very high temperatures. The River Thames now experiences currently about 30 days with

temperatures greater than 20 °C compared with around 5 in 1990 (Orr et al., 2010). Degree-day calculations are often related to fish growth and a small increase in temperature can lead to a large increase in number of degree-days if it is prolonged.

3.3 Rainfall

Change in rainfall patterns in the UK has been complex. Total rainfall in Britain has, on average, remained relatively steady since the 1760s, but the long-term trend in winter rainfall is of an increase (most prominent in Scotland and northern England) and of summer rainfall, a decrease since 1874 in central England. There are large fluctuations, however so that in the last fifteen years both trends have reversed, winters have been dry and summers very wet (Watts & Anderson, 2013). There appears also to be an increase in frequency of heavy rainfall events (Min et al., 2011; Slingo et al., 2014) and in flooding (Pall et al., 2011; Kendon et al., 2014) that are attributable to warming. Runoff is the amount of water draining from the catchments after evaporation has occurred. It tends to be higher in the cooler and wetter north and west than in the warmer and drier south and east, and has increased in winter since the 1960s in Scotland, Wales and parts of northern and western England, but not in summer and not in the southeast. Extreme winter flows and notable flooding have been more frequent over the past thirty years, particularly in the west and north. There is increasing confidence that these reflect climate changes (Slingo et al. 2014). The frequency of droughts yet shows no increase. There is a useful review (Jones, 2013) of the importance of extreme events in freshwater systems. It notes their main effects at the upper levels of food webs and the ability of freshwater systems to recover from them.

Rainfall (and snow melt) influence many aspects of freshwater ecology. First there are the physical effects of high flows in rivers. Invertebrates and fish are well-adapted to coping with these through behavioural and structural traits. Inadvertent drift of invertebrates (carriage of bottom-living organisms in the current) may increase at high flow, but drift is often adaptive for dispersal, particularly following low flow periods. The current and shear strength experienced by a bottom living animal or microorganism is very different and much lower in the microhabitats adopted by these organisms than in the open flow and conventional flow measurements may be of only limited relevance.

Secondly there is the transfer of organic and inorganic particulate matter. Undermining of banks and collapse of trees into rivers by high flows are ecologically important because downed timber provides habitats and snags for retention of small material like leaves that are the main energy base for headwater rivers and streams. It also helps retention of water in the channel and may help mitigate flooding where floodplains have been disconnected from the main channel by engineering operations downstream.

Thirdly runoff water carries dissolved organic matter and soluble nutrients, particularly phosphate and nitrate, that influence production in the river channel and in lakes to which the rivers discharge. Concentrations of these substances tend to increase as flow increases and much of the nutrient load may enter a river or lake in a relatively few pulses of high flow rather than in the steady base flows of the rest of the year. Conversely, increased flow dilutes point sources of pollutants including the effluents from wastewater treatment works, including nutrients and thousands of different organic compounds, some of them, such as endocrine disruptors, with significant ecological effects. In alpine lakes (Sommaruga-Wograth et al. (1997) there is a contrasting picture. Between 1985 and 1995, pH, conductivity, alkalinity, sulphate, and metal cations all increased and inorganic nitrogen decreased as temperature increased. These trends were in opposition to trends in the chemistry of

rainfall and were attributed to an increased weathering rate of surrounding rock debris uncovered by retreating ice and greater grassland plant uptake of nitrogen. In experimental tanks with inorganic sediments, conductivity also increased in warming treatments compared with controls and this could only be explained by increased sediment weathering because evaporation losses were topped up with deionised water (McKee et al., 2002 a,b).

However, chemical effects cannot easily be specifically attributed to the changing rainfall, run off and river flows in the UK in recent decades. The changing hydrology undoubtedly has effects but it has been masked by engineering modifications to river channels, the effects of land use, including irrigation, on organic and nutrient flows and the influence of the Urban Wastewaters Treatment Directive (European Union 1991) in reducing nutrient discharges from some wastewater treatment works.

3.4 Browning

There has been a prominent recent increase in dissolved organic carbon (DOC) in mainland European and British waters, where there has been almost a doubling in concentration in fifteen years. The substances involved are most obviously brown polyphenols derived from decomposition of wood and plant litter but there are many others, and the possibility of different causes for the increase of different compounds has not been explored. The process is called browning, or, by poor linguists, brownification. Worrall et al. (2004a) analysed changes in dissolved organic carbon monthly at 198 river and lake sites. The records vary in length from 8 to 42 years, going back as far as 1961. In 77% of sites DOC concentration significantly increased, and in 23% it showed no trend but no sites showed a significant decline. The increase was initially attributed to warming and decomposition of organic matter in soils and peats, but there is evidence that it is also linked with measures to combat acidification that have increased the pH values of upland waters slightly (Monteith et al., 2007).

The matter is not resolved (Evans et al, 2005; Clark et al., 2010). Modelling studies for Moor House in the Northern Pennines suggest that in peat-dominated catchments, the flux of brown substances should have increased by about 6%, for an observed temperature increase of 0.78 °C between 1970 and 2000, but the increase has been around 97%. However, a period of peat oxidation following drought may have been involved (Worrall et al., 2004b). One current position is that the trends in dissolved organic carbon are too consistent and widespread to be dependent on regional effects of rainfall, acid and nitrogen deposition, and local effects of land-use change, and that climate change, perhaps operating through increasing frequency and severity of droughts may primarily be responsible. The difference in opinion seems to be linked with where the studies were carried out (Clark et al. 2010), with effects of acidification recovery being associated with previously polluted areas and climate change with those not so affected. Increased browning reduces light availability sufficiently deep waters and leads to decreased euphotic zone depths (those where net photosynthesis is possible). This reduces the area of bottom available for plant colonisation, the most diverse part of lakes and rivers. Ecological effects on headwater rivers have not been investigated. Dissolved organic matter is important for the productivity of bacterial films on rocks, but browning compounds tend to be refractory and may be effectively inert.

3.5 Sea level rise

A further effect of climate change is in rising sea levels, particularly in southern and eastern England where the land is still subsiding as a result of isostatic adjustment to the retreat of the ice from Scotland. There are coastal lakes created behind sand or

shingle bars (for example, Lyn Coron, Loe Pool, Slapton Ley, the Little Sea, Dungeness pools) and areas like the Broads (which were man-made but several hundreds of years ago, and close to sea level). Many lowland rivers close to the sea have partly drained floodplain grazing marshes of conservation value and where flood defences may not be maintained indefinitely into the future. Sea level has risen by around 20 cm since 1920, with some geographic variation depending on land subsidence and span of the tide, for example a 312 mm rise at Liverpool (Department of Energy and Climate Change, 2013c).

Sand and shingle bars become vulnerable to breaching during storms as sea levels rise and Slapton Sands were severely damaged in 2001 (Watson, 2011). The likelihood is that some future storm will convert what is presently a freshwater system (and part of a National Nature Reserve) back to the estuary that it was three thousand years ago. This has already happened at Porlock in Somerset. All such coastal lakes and wetlands must be vulnerable.

The Broads are particularly at risk. They include one of the largest concentrations of SSSI and NNR in England, bordered by only a thin line of dunes, which has been breached several times in the past several centuries. Minimal sea defences protect the northern sections in the Thurne valley. The coast to the north is eroding rapidly. The southern part is buffered by an estuary and a large area of grazing marsh that is maintained presently as freshwater, but is vulnerable to a breach or overtopping of the floodbanks of the rivers. The whole freshwater system beyond the present tidal limit, where there are no embankments, will be subjected to increasing salinity (indeed already is (Moss et al., 1989)) as tides penetrate further upstream, or as drainage pumping close to the coast sucks in sea water (Holdway, Watson & Moss, 1978). Except in Hickling Broad and Horsey Mere, the salinity even at the highest tides still remains within that tolerated by most freshwater species, but the future is uncertain. The Fens around the Wash are well defended but for the sake of carrots, lettuces and wheat; their few nature reserves are far inland and well embanked.

3.6 Temperature, range, and phenology

Temperature (subject to biogeographical accidents and barriers) has long been considered to determine the ranges of organisms. Climate change, hitherto, has confirmed this (Thomas, 2010), with northward and upward colonisation by many organisms in Britain. Hickling et al. (2006), summarised data for several groups (including aquatic bugs; dragonflies & damselflies; fish; herptiles; birds and mammals). Overall the boundaries of 84% of over 300 species were moving northwards, two did not change and the rest were moving southwards.

In Ontario, Alofs et al. (2014) used contemporary and historical survey data to examine changes in northern range-boundary in 13 warm and coolwater freshwater fishes. Many of these fish now occur in lakes where climate was historically limiting. Piscivore northern range boundaries shifted northward significantly over nearly 30 years at about 12.9–17.5 km per decade, values comparable with range changes in other groups; in contrast, the northern range boundaries of forage fish often shifted southward. For 28 fish species in 196 European river basins, Lasalle and Rochard (2009) using known physiology and predictions from one climate model (A2RES Had CM3) suggest that 5 species would change little in distribution, 3 would expand and 14 decline. Atlantic salmon (*Salmo salar*) was predicted, other things being equal, to disappear from 30% of otherwise suitable basins in southern France and Portugal, to experience a marked decrease in abundance in northern France, and to diminish to a lesser extent around the North Sea and the southern Baltic. The populations would potentially remain high and intact in the UK. River lamprey (*Lampetra fluviatilis*) was predicted to lose most of its suitable basins in France and around the Mediterranean,

and to diminish in the south of the British Isles. Arctic charr (*Salvelinus alpinus*) would be lost from 70% of existing basins but would survive in north Norway and Iceland. Prediction of range shifts in UK fishes is complicated by the many transfers that are made in the interests of angling.

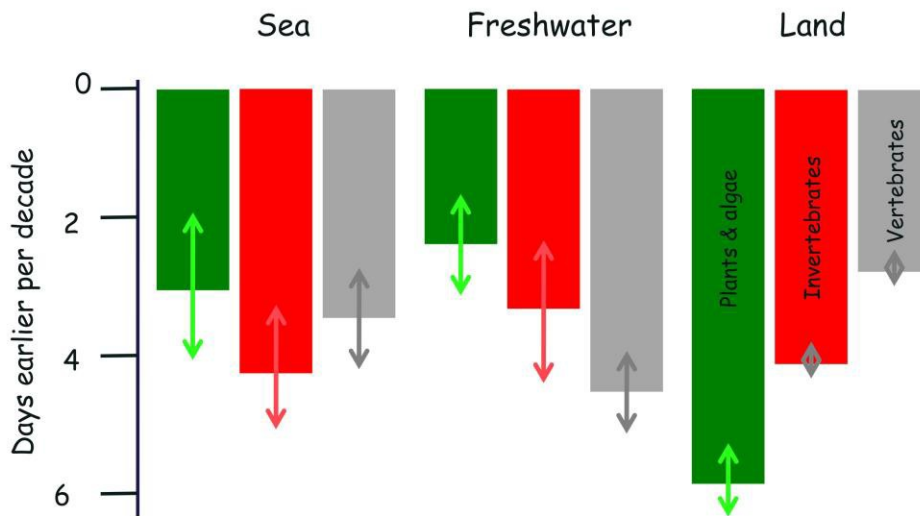


Fig. 2. Changes in phenology of plants, invertebrates and vertebrates in marine, freshwater and terrestrial habitats in the UK from 1975 to 2006, when temperatures rose by around 1°C. Values are shown as days earlier per year. Based on Thackeray et al. (2008).

At least one cold-water crustacean, the Arctic fairy shrimp *Branchinecta paludosa*, has shown a reduction in range, without a move northwards or upwards with warming (Lindholm et al., 2012). There had been a temperature increase equivalent to a 200-m upward shift of the local isotherms and the number of warm summer days had doubled in the lowest 200 m of the region, leading to reductions in oxygen concentrations.

Thackeray et al. (2010) analysed 25,532 rates of phenological change between 1976 and 2005, for 726 UK terrestrial, freshwater and marine taxa (Fig. 2). Most spring and summer events have advanced rapidly and accelerated in a way that is consistent with observed warming trends, with the greatest changes after 1986. Advances in timing were overall lowest (2 days per decade) for predators, and about the same (4-4.5 days per decade) for primary producers and grazers. The relative changes among plants, invertebrates and vertebrates differed among terrestrial, marine and freshwater habitats and there was no particular pattern among groups of finer taxonomic resolution. There were some biases in the coverage of freshwater organisms, determined by availability of data. There were no higher plants, six Cyanobacteria and 45 planktonic eukaryote algae, entirely derived from Cumbrian

Lake District data sets. Invertebrates were represented by 36 odonates, one other insect and one planktonic crustacean. There were four amphibians, two fish (perch and salmon), and nine birds, but no mammals.

3.7 Trends in organism size

There has long been an understanding (Bergmann's rule) that the sizes of warm-blooded animals, best expressed as the ratio of mass to surface area, tend to increase towards the Poles and this was attributed to the need to conserve heat in colder climates, though the rule is not always followed (Gardner et al., 2011). A similar relationship may exist for aquatic ectotherms. Daufresne et al (2009) found that bacteria, phytoplankton and a copepod in heated mesocosms (+2, 4 and 6°C) significantly decreased in volume with temperature and that among wild fish stocks subjected to warming trends, mean size within species and mean size of individuals within species tended to decrease with temperature, whilst the proportions of small species and the proportions of juveniles tended to increase.

Decreases in median size of diatoms have been associated with warming and water column stratification in the ocean and in Lake Tahoe (Winder et al., 2009a) but decreases in the proportion of large cells and colonies are often observed in response to reduced concentrations of limiting nutrients. Small cells have proportionately greater surfaces relative to their bulk and this is advantageous where nutrients are scarce. However, in small lakes, Finkel et al (2009) found a decrease in the median size of planktonic diatoms in response to higher nutrient concentrations. Climate-induced increases in the stability and length of stratification may select for smaller planktonic species in lakes owing to a reduction in nutrient availability and potential increase in sinking rates, while light limitation, stimulated by eutrophication and high chlorophyll concentrations, may select for smaller species within a community owing to their high light absorption efficiencies and lower sinking rates. The conservation significance of reduction in size with warming is yet not clear but it is claimed to be an emerging general principle. Size is important in food webs because the smaller an organism, the larger the range of grazers or predators that can take it.

3.8 Invasive species

Mainland Europe was separated from Britain and Ireland by the sea quite early and many species that had been present in former interglacial periods but eliminated by the last glaciation have yet to return. Some are still in the process of slow recolonisation. Freshwater triclads currently confined to England are capable of proliferating in Scotland but have not yet reached there (Reynoldson 1983). In a sense the UK yet has only pioneer communities in a grand succession that is still underway.

Many newly entering species, however, have not entered naturally. Exotic species are now common everywhere; not all become invasive, but a few do. Jeschke & Strayer (2005) found that about half of all introduced species established themselves and half of those spread. Warming may open new opportunities for invasives, especially where high nutrient levels are found, as in most lowland freshwaters. This is because most invasion inevitably comes from warmer latitudes, where the biodiversity is greater, and because high nutrient levels favour competitive species that can build up high biomass. Fish, bird and plant introductions are generally soon noted but those of invertebrates may often be overlooked and those of non-clinical microorganisms are barely sought.

Invasions of invertebrates may be very common but are often missed until the populations are well established. There may be increasing potential for damaging invasions of invertebrates (Gallardo & Aldridge, 2013a,b), and although the reasons are several, climate change is almost certainly involved (Hulme, 2012). Invasive freshwater shrimps (particularly *Dikerogammarus*) are currently of concern (Gallardo et al., 2012 ; McNeill et al., 2012) because they are voraciously predatory. *Cylindrospermopsis raciborskii*, an invasive freshwater cyanobacterium, originating in the tropics has spread to temperate zones over the last few decades (Wiedner et al. 2007). Its northernmost populations in Europe occur presently in North German lakes. An earlier rise in water temperature associated with climate change is believed to have promoted the spread of *C. raciborskii* to the temperate zone.

New arrivals and establishment of breeding birds are generally welcomed. Almost uniformly they are birds with previous distributions to the south and thus warming is likely to be key to their establishment in Britain. Examples include little egret, common crane, whooper swan, Cetti's warbler, goldeneye, Mediterranean gull, great white egret, purple heron, cattle egret, pectoral sandpiper, spoonbill, red necked grebe, little bittern, black-winged stilt, spotted sandpiper, little gull, bluethroat, black tern, ruff and Savi's warbler (Austin et al., 2014). Recent invaders that have begun to breed have first established themselves in protected areas such as SSSI (Hiley et al., 2013). Such areas offer the highest quality habitats available and invasion of such places is unlikely by aggressive species likely to become pests. That is probably not true of exotic species among invertebrates and plants and probably of fish. They are likely to enter via estuaries (from ship ballast water), aquaculture, water gardening, discarded live bait imported from overseas, and disenchanting aquarists (Hill et al., 2005), though also on the bodies or in the guts of migratory birds. Such species often are first found in canals, lowland rivers and reservoirs, all of them more challenging habitats than most SSSI. Such species are therefore likely to be good competitors with a greater chance of becoming invasive problems.

4. Summary of future general effects of climate change on freshwaters in Britain and Ireland

4.1 Steady change or tipping points

Climate projections indicate that present trends in temperature, rainfall and sea level will continue (IPCC, 2013), though whether steadily or with abrupt changes in effects is not known. There is much discussion on 'tipping points' and evidence, for example, from shallow freshwaters of abrupt changes that cause diverse plant-dominated systems to switch to turbid phytoplankton dominated ones, and some indication that climate change is likely to worsen the present risks through exacerbation of eutrophication symptoms (Moss et al., 2011) (Fig. 3). Switches in the past have occurred, for example, owing to introductions of carp, through pesticide leakage and through major storms (in Florida) (Moss et al., 1996) and all of these may be intensified by climate change in future (Mooij et al. 2005). However, it is more

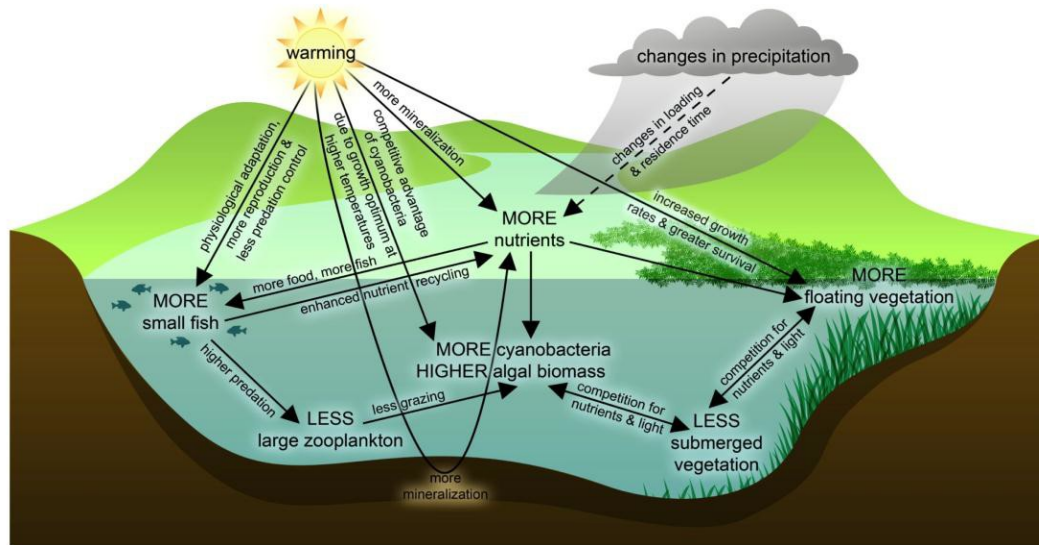


Fig.3 Climate change intensifies the symptoms of eutrophication through a variety of mechanisms. From Moss et al. (2011).

conservative to assume steady changes in effects. The approach to predicting these is generally to use a sequence of climate then hydrological then nutrient and finally ecological models. Hydrological models go some way towards future prediction of nutrient chemistry in rivers (Whitehead et al. 2009a,b) but all models rest on how societies in many countries of differing aspirations may react in future towards mitigation of climate change and this is presently unpredictable. Another uncertainty is the extent to which water quality and ecosystem structure may be improved as a result of the Water Framework Directive (European Union 2000), the current most significant legislation on water and ecological quality in Europe. Present indications are that progress is likely to be very slow but there is a potential for significant improvement.

4.2 Flowing waters

For streams and rivers, predictions for the future are that warming might lead to more extreme winter flows (IPCC 2013). This will likely mean replenishment of large woody debris in rivers (particularly if policies change to favour reforestation of upland catchments (Curtis et al., 2014) and retention of upland river timber to mitigate lowland flooding). These in turn would increase habitat diversity and biodiversity. Future nutrient loading in rivers and lakes will likely increase *per se* with more storminess but the effects may be masked by changing land use (restrictions of fertiliser application, increase in fertiliser prices, creation of buffer zones, reforestation), and installation of phosphorus and nitrogen removal at more wastewater treatment works).

Changes in rainfall patterns and temperature may influence the delivery of pesticides to surface and groundwaters (Bloomfield et al., 2006). There is no evidence of effects yet and they are likely to be very variable and difficult to predict, though Kattwinkel et al. (2011) used a model based on space-for-time comparisons of existing fertiliser use and predicted changes in arable area, to suggest increased problems in streams in northern Europe. Land-use change driven by changes in climate is predicted to increase arable production by 20–30% by 2080.

Johnson et al. (2009) predicted the possible effects of changing climate on the Thames and the Yorkshire Ouse. They used a hydrological model and one particular climate projection together with collective expert judgement. The model predicted lower flows for both rivers, in all seasons except winter, longer residence times (by up to a month in the Thames), and increase in nutrient, organic matter and other pollutant concentrations by 70–100%, assuming sewage treatment remains unchanged. More phytoplankton would grow in the Thames. Warmer winters and milder springs would favour riverine birds and increase the recruitment of many coarse fish species, but the incidence of fish diseases would increase and conditions would be less favourable for Atlantic salmon. Accidental or deliberate, introductions of alien plants and fish might change the range of native species in the rivers. No predictions could be made for particular species.

4.3 Lakes

The same modest level of detail applies to predictions for lakes. Ice cover will become rarer, summer stratification will become stabler. In shallow but stratifying lakes, hypolimnial deoxygenation will become more intense and in very shallow lakes there will be increased sediment mineralisation and release of phosphate. Available nitrogen may decrease because of increased denitrification rates and reduced redox potential. Collectively these might be associated with increased production or decreased production depending on the degree of nutrient enrichment from the inflows. Climate change tends to intensify the symptoms of eutrophication (through increased rainfall and nutrient loading, sediment release and food chain effects (Fig. 3 and see below), Moss et al., 2011) but pressures from the Water Framework Directive should tend to reduce nutrient loads. Effects of climate change on Esthwaite Water have been masked by changes in nutrient loading from other sources (Dong et al., 2012). Conditions may become more eutrophic and maintaining the status quo will therefore require additional measures. It is unlikely that conservation status of lakes in the lowlands will be improved. There may be building of some new reservoirs, with possibilities of habitat creation for conservation if predicted reductions in summer rainfall and increasing severity of summer droughts are borne out, but the high variability of annual rainfall and the long planning time needed for reservoir creation make this unlikely in the immediate future. Coastal lakes dammed by shingle and sandbars will become flooded with sea water and return to estuarine conditions.

Conventional wisdom on the functioning of wetlands and evidence documented under specific headings below suggest that rising temperatures will intensify the degree of deoxygenation of the soils, but since these are already naturally deoxygenated when waterlogged, there may be only minor changes in community composition. Water levels will be higher in winter, lower in summer and periods of drying out will become more frequent, possibly resulting in a reduction of wetland area and conversion to damp grassland. Changes in policy on flood prevention may lead to re-establishment of wetland on some floodplains as a means of increasing water storage. Grazing marshes may also return to estuarine conditions as it becomes uneconomic to maintain flood defences to protect grazing land; coastal

freshwater wetlands may become brackish as sea water penetrates further upstream, even if flood defences downstream are maintained. More details of what might happen to plankton communities, wetland and littoral plant communities are discussed below after the evidence of existing change has been presented.

5. Existing and future influences on particular communities and groups

Freshwaters are not so diverse absolutely as marine systems but there are relatively many more species in freshwaters when calculated per unit volume of water (Balian et al., 2008; Strayer and Dudgeon, 2010) and inevitably this biodiversity is threatened by the many impacts on freshwaters. A handful of freshwater species is already considered vulnerable, endangered or critically endangered in England (Natural England 2010): sturgeon (*Acipenser sturio*), eel, (*Anguilla anguilla*), schelly, (*Coregonus lavaretus*), vendace, (*Coregonus albula*), freshwater pearl mussel (*Margaritifera margaritifera*), aquatic warbler (*Acrocephalus paludicola*) and white clawed crayfish (*Austropotamobius pallipes*). Since 1800, 2/7 amphibian species, 4/25 stoneworts, 4/30 stoneflies, 3/37 dragonflies, 2/35 freshwater fish, 3/193 caddis, and 6/386 water beetle species have been lost for a variety of reasons but climate change has not been implicated (Natural England, 2010). However, among a variety of pressures, climate change is now included as a possible threat to many Biodiversity Action Plan (BAP) species, though not on any specific evidence. On the BAP list are 44% of British amphibians, 38% of freshwater fish, 31% of stoneworts, but fewer than 5% each of dragonflies, water beetles, stoneflies and caddisflies.

5.1 Plankton systems

Freshwater plankton is a particularly useful system for detecting effects of climate change because the life histories of its members are short, and there is naturally a huge seasonal turnover in communities, so that responses are prompt. The literature on ecological effects of climate change is greater for the plankton than for any other aspect of freshwaters. Warming and associated hydrological effects have led to changes in seasonality of phytoplankton (Gerten & Adrian, 2000, 2002; Catalan et al., 2002), an extension to growing seasons and increases in lake productivity (Blenckner et al. 2007; Kerfoot et al. 2008) but there is not always a response. In experimental lake mesocosms (albeit plant-dominated), McKee et al. (2003) found no effects on mean phytoplankton chlorophyll a with a 3°C rise in temperature and Moss et al (2003) in the same experiment found that of 90 algal taxa, two were significantly increased in numbers by warming, two were decreased and the remainder were unaffected. In a subsequent experiment in the same mesocosms, using a 4 °C rise in temperature, chlorophyll a did increase significantly. The composition of the community was not systematically monitored as a result of the discouragement caused by counting over 3000 phytoplankton samples in the previous experiment with little influence of temperature.

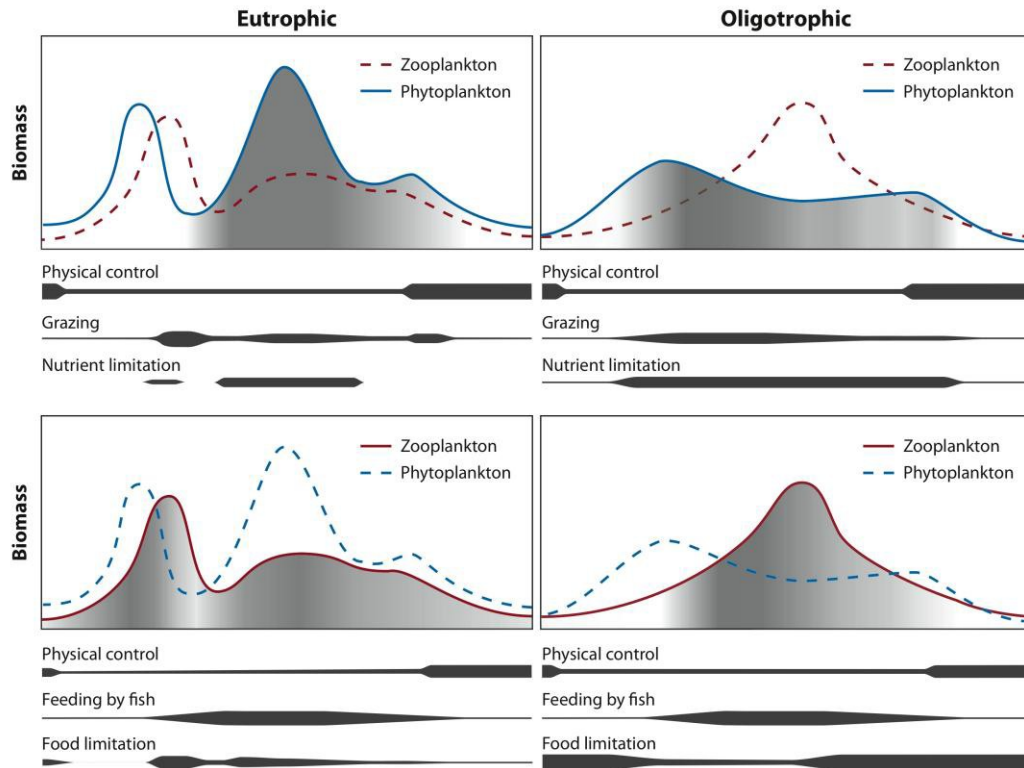


Fig.4 The Plankton Ecology Group model, with emphasis on phytoplankton at the top and zooplankton below. Shading for phytoplankton indicates relative inedibility (the darker the less edible). Shading for the zooplankton indicates animal size, with light shading meaning large animals and heavy shading smaller. Horizontal axis runs from mid winter to mid winter. From Sommer et al. (2012).

In Lake Baikal, warming by 1.2 °C since 1946 has been associated with increases in chlorophyll a and cladoceran zooplankton biomass (Hampton et al, 2008). These results are particularly significant because such a huge mass of water might be expected to be more resistant to warming trends than the much smaller lakes of Britain and Ireland. Clarke et al. (2005) took sediment cores from 209 high altitude lakes from 11 countries in Europe and compared diatom communities between present and pre-industrial conditions. Most lakes studied show an increase in planktonic diatom species and changes in the ratio of planktonic to non-planktonic diatoms were likely related to changes in nutrients, through increased mineralisation, decreased ice-cover and increased erosion, all linked with climate warming.

The bulk of the literature concerns the substitution of one species for another and the relative timing of changes in the phytoplankton, zooplankton and fish communities. Understanding of the functioning of plankton systems is summarised in the Plankton Ecology Group (PEG) model (Fig. 4) (Sommer et al., 2012), which is a widely accepted description of seasonal changes in the plankton of temperate lakes and is used as the basis of the following discussion.

5.1.1 Spring and early summer plankton

Phytoplankton is not inert in winter, but activity increases greatly in spring when nutrients, accumulated from the inflows over winter, coupled with rising light availability and temperature, stimulate a spring growth of phytoplankton, generally dominated by diatoms. The size of the peak is determined largely by the availability

of nutrients (variously P, N or Si are most critical) coupled with the timing of onset of stratification (diatoms are heavy and favoured by mixed water) and the zooplankton grazer population. Warming induces earlier stratification and because diatoms require wind-induced eddy currents to maintain them in suspension, warming may terminate the spring bloom earlier. In Windermere, Thackeray et al. (2008) found that warming had advanced the peak biomass of a *Cyclotella* species but *Asterionella* was influenced much more by nutrient enrichment, and for both genera the trend was very irregular.

Horn et al. (2011) examined data from a German reservoir and found that the diatom, *Asterionella formosa* was dominant until 1990, but another diatom, *Aulacoseira subarctica* became more frequent at the end of the 1990s and was particularly abundant in years with short, mild winters that were frequent after 1988 and led to early ice melt and long-lasting spring circulation. *A. subarctica* is a rather heavy diatom, needing high turbulence to survive. Feuchtmayr et al. (2012) investigated phenology of three phytoplankton taxa (*Asterionella formosa*, *Aulacoseira* spp. and *Cryptomonas* spp.) in four lakes of the English Lake District situated within the same catchment over a 58-year period (1945–2003). Timing of the spring bloom advanced over the study period for *A. formosa* but was delayed for *Aulacoseira* spp. and *Cryptomonas* spp. These changes were consistent in all four lakes. They tested several climatic and nutrient drivers. Temperature significantly advanced *A. formosa* and *Aulacoseira* spp. in the North Basin of Windermere but significantly delayed *Cryptomonas* spp. peaks in three lakes. Overall, phosphate concentration had a more consistent effect upon phenology, affecting all taxa in nearly all lakes.

Planktonic algae, like all organisms, have parasites, including viruses, protozoa and chytrids. Changing temperatures influence these infections. Ibelings et al. (2011) describe host–parasite relationships between the freshwater diatom *Asterionella formosa* and two highly virulent chytrid parasites (*Rhizophyidium planktonicum* and *Zygorhizidium planktonicum*) in Lake Maarsseveen in The Netherlands, during a 30-year trend of significant warming that was strongest in spring. In years with cold winters, a dense *Asterionella* population became heavily infected, but this did not happen in milder winters. The parasites do not infect below 3 °C and warming has reduced periods in which water temperature remains <3 °C, reducing the period for uninfected growth. In warm winters *Asterionella* continuously suffers from low-level infection, and does not increase in numbers so rapidly, which allows other diatoms to grow simultaneously. In mild winters, chytrid infections are not epidemic because transmission is impaired at low host densities. Warming thus denies the host a bloom and the parasite an epidemic. The mixed diatom community of mild winters may benefit the food web, because of the poor edibility to zooplankters of *Asterionella*, though the numerous chytrid zoospores produced during epidemics may be eaten. Warming has revealed a paradox: reduction in epidemics would seem to benefit the host, but this was not the case.

Zooplankton is also influenced by weather and trends of change in it (George & Harris 1985; George et al. 1990; George & Taylor 1995; George 2000; George et al., 2000). Lake Washington (USA) has warmed by 1.5 °C since 1962 and stratifies for about four weeks longer than previously. Its most prominent calanoid copepod (*Leptodiaptomus ashlandi*) has greatly declined in population density, but productivity has been maintained because of an increase in the production to biomass ratio and a life cycle shift from an annual to a 6-month cycle during the past two decades (Winder et al., 2009b). The shift from one to two generations per year most likely resulted from a longer and warmer growing period, combined with changing fluctuations in phytoplankton availability.

Analysis of long term records (1982-2007) from the Muggelsee in Berlin, has given many insights into how plankton systems react to increased temperature and its consequences for stratification (Wagner & Adrian, 2011). Muggelsee formerly did not stratify. Now it does so intermittently with several periods of summer mixing and stratification, each 2-8 weeks long. When the lake was stratified, higher surface water temperatures and lower epilimnetic nutrient concentrations were found, and as the length of a period of stratification increased, the phytoplankton shifted towards a higher proportion of buoyant cyanobacteria capable of N-fixation (*Aphanizomenon*, *Anabaena*), and fewer diatoms. Zooplankton species with high thermal tolerances (*Thermocyclops oithonoides*, *Thermocyclops crassus*) and/or rotifers that grow quickly at high temperatures became more common. There was no short-term effect on cyanobacterial diversity because of species replacements. In the long term, diversity of cyanobacteria and cladocerans declined while that of rotifers increased.

In the Muggelsee, Gerten & Adrian (2002) found that this trend towards warm springs and summers has also affected the population dynamics of the several cyclopoid copepods. The growth phase of the copepods was prolonged both in spring and autumn. *Thermocyclops oithonoides* emerged from eggs earliest (May in the warm years, July in the cool years) and this was probably related to high water temperature in late spring. A later onset of winter diapause in all species may have been coupled to raised temperature in late summer and autumn. The annual peak abundance of the two thermophiles, *Mesocyclops leuckarti* and *T. oithonoides* increased significantly in the warm period, in the latter case, probably because of the early start to population growth and in the former, which has a short development time, primarily owing to mid-summer heat waves. The increase in population size of both species resulted from development of an additional generation (three instead of two cohorts per year). In contrast, the coexisting *Acanthocyclops robustus*, which grows over a broader temperature range, did not respond noticeably to the warming trend. Effects were therefore through seasonality and life history and highly species-specific.

Experimental work in mesocosms amplifies these findings from lakes (Feuchtmayr et al., 2010). With a 4 °C warming, the timing of the chlorophyll a peak and crustacean zooplankton peak abundance, dominated by *Daphnia pulex*, responded strongly to temperature and nutrient addition. *Daphnia* numbers reached peaks 22–24 days earlier in heated than in unheated mesocosms. Very high zooplankton abundances occurred with warming and high nutrient loadings, inducing a clear water state in all the tanks owing to heavy zooplankton grazing, despite high nutrient concentrations.

Predatory Cladocera as well as filter feeders have also been affected. In Lake Maggiore, Italy, Manca & DeMott (2009) recorded a more than 10-fold increase in the mean annual population density of *Bythotrephes longimanus* between 1987 and 1993, when high values of the NAO winter index indicated warmer winter and spring temperatures across Europe. *Bythotrephes* remained abundant and increased even more during the following ten years, as water temperature continued to increase. It needs a warm, low-light, deep-water refuge from fish predation; this was more extensive during the warm years. *Bythotrephes*' first appearance shifted from late August to May, linked with earlier thermal stratification and earlier establishment of the predation refuge. *Daphnia hyalina galeata*, the dominant grazer, and a prey of *Bythotrephes*, decreased sharply as *Bythotrephes* increased.

Matters are not always straightforward. A laboratory study of the native *Daphnia pulex* and the introduced tropical *Daphnia lumholtzi* showed greater productivity of the latter in single-species cultures in lake water at high temperatures, but in mixed

cultures at the same temperature, especially when cyanobacterial food was provided, the native species outcompeted the invader, despite its greater temperature optimum (Fey & Cottingham, 2010).

5.1.2 Late summer plankton

Fish tend to spawn late in spring and the young-of-the-year become very abundant in May or June as the zooplankton also reach high numbers and the spring algal growth is in decline. Young fish are mostly zooplanktivorous in the UK and select the more vulnerable (large and slow moving) cladocerans such as *Daphnia*, leaving more predator-resistant rotifers and copepods that are less efficient grazers. The phytoplankton community then recovers to a mixed assemblage during summer, with some slow-growing species then reaching their zenith in the warmer waters. Cyanobacteria are favoured in summer. They are an ancient group, having evolved in the warm seas of the Precambrian and are favoured by high temperatures and also by deoxygenated conditions at the interface between the hypolimnion and epilimnion. Some cyanobacteria use the formation and collapse of gas vesicles to make complex movements between the top of the hypolimnion (where they can acquire nutrients, and the epilimnion where light is greater).

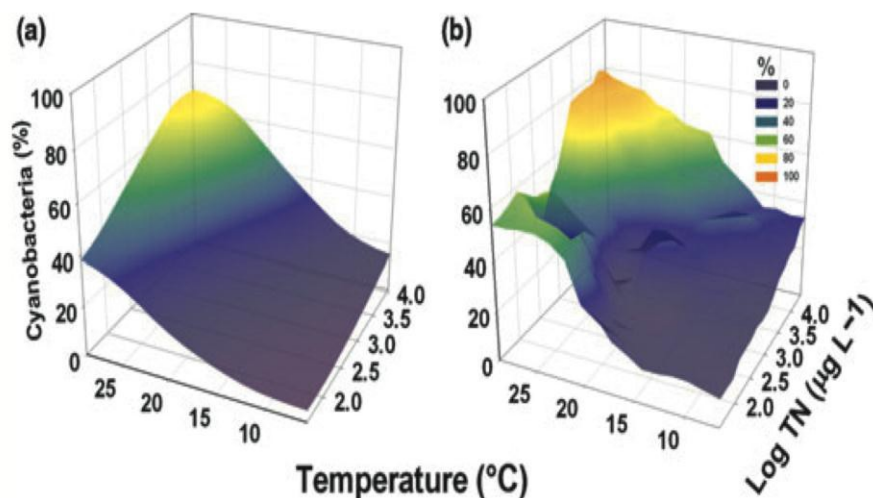


Fig. 5 Percentage of Cyanobacteria in lake plankton from a series of lakes along a climatic gradient in Europe and South America, in relation to water temperature and total nitrogen concentrations. The two diagrams are derived from two different statistical models. From Kosten et al. (2012).

Zooplankters reproduce rapidly, often parthenogenically, and when they increase in numbers earlier with warming, the earlier grazing may truncate the spring algal growth before nutrients become scarce. This has implications for the summer algal communities, though the details are not easily unravelled; one may be in stimulation of cyanobacterial growth. Warming trends are predicted to favour Cyanobacteria

(Paerl & Huisman, 2008). Space-for-time studies in a gradient of shallow lakes in Europe and South America showed increasing incidence of Cyanobacteria in warmer waters (Kosten et al., 2012) (Fig. 5). Cyanobacteria, (or at least the larger species) can be problematic in that they are relatively poor food for zooplankters, may produce toxins that can be lethal to mammals, and possibly other vertebrates and zooplankters, result in particular tastes in drinking water, and are difficult to filter out in purification of water supplies.

It is unlikely that temperature *per se* is responsible entirely for increasing biomass of Cyanobacteria (they have probably been abundant in the West Midland Meres for millennia (McGowan et al., 1999)) but the complex of indirect effects of warming probably is. In shallow lakes, warming increases release of phosphate from sediments and also the rate of denitrification. A low available N to available P ratio is associated with high cyanobacterial incidence. Modelling studies (Elliott 2012) and specialist reviews (Paerl & Paul 2012) conclude that the most prominent climate effect would be to increase the duration and proportion of Cyanobacteria in the phytoplankton but not to increase the annual biomass of the phytoplankton community; the more nutrient rich the lake, the greater are the modelled Cyanobacteria populations; and earlier depletion of nitrogen by the spring algal growth could favour earlier onset of non-nitrogen fixing Cyanobacteria. Increase in Cyanobacteria would lead to reduced energy flow owing to their relatively low edibility for zooplankton and potentially to changed fish production or the balance between open water and bottom-living fish.

5.1.3 Match and mismatch relationships

Weather-related differences in timing of phytoplankton peaks, zooplankton growth and fish hatch in the sea were shown many years ago to be related to fish production (Cushing 1995) and this idea has stimulated work on what could be similar effects with warming in freshwaters. Thackeray et al. (2013) compared phenological change for phytoplankton (chlorophyll a), zooplankton (*Daphnia*) and fish hatch (perch, *Perca fluviatilis*) in the two basins of Windermere over 40 years to determine whether change has differed among trophic levels. Seasonal events shifted earlier for all three and were correlated with raised temperature. Zooplankton advanced most, and fish hatch least rapidly.

However, these shifts were also linked with changes in nutrients. Lower silicate, and higher phosphorus concentrations accompanied earlier phytoplankton growth, and earlier phytoplankton growth was associated with earlier zooplankton growth. Thackeray et al. considered that mismatch between perch hatch and zooplankton food may ultimately affect fish survival. In Lake Washington, Winder & Schindler (2004) found that increasingly warm springs have advanced thermal stratification, the spring diatom bloom and the growth of *Daphnia*, but at different rates, so that *Daphnia* biomass has declined for lack of food at the right time. However, Hansson et al (2012), in a mesocosm experiment, found that phytoplankton and zooplankton advanced their spring peak abundances similarly in response to a 3 °C temperature increase, and there was no support for a mismatch between grazers and food.

Temperature increase in a series of Russian lakes was associated with a shift from copepods to cladocerans, resulting in the highly unsaturated fatty acid content of the community falling and thus providing food of reduced quality for fish (Gladyshev et al. (2011) irrespective of timing. There may be more subtle changes through changing element ratios. As CO₂ concentrations rise, and stratification leads to depletion of nutrients in the surface layer, phytoplankton with a higher carbon-to-nutrient content may provide poor-quality food for zooplankton, which may shift the community

composition to less nutrient-demanding species. There may then be effects on fish communities (Waal et al, 2010).

5.1.4 Future plankton communities

Work on plankton has picked up particularly readily the nature of influences that climate change will have and gives hints as to the sorts of changes and their complexity that may also come to bear on communities of larger organisms. The evidence is overall of substantial change in phenology, community composition, life history strategies, productivity and linkages among trophic levels. Future changes will have implications for water supply but also for conservation in that littoral plant communities and plankton communities compete for light and nutrients, and that particular value is placed on the conservation of plants and fish.

The spring growth of diatoms will advance until it becomes a winter peak and the lake starts to behave like those in warm temperate regions, subject to the fact that light may be limiting in mid-winter, which will put some check on the process. Recruitment of cyprinid fish will be favoured (see below), leading to reduced cladoceran populations and grazing potential on algae (Gyllstrom et al., 2005). Total algal population in spring will increase and Cyanobacteria will become commoner in summer, though scarcer nutrients in stratified lakes may result in reduced summer crops overall. Rivers only have plankton in their lower reaches. It is subject to continual mixing and dominated at all times of year by diatoms and green algae rather than Cyanobacteria. Predictions of climate change effects relevant to the spring growth for well mixed lakes are applicable for all of the growth season in rivers.

There are possibilities of many different outcomes in plankton communities as increased temperature couples with climate-induced changes in hydrology and nutrient loading. Such adjustment is a normal feature of plankton systems however and fluctuation in weather between years, even without long-term trends, is associated with a great deal of variation in the plankton. There are common main events and some species tend to occur every year but exact timings can be very variable and sudden surges of previously less abundant species are usual. Concerns about match and mismatch are probably premature. The key findings concern Cyanobacteria in lakes for they have implications for recreation and water supply. Cyanobacterial blooms may accumulate at the lake surface on still, hot days, probably through a breakdown in their buoyancy regulation mechanisms, and if windrowed to the edges will decompose and may release toxins that can kill stock and dogs drinking the water. There was a notable example at Rutland Water in 1998.

5.2 Aquatic plants, wetlands and littoral zones

Many northern aquatic plants have wide ranges and some are circumboreal (Santamaria, 2002) Climatic factors probably have limited effects on their distributions, beyond major disjunctions (tropical–temperate–subarctic). Dispersal has been effective enough to assure quick colonisation following glacial retreat, but there are some geographic barriers. Aquatic plants show limited within-species genetic variation, but variation among populations is relatively high, because of the persistence of long-lived clones (Santamaria, 2002). Aquatic habitats are stressful for plants, with low carbon availability, high shade, sediment anoxia, potential damage by water movement, restrictions to sexual reproduction, and sometimes also osmotic stress and limited nutrient supply. There has thus been selection for stress-tolerant taxa with broad tolerance ranges, for clonal growth and multiplication, and for long-distance dispersal of sexual propagules with high local dispersal of asexual clones, often by birds. Aquatic plants, in general are tough survivors.

There are four main groups in a continuum that leads from the land-water interface, from emergent plants in fens, carrs and reedswamps, to floating-leaved plants, floating and then completely submerged plants in lakes and sedimented rivers. Few variables limit emergent growth, given a habitat that is waterlogged for much of the year, with plentiful soil nutrients that have accumulated from soil eroded from higher land, and the maximum light available for their location. Emergent communities are likely to be resistant to climate change. They survive dry years and deep flooding, reflecting their competitive nature. There are instances of loss of reed (reed die back) but these have been attributed variously to grazing by introduced mammals (coypu) and overgrazing on young shoots by feral geese. There has been loss of floating mats (play) owing to increased nitrate levels altering the balance of biomass between the shoots and the roots and rhizomes, leading to instability and vulnerability of the mat to wind (Boar et al., 1989). No good evidence of changes to wetlands through existing warming has been found, but this may be due to masking by many other impacts: drainage, local reduction in groundwater levels through irrigation, eutrophication by nitrate in rain and from fertilisers (Stevens et al., 2004; James et al., 2005), and deliberate management for reed and fen crops, and wetland birds like bittern (*Botaurus stellaris*).

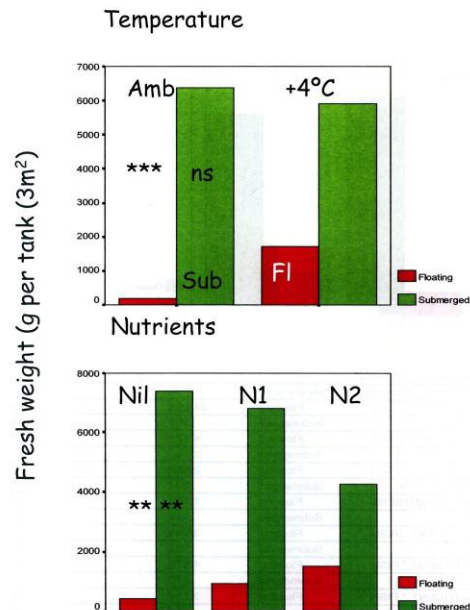


Fig. 6 Effects of warming by 4 °C and addition of two levels of nitrate (N1 and N2) on submerged and floating plants in a mesocosms experiment. ns, not significant, ** P<0.01, *** P<0.001. Based on Feuchtmayr et al., 2009.

Floating-leaved plants have many characteristics similar to reedswamp plants and are also resilient. Heterophylly, with both submerged leaves and leaves at the water surface, may give them both advantages and disadvantages. They are vulnerable to loss through disturbance, for example by boat wash, and *Nuphar*, with submerged leaves, may disappear earlier as nutrient loads increase and competition with phytoplankton and periphyton increases, but it is unlikely that climate change, unless extreme, will displace any of the commoner species. Floating plants, like the

duckweeds, are generally small in the UK and most persistent where they are sheltered from wind. There is evidence that they are favoured by warming, especially when coupled with eutrophication. The reasons are obscure but may involve deleterious effects of deoxygenation on other plants in dense beds further shaded by a floating cover. In one experiment in controlled mesocosms, warming increased the biomass of lemniids whilst not affecting that of submerged species, whilst increase in nitrate also increased biomass of lemniids but reduced that of submerged plants (Feuchtmayr et al., 2009) (Fig.6). In Dutch ditches (Netten et al. 2011), cover of both free-floating plants and evergreen overwintering submerged plants was positively related to mild winters (positive NAO winter index). High cover of submerged plants that die back in winter coincided with cold winters (negative NAO winter index). The effects were strongest where nutrient supply was greatest. In several mesocosm experiments using shallow-lake communities it has been concluded that the effects of eutrophication were much greater than those of increased temperature (McKee et al, 2002a,b; Christoffersen et al. 2006; Feuchtmayr et al 2007, 2009).

Submerged plant communities are often used in conservation assessments. Particularly valued are isoetid and charophyte communities. The former occur in low alkalinity water, the latter in harder water and particularly calcareous lakes. The occurrences of these, and also another category, listed in the Habitats Directive European Union, 1992), of naturally eutrophic lakes with *Potamogeton* species and *Hydrocharis*, are strongly influenced by water chemistry. It is unlikely that they will be directly affected by climate change but indirect effects could be significant. They might occur through increased run off and nutrient loadings, though, *per se*, likely increments are likely to be small compared with agricultural and effluent loads. Nitrate is a determinant of submerged plant species richness (James et al., 2005) and increased runoff, especially in winter, means increased nitrate levels. Actual concentrations, however, are already high and well above the threshold for declining richness in much of the UK, and likely to be increased by changes in land management, which will mask direct climatic effects.

Submerged plant communities are nonetheless the most vulnerable to environmental change of all aquatic plant communities and have already been seriously damaged in the lowlands (Morgan, 1972; Carvalho & Moss, 1995; Moss et al. 1996; Egertson et al., 2004; Madgwick et al, 2012). Their growth is influenced by competition with overlying phytoplankton, which worsens the underwater light climate, and is determined by the balance of availability of nutrients and the grazing pressure from zooplankton. In turn stocks of forage fish influence the zooplankton community, the relationship being further fed back by the availability of plants to provide refuges for zooplankters against such fish predation. Among broadly similar physical and chemical conditions, shallow lakes may have clear water, plant dominated states or turbid-water, phytoplankton-dominated states, determined by this interplay among nutrient loading, competition, grazing, and external factors which may damage the plants, such as grazing by introduced fish and birds, biocides and mechanical disturbance. Although the plants are resilient, phytoplankton, being higher in the water column has the inherent advantage.

Studies on sediment cores from some northern Russian and Lapland lakes (Valiranta, 2006) have shown much greater abundance and diversity of submerged plants in the warming millennia up to about 5000 BP and then a decline thereafter, attributed to cooling, oligotrophication (a natural process of decline in nutrients as soils in pristine catchments become leached out) and reduction in the ice-free season. Current warming is predicted partly to reverse this trend and may be relevant for the remoter lakes of Scotland. Rooney & Kalff (2000) monitored the biomass and distribution of submerged plant communities in five Canadian lakes, in

two climatically different growing seasons. The warm year allowed for earlier growth, much deeper plant colonization and greater biomass but these were relatively infertile lakes and the phytoplankton was overall sparse.

Against this is a possibility that warming, by increasing nutrient loads in cold lakes, could shift dominance by bottom littoral communities with diverse plants, towards plankton dominance (Rautio et al. 2011, Kosten et al. 2009). The tendency for weathering in the catchment to increase with warming and to increase alkalinity and conductivity may also favour pondweed communities over isoetid communities. Warming through 3 °C or 4 °C in two controlled mesocosm tank experiments had no effect on submerged plant biomass (McKee et al., 2002b); Feuchtmayr et al., 2009) but advanced the start of spring growth and changed the community composition in favour of an introduced species, *Lagarosiphon major* in a community otherwise containing *Potamogeton natans*, and *Elodea nutalli* (McKee et al., 2002b).

Warming has been associated with a decline in charophyte biomass in a Dutch lake (Rip et al., 2007). Lake Botshol alternates between clear water with abundant charophytes and turbid water with phytoplankton. In wet winters phosphorus and dissolved brown organic matter entered and phosphate from runoff was stored in the lake bottom. It was released the following spring and summer under anaerobic sediment conditions, resulting in increased phytoplankton density and light attenuation in the water column. In years with dry winters, the phosphorus and humic acid loads were reduced, and growth of charophytes increased in clear water. In the first half of the 20th century variation in precipitation between years was not sufficient to cause large changes in internal P flux in Botshol, and submerged plant populations were stable.

A similar situation appears to hold in Lake Takern in Sweden (Hargeby et al. 2004), which shifts between clear-water and turbid states. In 1995–1997, submerged vegetation declined after 30 years of clear-water and abundant vegetation. This was unlikely due to long-term changes in external input of phosphorus, fluctuations in water level, or changes in zooplankton grazing pressure. The most likely scenario was a series of mild winters with short ice cover and no winter-kills of fish, leading to high biomasses of benthivorous and planktivorous fish, increased sediment disturbance and nutrient release, coupled with unusually cool and windy springs before and during the shift, leading to unfavourable conditions during the establishing phase of the submerged plants. Shorter periods of ice cover and high wind velocity in winter and spring were associated with changes in the NAOI.

Mesocosm experiments in Sweden (Mormul et al. 2012) tested the effects of raised temperature (3 °C) and browning on native and non-native aquatic plant production. *Elodea canadensis*, an invasive aquatic plant, had higher relative growth rate as well as higher weight to length ratio when grown in brown versus clear water but did not respond to increased temperature. Native producers (phytoplankton, periphyton, plants) showed different relationships, with the native plants decreasing in biomass in browner water, where they represented about 40 % of total biomass compared with 85 % in clear water.

The evidence is that submerged plant growth can increase, be unaffected or decrease with warming, but on balance, because of indirect effects operating through increased nutrients and fish survival, a decline is most often to be expected. The situation is further complicated because vascular plants can sometimes be substituted by extensive skeins of filamentous green algae, which also seem to increase with warming. Filamentous green algae often proliferate in nutrient-rich rivers under low flow conditions. Trochine et al. (2011) used microcosm experiments to demonstrate that filamentous green algae strongly suppressed the growth of

natural phytoplankton at non-limiting nutrient conditions and that the effect increased by up to 49% with increased temperature. Filamentous green algal growth increased in a Canadian riverine lake under hydrological conditions associated with increased warming (Cattaneo et al., 2013). Hydrological (depth, water level change) and meteorological (hours of sunshine, wind velocity) variables were the best predictors of filamentous green algal occurrence but no water quality variable was significant. Years of low water levels coincided with early occurrence, highest prevalence and longest seasonal persistence of these algae.

5.2.1 Future wetlands and littoral zones

There are four components that may damage future freshwater plant communities with increased warming: reduced summer water availability, increased nutrient loading, greater abundance of benthivorous fish, like common carp (see below) and the ready availability of invasive plant species. Fens will become more vulnerable if groundwater levels decrease in summer (Curreli et al., 2013) and water becomes richer in nitrate (from more intensive farming and greater winter runoff). Stuart et al. (2011) predict that nitrate in groundwaters may double by 2100.

Shallow lake littorals, are, on balance, likely to decline in quality as changes in nutrient loading and influences on fish communities further favour development of phytoplankton. A space-for time set of mesocosm experiments (Moss et al., 2004) carried out along a gradient between Finland and Spain suggested a greater dominance of effects of nutrients in warmer climates as fish removed zooplankton grazer populations more effectively. Such circumstances favour emergent, floating-leaved and floating plants, which are less susceptible to the light climate in the water, and particularly floating species which have no underwater stages and are unaffected by deoxygenating conditions in the sediments. Swards of lemniids and perhaps of some larger introduced floating plants, may increase during the calm periods of increasingly hot summers.

In warmer regions, large floating species occur (*Pistia stratiotes*, *Eichhornia crassipes*, *Salvinia rotundifolia*) and these plants or congeners often dominate the littorals of tropical lakes. This may be because water level changes are greater in warmer climates and floating plants are independent of these, whilst rooted plants may dry out or be unable to extend their shoots high enough in the deep water of the wet season. Several such warm water species have been introduced for water gardening in the UK but have not spread because they fail to overwinter. A rise in water temperature may permit this (Netten et al. 2010). Indeed many plants introduced for water gardening come from warmer regimes and, with the inherent aggressiveness of many submerged species, may gain dominance over native communities in shallow water that has become increasingly eutrophicated.

In this respect, Riis et al. (2012) studied the effect of summer temperature (20, 25 and 30 °C) and light availability (25% and 50% of incident light availability) on performance of three invasive aquatic plants (*Elodea canadensis*, *Egeria densa* and *Lagarosiphon major*) in Denmark. *E. canadensis* was the most competitive in both high and low temperature and light availability. *E. densa* fared best in warm water and *L. major* in cooler water. *E. densa* will likely dominate warmer, shallower waters, whereas *L. major* will dominate in colder, clear-water lakes, while *E. canadensis* continues its established role as a pioneer species that is quickly replaced by the two taller species after their arrival.

5.3 Odonates

Dragonflies and damselflies produce aquatic nymphs that are predators on other invertebrates and sometimes on hatchling fish and tadpoles. They have vigorously flying adults and are charismatic and well monitored by amateur naturalists. There is good evidence that ranges of southern species are extending northwards (Hickling et al. (2005), Brooks et al., 2007).

All but two of the 37 non-migratory British odonates have increased in range size (mean change +55 10-km grid squares), and all but three species shifted northwards at their range margin (mean 74 km) between 1960–1970 and 1985–1995. Southern species increased in range size (mean change + 52 squares) and, on average, shifted northwards at the range margin by 88 km. The species which colonized the most new grid squares in the second period was *Coenagrion puella* and that which expanded furthest northwards at its range margin was *Sympetrum striolatum*, another common southern species, shifting 346 km north between the two periods. The increases in range size could be attributed to increased temperatures but also could have coincided with improved water quality in some places. Two northern species (*Aeshna caerulea* and *Leucorrhinia dubia*) showed declines in range size (as well as northwards shifts), which tends to suggest a greater influence of warming. Phenology of British Odonata also changed between 1960 and 2004, with a significant advance in start of the flight period by a mean of 1.51 days per decade or 3.08 days per degree rise in temperature (Hassall et al., 2007).

In mesocosm experiments, warming through 4 °C decreased the proportions, among total macroinvertebrates, of invertebrate predators overall, but increased the proportions of odonate nymphs (Moran 2009). The group is generally tropically distributed. Another set of experiments demonstrated an unexpected role of numbers of odonates in small ponds (Knight et al., 2005). Where fish predation on them was reduced, odonate numbers and hatching increased, leading to more adults, greater predation on bumblebees and thence reduced pollination of *Hypericum*, a plant growing around the pond edges. Warming could reduce fish populations and favour an increase in odonates. It could also increase numbers of small fish (see below) and have a contradictory effect.

Odonates are generally declining in Western Europe as a result of post-war intensive agriculture (Corbet & Brooks, 2008; Raebel et al., 2012). Despite recent increases in range of many species owing to climate change, three have become extinct, four are classified as 'endangered', two as 'vulnerable', and six as 'near threatened' from a total of 46 species in Britain (Daguet et al., 2008). The underlying causes are habitat loss and fragmentation, changes in farm management (drainage, neglect, and infilling of ponds), eutrophication and increased use of agrochemicals. Lack of a landscape-scale consideration of aquatic habitats (Davies et al., 2008) may be preventing the current situation from improving. A general tendency for shallow lakes to become phytoplankton-dominated with warming will not help.

5.4 River algae and invertebrates

Streams figure prominently in the hydrology of the UK and much effort has been devoted to determining the effects of environmental factors on stream and river communities. Streams have also been heavily modified by removal of trees from the bankside (riparian) zone to reduce summer flood risk were they to collapse into the water, by intense cultivation to the water's edge, and by overgrazing. Woody debris, however is important in the functioning of pristine streams for it retains leaf litter that forms the food base of the invertebrate community. There has been realisation of this and some moves to re-establish riparian woodland (Capon et al., 2013).

Streams within a small area in Iceland that offer a temperature range from 5 °C to 21°C, with broadly similar chemistry, have been useful in showing effects of temperature, (Gudmundsdottir et al., 2011 a,b, 2012; Hannesdottir et al., 2013) though over a greater range than is likely to be experienced in Britain. With increasing stream temperature, the cover of mosses increased significantly, offering a more complex environment, and the invertebrate communities changed from chironomid-dominated in the colder streams to increasing growth of snails and simuliids in the warmer. There were more generations per year among macroinvertebrates in warm streams. Species in the coldest streams were either uni- or bivoltine, while those in the warmer streams were mostly bivoltine or multivoltine. Flies emerged mostly in summer in the colder streams, year-round in the warmer streams. Macroinvertebrates grew faster with increasing temperature, had greater population biomass and secondary production in the warmer streams, and were able to support trout populations.

Hogg et al. (1995) raised the water temperature of a stream by 2.0-3.58 °C over 2 years. This suppressed total invertebrate abundance but stimulated growth rates. Barlocher et al. (2008) heated the hyporheic (sub-gravel) zone of streams by up to 4.38 °C, a change that accelerated leaf litter decomposition rates, and in turn led to lower abundance and diversity of aquatic hyphomycetes (the fungi that decompose leaves and provide protein-rich food for shredding invertebrates) owing to reduced substrate availability. Many observations were made on the effects of thermal pollution from power stations on fresh waters during the 1970s and 1980s (e.g. Langford 1990), generally indicating raised activity and metabolism of the river communities. Boyero et al. (2011), analysing litter decomposition rates in streams over a latitudinal gradient, found that overall rates did not change with temperature, but that the microbial activity increased and the invertebrate activity decreased with increasing temperature.

The diversity of stream invertebrate communities has increased in British rivers in recent decades. Family level richness increased on average by nearly 20% during 1991–2008, particularly in urban catchments, with a widespread shift towards taxa of well-oxygenated and less polluted waters. There has been localized deterioration in some streams draining upland areas and in the lowland south east. The changes are explicable largely by improvements in waste water effluents and cannot be traced to climate change (Vaughan & Ormerod 2012).

There is, however, some evidence of direct warming effects on stream communities in the Welsh uplands (Durance & Ormerod 2007). Spring crops of macroinvertebrates declined with warming in circumneutral streams, and could decline by 21% for every further 1°C rise. Many core species could persist if temperature gain reached 3 °C, but 4–10 mostly scarce taxa (5–12% of the species pool) would risk local extinction. Climate effects maximally explained 37% of the variation in community and 23.3% of abundance, when the effects of changing pH had been eliminated. Acidification however had simplified the communities and probably made them more vulnerable to climate effects, which conversely might offset biological recovery from acidification. Hitherto biological improvement has not been so great as chemical recovery in acidified waters.

Macroinvertebrate communities are central to ecological assessments of stream ecological quality under the Water Framework Directive. Systems by which these assessments are made could be upset by effects of climate change (Hassall et al., 2010); for example range shifts in Odonata could change scores derived from the Biological Monitoring Working Party (BMWP) system that is used and have effects consequently on conservation monitoring and assessments. Ranges are changing

also for other important groups including bugs (Hickling et al., 2006), Plecoptera, and aquatic beetles (Heino, 2002), and Diptera (Burgmer et al., 2007). These five groups (Odonata, Coleoptera, Hemiptera, Plecoptera and Diptera) comprised 35 out of 81 families in the revised BMWP scores of Walley & Hawkes (1996), suggesting that the impact of climate-induced range shifts on biological water quality indices may need to be assessed in all groups of interest. The Plecoptera are particularly crucial, since they have been allocated some of the highest BMWP scores and have been shown to be “cold-adapted” (Pritchard & Leggott, 1987) and to decline in species richness with increasing temperature (Heino et al. 2009).

The future of stream and river systems has been discussed in general in Section 4 but projections of hydrological models suggest deterioration in stream invertebrate communities on warming, primarily through decreasing summer flows, though also through loss of cold-adapted species (Harper & Peckarsky, 2006; Domisch et al. 2013; Fung et al., 2013; Laize et al., 2014). Pearl mussels (*Margaritifera margaritifera*) may be particularly vulnerable to increased high floods (Hastie et al., 2003).

5.5 Fish

Fish are the charismatic species of freshwaters and there is much interest in their potential reaction to warming. Thermal tolerances are generally well known and are greater for growth than for spawning. UK species can be broadly categorised as cold water species, (physiological optima <20 °C) with some of them, such as the coregonids (*Coregonus* spp, grayling (*Thymallus thymallus*), charr (*Salvelinus alpinus*) and bullhead (*Cottus gobio*) possible glacial relicts (Hanfling et al., 2002), and some of them anadromous, like the Atlantic salmon and sea trout (*Salmo trutta*), and warm water species (physiological optima 20-28 °C). The latter were pushed southwards by the ice but then moved back when land bridges connected Britain and Ireland to the mainland until about 7000 years ago. They include a range of species of increasing temperature tolerance from pike (*Esox lucius*), minnow (*Phoxinus phoxinus*) and perch (*Perca fluviatilis*) to roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus*), bream (*Abramis brama*), three-spined stickleback (*Gasterosteus aculeatus*), tench (*Tinca tinca*), and crucian carp (*Carassius carassius*). A third group, which comprises around half of British fish species, is introduced and includes largely fish from warmer climates, including carp (*Cyprinus carpio*), and wels (*Silurus glanis*), with physiological optima >28 °C, some of which find low temperatures limiting to their spawning in northern areas, but which will spawn more easily with a modest degree of warming.

Fish have major effects on freshwater systems through their predation or foraging, and carp in particular can stir up sediment in their search for invertebrates, destroy aquatic plant communities and switch clear water plant-dominated lakes to turbid phytoplankton-dominated ones of much lower overall biodiversity (Moss et al., 1996). For example, Grieg et al. (2011) used outdoor mesocosms to investigate the combined effects of warming, eutrophication, and sticklebacks on the flux of biomass between aquatic and terrestrial ecosystems. Fish reduced the emergence of flies and suppressed the decomposition of terrestrial plant detritus (by removing detritivorous invertebrates). In contrast, warming and nutrients increased emergence and decomposition, and these effects were strongest in the absence of predators. Warming advanced, whilst predators delayed emergence of insects.

Hitherto it has been difficult to assess changes with existing warming in the UK because fish are so highly managed and influenced by other impacts, but there is evidence of changed communities and growth rates elsewhere (Daufresne et al., 2003; Hari et al. 2006). Jeppesen et al. (2012) reviewed published and new long-

term (10–100 years) series of fish data from 24 European lakes (but including only Windermere from the UK). Along with a temperature increase of about 0.15–0.3 °C per decade, considerable changes have occurred in either fish assemblage composition, body size and/or age structure during recent decades, with a shift towards higher dominance of warmwater species. These changes took place despite a general reduction in nutrient loading and occurred in many lakes that should have benefited the larger-sized individuals and species typically inhabiting cold-water, low-nutrient lakes. Arctic charr (*Salvelinus alpinus*) have been particularly affected and become less abundant in most lakes. Helland et al (2011) show that increasing ice cover correlates with lower trout biomass when Arctic charr co-occur, but not in charr's absence. In experiments, charr grew better in the cold and dark of ice-covered lakes. Decreasing ice cover with warmer winters could mean more trout and fewer charr. Species interactions can strongly modify responses to climate change.

The harvest of cool-stenothermal brown trout has also decreased substantially in two southern lakes (Jeppesen et al., 2012). Whitefish (coregonids) and smelt (*Osmerus eperlanus*) showed varied responses depending on lake depth and latitude. Perch has apparently been stimulated in the north, with stronger year classes in warm years, but its abundance has declined in the southern Lake Maggiore in Italy. Where introduced to northern waters, roach (*Rutilus rutilus*) seems to have taken advantage of higher temperature after years of low population densities. Eurythermal species such as bream, pikeperch (*Sander lucioperca*) and/or shad (*Alosa* spp) are apparently on the increase in several of the lakes. The response of fish to warming has been surprisingly strong and fast in recent decades.

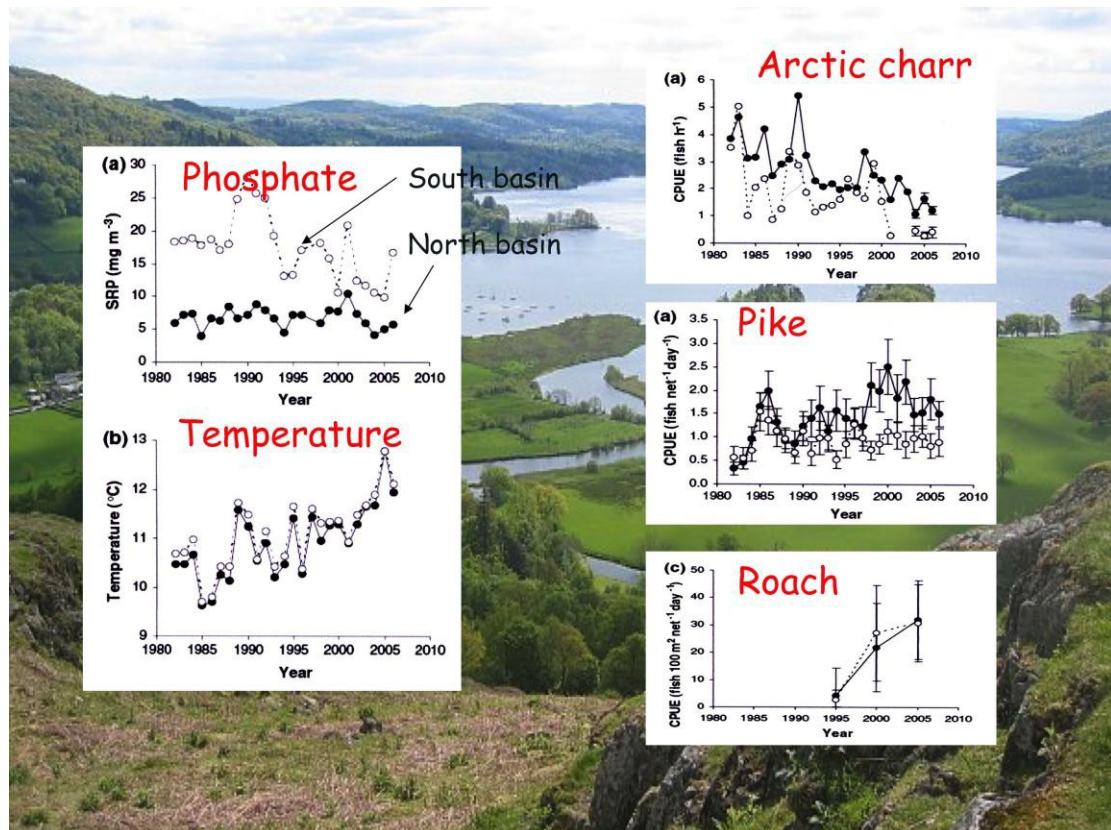


Fig.7 Changes in environment and fish populations in Lake Windermere. Data from Winfield et al. (2010b).

The most notable effect in the UK has been a decline in charr in large lakes like Windermere (Winfield et al., 2008), but this effect is compounded by other changes such as introduction of roach (Fig. 7). The north and south basins of Windermere support autumn- and spring-spawning populations of Arctic charr. The south basin has been significantly eutrophicated, while both basins have shown raised water temperatures and increasing roach populations, following their introduction as live-bait for pike, by anglers. Despite the introduction of phosphate stripping in 1992 and some subsequent initial improvement, the hypolimnion of the south basin still remains significantly deoxygenated and the charr fishery catch-per-unit-effort in this basin is now at record low levels. In addition, roach has become a significant part of the fish communities of inshore and offshore surface waters, where it may compete with Arctic charr for zooplankton prey. Current charr abundance in the north basin, where eutrophication is limited and the local roach population has increased only recently, is also declining. Charr elsewhere are particularly vulnerable to competition with trout as temperatures rise.

About half of English SSSI with standing waters were already damaged by 1995 through introduction of carp (Carvalho & Moss, 1995). Carp are very likely to extend their range with warming and they are already widely redistributed because they are favoured angling fish, especially in commercial fishing ponds, from which they may escape in floods. Carp are also one of the few species likely to survive warming through several degrees and to cause extensive damage (Britton et al. 2010). Wels (an introduced Danube catfish) may also spread, though may be less damaging. Experiments in mesocosms using the very tolerant three-spined stickleback showed that the fish did not survive warming by 4 °C in tanks that were eutrophicated to a degree characteristic of many lowland lakes (Moran et al., 2010) and there were fish-kills even with a 3 C increase (McKee et al., 2003). Sticklebacks are more thermally tolerant than most native British fish species, including many of the warm water species. Sticklebacks, however, failed successfully to reproduce in experiments in the laboratory when the temperature was increased over the likely future range (Hopkins et al 2011). Males were less assiduous in courting and mating and then, if they had mated, in guarding and fanning nests, so that fewer young survived. The implications are that even a modest degree of warming will lead to major changes in fish communities.

Coregonids like vendace (*Coregonus albula*), which was confined to Derwentwater and Bassenthwaite Lake in Cumbria, are vulnerable to temperature increase, which in summer limits the cold, well oxygenated habitat they require. Vendace has all but disappeared from Bassenthwaite but probably for reasons of eutrophication, soil erosion and siltation of its spawning beds. Other coregonids like the schelly, powan and gwyniad (*Coregonus lavaretus*), are cold-water fish of very restricted distribution in the UK and are probably in decline owing to reduction in the well-oxygenated deep cold waters that they require for survival in summer (Winfield et al., 2010a).

There are also subtler influences at work. Parasites are normal components, indeed in terms of species richness probably the most abundant organisms in all ecosystems, and their infectivity is influenced by the physiological state of their hosts. Macnab & Barber (2011) found that raised temperatures affect a critical phase of the life cycle of the bird tapeworm *Schistocephalus solidus* – the growth of plerocercoid larvae – in three-spined sticklebacks. By 8 weeks post-infection, plerocercoids taken from experimentally infected sticklebacks held at 20 °C, weighed on average 104.9 mg, with all individuals more than 50 mg, the mass considered consistently infective to other hosts. In contrast, plerocercoids from sticklebacks held at 15 °C weighed on average 26.5 mg, with none exceeding 50 mg. As small increases in plerocercoid mass affect adult fecundity disproportionately in this parasite, greater plerocercoid

growth at higher temperatures predicts dramatically increased production of infective parasite stages. Subsequent screening of thermal preferences of sticklebacks from a population with endemic *S. solidus* infection showed that fish with infective plerocercoids preferred warmer water. Parasite transmission might therefore be affected in at least two ways by warming: increasing rates of parasite growth and development; and increasing the likelihood of hosts seeking warmer microhabitats where the parasites grow better. This suggests a potential for positive feedback between parasite growth and host thermal preferences, which could dramatically increase the effects of even small temperature increases.

5.5.1 Future fish communities in the UK

Fish figure prominently in public perceptions of freshwaters and possible influences of climate change. They have key roles that were underappreciated when fisheries and freshwater science developed separately. Britain and Ireland have a limited native fish fauna, with a cold-water prominence of salmonids and a warm-water prominence of cyprinids, a scarcity of coregonids, a wide distribution of perch and pike and an abundance of introduced species. Most species straddle both standing and flowing waters in their distribution with wide niches that mean that few can be distinguished as specifically river or lake fish.

Space-for-time studies across latitude are beginning to reveal trends in the traits of organisms that give hints as to what might be expected as northern latitudes continue to warm. For shallow lakes, for example, Meerhof et al (2011) found greater richness at warmer locations for fishes, phytoplankton and periphyton, but the opposite for macroinvertebrates and zooplankton. With decreasing latitude, the biomass of cladoceran zooplankton and periphyton and the density of zooplankton and macroinvertebrates declined whilst fish biomass and density increased. Fish and cladoceran zooplankton showed reduction in body size with higher temperature. There was stronger predation by fish (whose communities are increasingly dominated by omnivores (Moss, 2010; Gonzalez-Bergonzona, 2012)) and weaker grazing pressure of zooplankton on phytoplankton with increasing temperatures. As waters warm in Europe (Hering et al. 2010) fish species or individuals will become smaller, and more benthivorous. Egg incubation times will shorten and egg size decrease. Increased precipitation is associated, in river fish, with later maturity and less time spent on parental care. Parallel traits have been shown in the Murray-Darling basin in Australia (Chessman 2013).

The general predictions with warming are that piscivorous fish will be disadvantaged, because their oxygen requirements are high and oxygen solubility decreases with increasing temperature; survival of forage fish will therefore increase and increased competition among them will lead to smaller individual size and a lengthier period spent as feeders on small invertebrates. They will breed earlier and young-of-the-year survival will be greater. Zooplanktivory will therefore increase, leading to greater algal crops for the available nutrients and a tendency for grazer-resistant large algal species, not least Cyanobacteria, to develop. In turn this will make mitigation of the symptoms of eutrophication more difficult, will increase the loss of biodiversity in the system in general, will change the nature of fish populations for angling and will increase the costs of drinking water treatment. The data on fish contribute to the general finding that warming effectively intensifies the symptoms of eutrophication in many respects (Fig. 3) (Moss et al. 2011).

Much work on fish rests on knowledge of thermal tolerances and predictions assume that these will remain constant, though fish evolve rapidly and there is much local

adaptation (Holt, 1990; Crozier & Hutchings, 2014). The eggs and juvenile stages are always less tolerant than the adults (Elliott & Elliott 2010; Souchon & Tissot, 2012) and studies that use tolerances for adults may therefore underestimate future effects. In the UK, coregonid fishes may not survive because the lakes where they occur are too small and vulnerable (Elliott & Bell, 2011; Murdoch & Power 2013) though translocations to higher and northern lakes may help (Winfield et al. 2012). Charr may survive only in the cooler Scottish lochs (Winfield et al., 2010). Predators like perch and pike may be disfavoured. Cyprinid fish will spread rapidly. Further introductions of species from lower latitudes will likely survive and spread. Carp will begin to dominate lowland communities.

The fate of Atlantic salmon and sea trout is likely to be continued decline in the UK (Conlan et al., 2007; Walsh & Kilsby 2007; Moore et al, 2012) but a northward movement with increased stocks in northern Norway, Canada and elsewhere in the Arctic (Jonsson & Jonsson, 2009; Hedger et al., 2013). Brown trout is more resilient and a several degree increase in temperature would be needed to give a marked decrease in trout growth (Elliott & Elliott, 2010). There are many factors already contributing to salmon decline and warming may only exacerbate the inevitable. The situation for lampreys, all three species of which are listed in the Habitats Directive, is unknown. The future of eels (*Anguilla anguilla*) is very uncertain. Numbers are at unprecedentedly low levels, but the reasons are not clear.

The warmwater fishes will fare better, except in extreme scenarios (Graham & Harrod (2009). Roach, for example, are likely to benefit, though with much oscillation in growth rates from year to year, from warm and wet summers, though not dry ones (Nunn et al, 2010). Pike will benefit from increased temperature, and models using extensive data from Windermere suggest that the population will have fewer small and large fish but a dominance of intermediate-sized ones (Vindenes et al., 2014). Introduced cyprinids and percids are likely to spread in Lake District lakes to the detriment of cool-water fish (Winfield et al 2010a). Models based on predicted changes in a large number of central European catchments suggest that fish extinction rates will be dominated (to the extent of two orders of magnitude) by other factors and not warming (Tedesco et al. 2013). Temperature increase tends to increase spread of fish diseases (Marcos-Lopez et al., 2010) though the dangers are greatest for aquaculture of salmonids and carp. Finally escapes during summer flooding of the Sussex Ouse allowed modelling of the likely spread of pond populations of the exotic pumpkinseed (*Lepomis gibbosus*) into rivers and, with experiments in warmed mesocosms, suggested that this species could be come invasive in future (Fobert et al., 2011, 2013).

In an extreme case of warming by above 4° C, most native species other than crucian carp and tench will disappear from southern England and lowlands everywhere, and carp may dominate near monospecific communities.

5.6 Amphibians

Amphibians are declining in numbers almost everywhere, mainly through loss of habitat but also, it is suggested, from increasing UV radiation, chytrid disease, alien species, direct exploitation and climate change. Beebee (1995) and Beebee & Griffiths (2005) found no evidence that tolerance limits of temperature or moisture have been exceeded for UK amphibians, but that three newt species (*Triturus vulgaris*, *T. helveticus* and *T. cristatus*), *Rana esculenta*, and *Epidalea* (*Bufo*) *calamita* were breeding earlier. There had been no change in *Rana temporaria* or *Bufo bufo*. The latter pair breed early and abundantly, the former group over a longer period. Amphibians often have rather long generation times that mitigate against quick response to impacts. Their tadpoles are often vulnerable to fish predation and

the stock of suitable fish-free ponds in the UK is in decline and may decline further in dry summers.

The UK's rarest native amphibian, the natterjack toad (*Epidalis calamita*) is at its northernmost limits and may be favoured by climate change. McGrath & Lorenzen (2010) found that British populations have declined since at least 1960. They investigated the effects of 25 climatic, site and management variables on population trends. Rainfall was correlated with declining populations but the effect was strongly influenced by three sites with very high rainfall. Climate change over the next 50-100 years is predicted to have limited impacts on most natterjack populations in Britain, but strongly positive impacts on the most threatened populations located at the very edge of species' range that will benefit from reduced precipitation.

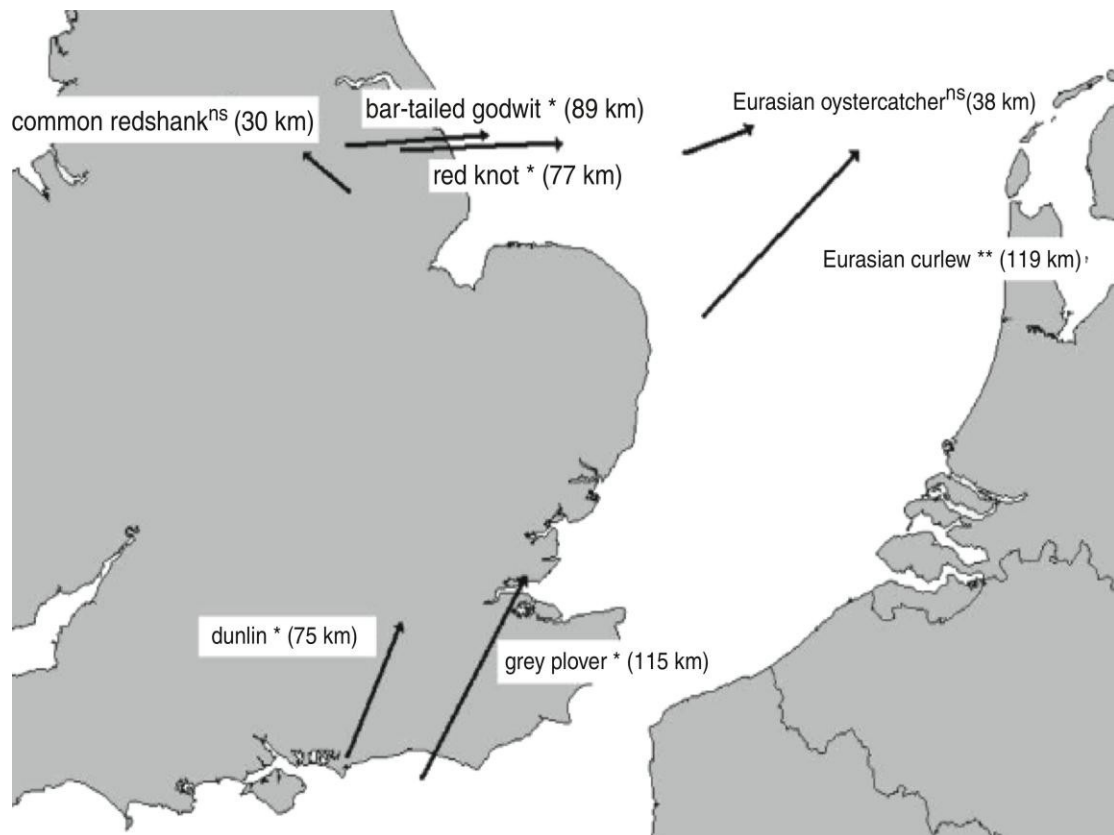
The future may pose problems for other amphibians as warming intensifies. D'Amen and Bombi (2009) looked at patterns of 19 recent amphibian declines in Italy to examine effects of climate change, habitat alteration, and high levels of incident solar radiation. Many factors had contributed to the declines but a common pattern of disappearances among very different species suggested climate change, acting through temperature directly and drought, as a major cause of population disappearances.

5.7 Wetland birds

Excellent data exist on trends in numbers of wintering waterbirds in the UK as a result of the Wetland Bird Survey (Austin et al., 2014). However explaining trends is not easy. About 70% of wetland species have shown declines since 2000, and about 43% over the past twenty-five years. Numbers include estuarine as well as freshwater sites.

Steady declines have been recorded for Bewick's swan, European white fronted goose, shelduck, mallard, pintail, pochard and scaup, goldeneye, red breasted merganser, ruddy duck, oystercatcher, ringed plover, purple sandpiper, dunlin, bar-tailed godwit and turnstone. Continued increases have been found for whooper swan, pink footed goose, Icelandic greylag goose, British greylag goose, Canada goose, Greenland barnacle goose, Svalbard barnacle goose, light bellied brent goose, gadwall, avocet, sanderling and black-tailed godwit. Coherent reasons linked to climate change can only be proposed for some of the ducks and waders, and recent invaders that have begun to breed, such as great white egrets, which bred for the first time in the UK in 2012 (Holt 2013). Predicted changes in climate are expected to be beneficial for such species.

Lehikoinen et al. (2013), working in Finland, noted that early winter temperatures had increased by 3.8 °C over the 30-year study period. Spring arrival dates of several waterbirds in the flyway were linked to climatic change, and several species in Europe and Siberia have increasingly delayed their southward autumn migration in response to warming. There are profound implications for winter duck populations. Prior to the onset of milder winters in recent decades, wetlands in northern latitudes of Europe tended to remain frozen throughout the winter. However, such water bodies have become increasingly available to be used by waterbirds in winter. Numbers of tufted duck, goldeneye and goosander have increased exponentially in Finland, while in northern Sweden the total for all three species combined rose by over 80,000 birds. Goldeneye have increased by 4,320% in Finland and 269% southern Sweden.



*Fig. 8 Movements of the centroids of populations of seven wader species between 1981 (bottom of arrow) and 2000 (tip of arrow). Ns no significant change, * $P < 0.05$, ** $P < 0.01$. From McLean et al. (2008).*

At the other end of the flyway, there is a different story from that in Scandinavia. The wintering population of tufted ducks in Britain has changed little but neighbouring regions at the southwest edge of the flyway have experienced marked declines. For example, tufted ducks have decreased by 46% in France, 43% in Ireland and 39% in Switzerland, amounting to a combined loss of 104,000 birds. Goldeneyes decreased significantly by 63% in Ireland and 35% in Switzerland over the three decades, meaning a loss of 12,000 birds from those two countries alone. Recent shorter-term declines have also occurred in Great Britain, France, and The Netherlands. At the south-western end of the flyway used by goosanders, numbers have declined in The Netherlands (by 66%), Denmark (41%) and southern Sweden (21%). Birds are likely increasingly to move from sites further south and west in the wintering ranges and this will deplete many sites in the south and west of the UK but may benefit those in the north-east. A similar move towards the east or north-east, by an average so far of over 100km, has occurred in five (bar-tailed godwit, red knot, Eurasian curlew, dunlin and grey plover) out of eight species of waders (Maclean et al. 2008) (Fig.8). In future many wetland birds may winter nearer to their breeding grounds (staying in continental Europe) or their populations may decline because their Arctic breeding grounds become unsuitable through melting of the permafrost and encroachment of forest. Some of the populations of wintering and passage waterbirds in England may then no longer retain their international importance (Natural England 2008).

Mooij et al. (2005) suggest that climate change in the Netherlands will reduce numbers of several species of waterbirds. Shallow lakes in the Netherlands harbour many species owing to the abundant nutrient-rich and shallow lakes and dykes, located along the main East Atlantic flyway and positioned just south-west of the 0 °C January isotherm, which means little long-term ice cover in most winters. The same conditions apply to the UK. The forecasted increase in winter temperatures will shift the 0 °C January isotherm to the northeast. The shallow lakes of the Netherlands are expected to lose their importance for whooper swan and goosander, which currently move in during severe winters. Gadwall, teal, pochard, tufted duck, and scaup, which often overwinter in large numbers in the Netherlands, are expected to do so further north-east, in the Baltic region. Such shifts in non-breeding distribution in response to climate change have also been observed in waders (Austin & Rehfishch 2005). Northern waterfowl tend to overwinter as close as possible to the breeding grounds in order to return there early, but food limitation further north may preclude such a shift. Water depth is also critical in water birds that feed by diving and up-ending. Increased winter rainfall could hinder this by creating longer periods of deep water and trigger earlier departure.

Climate change may also trigger more outbreaks of botulism in waterfowl (Rocke & Samuel, 1999; Lafrancois et al., 2011). *Clostridium botulinum* type C, the major cause of botulism outbreaks in wild waterfowl is ubiquitous in lake and marsh sediments, grows under anaerobic conditions and can persist for long periods. Warming, through reduced summer lake levels and exposure of festering muds increases the risk of outbreaks. Increased temperature stimulates the production of botulin toxins and increased frequency of storms may resuspend the bacteria with the sediment. Blooms of toxic cyanobacteria may co-occur with botulism and *Closterium* tends to proliferate in windrowed algae. Outbreaks of botulism in waterfowl in the Netherlands and in British reservoirs and the Broads have occurred mostly in exceptionally warm summers.

Unfortunately the different emphases of research on birds from that on other aspects of freshwater ecology makes it impossible to assess the consequences of likely changes in bird populations for freshwater systems. Hurlbert & Chang published a seminal paper on "ornitholimnology" in 1983 but it has yet had little effect on research on the role of birds in aquatic systems (Comin & Hurlbert, 2012). Ornithologists tend to focus on the population ecology of their study species, without considering their influence on the ecosystems they inhabit. Aquatic ecologists tend to ignore animals above the water surface. However, birds may be as important as fish in many freshwater systems, especially shallow or temporary ones. As predators and grazers they have considerable influence on the abundance of other organisms (Green & Elmberg 2013). They influence sediment stability and suspension, and the switch between clear water and turbid water states. Owing to their movements between land and water, they have a role in nutrient cycling and can cause guantrophication. They influence methane production and other aspects of biogeochemical cycling in wetlands. As vectors for the dispersal of plankton, plants and invertebrates they have a role in maintenance of biodiversity and in metapopulation dynamics, and may be especially important in the redistribution of these organisms in response to climate change. Waterbirds also disperse parasites, pathogens and invasive species between aquatic systems.

Concern for the future of waterbirds in the UK is not so much for any decline in absolute numbers, but for the legal status of designated conservation sites where numbers may fall and for the need to give such status to new areas to which the birds have moved. Declines by 25% or more than half of internationally important populations have been predicted for a 4°C rise in temperature, but models suggest

that all existing Special Protection Areas would retain their status (Johnston et al. 2013).

6. Freshwaters and global carbon balance

Assuming a steady state among terrestrial ecosystems, there is a net production of fixed carbon, which is calculated by difference rather than directly measured, as around 2.5 Gt yr^{-1} , and treated as a sink in global carbon budgets. It is assumed to be stored as wood or in soils. Recent measurements suggest that most of this material is washed into freshwaters and processed there. Lakes and wetlands receive about 1.9 Gt C yr^{-1} from the land, respire 0.8, store 0.2 and export 0.9 to the ocean (Cole et al., 2007; Tranvik et al., 2009). There is uncertainty about the precision of the values, but not about the reality of the magnitude of the processes. Storage of carbon in freshwaters is about the same as that in the global ocean.

Current understanding (Reynolds, 2008; Cole, 2013) is that pristine freshwater systems are net heterotrophic: they depend about as much on energy entering as dissolved and particulate organic matter from the catchment to support production of bacteria and animals, as that fixed by photosynthesis within the wetted perimeter, though eutrophication may alter this balance (Pacheco et al., 2013). Most lakes and rivers are supersaturated with carbon dioxide (Cole 2013) and, together with much evidence from stable carbon isotopes, which allow tracing of food sources, this is taken as evidence for net heterotrophy. Humborg et al. (2010) and Maberly et al. (2013) challenge this, suggesting that the excess carbon dioxide comes from respiration in the catchment soils, but both mechanisms can be simultaneously maintained. There are also significant methane emissions from lakes and freshwater wetlands. The present estimate of global methane emissions (almost entirely from wetlands and lakes) is $0.65 \text{ Gt C yr}^{-1}$ (Walter, 2006; Bastviken, 2011). Whitfield et al. (2011) measured emissions from 121 Irish headwater lakes and found the majority were supersaturated (relative to the atmosphere) with CO_2 and N_2O while CH_4 was above saturation in all lakes. Estimated fluxes of CO_2 , CH_4 and N_2O to the atmosphere were substantial. Huttunen et al. (2003) found even higher values from eutrophicated lakes in Finland.

Understanding possible effects of climate change on these global carbon processes is clearly very important. Kosten et al. (2010) analyzed patterns in carbon dioxide partial pressure (pCO_2) in 83 shallow lakes over a large climatic gradient in South America and found a strong, positive correlation with temperature. They thought that higher pCO_2 in warmer lakes may be caused by increased mineralization of organic carbon and suggest that cool lakes may start to emit more CO_2 when they warm because of climate change. However, Sobek et al. (2005) using a sample of 4902 largely northern lakes, within a narrower temperature range, found that temperature was not an important regulator of pCO_2 . Instead, the concentration of dissolved organic carbon (DOC), explained significant variation in lake pCO_2 . Their view is that effects of climate change on the carbon balance of lakes will not be due to rising temperature *per se*, but rather to climatically induced changes in the export of DOC from terrestrial soils to aquatic habitats.

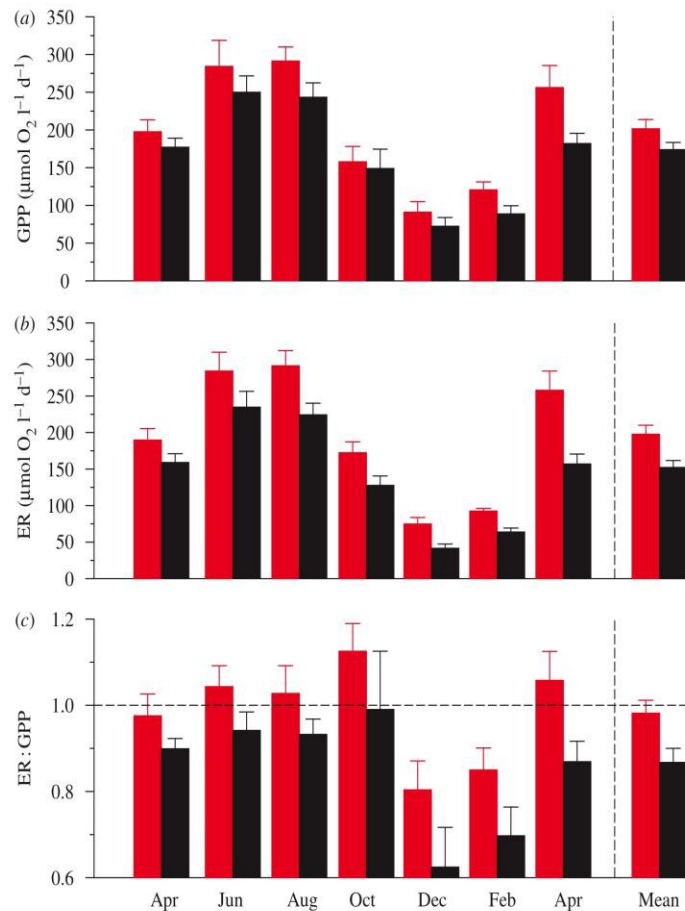


Fig.9 Changes in gross photosynthesis (Gross Primary Productivity, GPP) and ecosystem respiration (ER) and the ratio between them in experimental mesocosms at ambient temperature (black) and subject to a 2-3 °C temperature increase (red). From Yvon Durocher et al. (2010).

Two sets of experiments in freshwater wetland mesocosms have shown an increase in community respiration to gross photosynthesis ratios: of 18% with warming of 2-3°C (Yvon-Durocher et al., 2010) (Fig. 9), and 35% with warming of 4°C (Moss, 2010). Although there are few data and the methods used (based on oxygen exchanges) have limitations, the order of magnitude of the changes is disquieting and is supported by measurements made in wet and dry years in boreal peatlands (Gazovic et al., 2013). Net ecosystem production (gross photosynthesis minus community respiration) was $-83.7 \pm 14 \text{ g C m}^{-2}$ the dry year and $-134.5 \pm 21 \text{ g C m}^{-2}$ in the wet year, a reduction in the dry year of 38%. In a series of Icelandic streams at different temperatures, Demars et al. (2011) found a doubling in net carbon dioxide emissions and a halving of net ecosystem production for a 5°C-rise in mean annual temperature.

Moreover current estimates of methane emissions show that freshwater wetlands are major sources of methane and are equivalent, in carbon dioxide equivalents for radiation absorption, to about 25% of the calculated total terrestrial greenhouse gas sink (Bastviken et al. 2011). Streams are also major sources (Campo & del Giorgio, 2014) and emissions from bubbling are very significant (Crawford et al., 2014). Emissions of methane will increase with rising temperature (Walter et al., 2006; Campeau & Del Giorgio, 2014). Marotta et al. (2014) measured release of carbon

dioxide and methane from tropical and boreal lakes and found much higher combined rates, by 2.4-4.5 times in the former. Allowing for comparative areas they estimate future increases, using conservative climate models of 9-61%. The implications of these findings for net emissions are severe. The wetlands of the boreal zone contain 30% of the Earth's carbon store and lake sediments alone comprise 15% (Benoy et al. 2007). Marotta et al. (2014) write of potential large-scale positive feedback to climate change.

7. Rehabilitation and adaptation

There is high confidence that climate change is occurring, that it is largely man-made, that it is likely to give effects more rapidly than optimists might like, and that it must inevitably have direct and indirect effects on freshwater systems. The problem cannot be tackled on the basis of individual sites but must at least consider the catchment and even greater scales. Existing climate change has had demonstrable effects but other influences are likely to have been masked by the many other impacts on freshwaters. Temperature rises of several degrees will cause prominent changes but there is little confidence in the predicted details.

Freshwater systems are generally resilient, there is great natural flux in their communities and inherent evolved abilities to cope with change. Change may come directly from warming and particularly through hydrological influences on catchments. Changing catchment management in response to climate change may have both positive and negative effects. Reducing flood risk, for example, may result in greater areas of drained floodplains being returned to wetland, but increased demands for summer irrigation may deprive fens of groundwater supplies and lead to chalk rivers drying out for longer periods. Movement of intensive crop cultivation northwards may increase nutrient loading on lakes and rivers that are presently surrounded mostly by pasture and rough grazing, whilst areas in southern England may revert to heathland or grassland because water supplies may be insufficient to maintain crop agriculture. Increased numbers of people, perhaps including refugees, may increase the need for urbanisation and hence pollutant effects from wastewaters, whilst also creating a stronger lobby as local extreme weather increases distress and inconvenience. The details of most of these effects will not emerge until after they have happened. Attempts to protect freshwater systems must then be planned in very general terms. A particular problem for species-based conservation is the idiosyncratic response of different species in communities that may contain hundreds of species with thousands of potential interactions. Conservation based on ecosystem services, particularly regulatory services, may be a better strategy for the future.

The Water Framework Directive, although currently disappointing in its achievements (European Environment Bureau, 2010), in theory at least should result in improved freshwater habitats. There are currently no plans by the European Commission to modify the Directive or to incorporate the effects of climate change into it, though individual Member States are sometimes taking cognisance (Wilby et al., 2006). The current emphasis on ecosystem goods and services should also be useful, but the most important services, the regulatory ones, are among those least amenable to valuation. These instruments may counteract some negative effects of climate change, but it is impossible to make specific projections, given the detailed uncertainties in climate models, ecosystem responses and future policy. Many effects of climate change are likely to exacerbate those created by existing pressures like eutrophication, drainage, river engineering and introduction of alien species and so a sensible strategy is to intensify efforts to counteract these. This will likely need much more ambitious, indeed revolutionary, policies than are presently contemplated

to make significant differences if the deeper problems of the Earth's carbon balance, that underly the current concern for rapidly reducing biodiversity are to be solved.

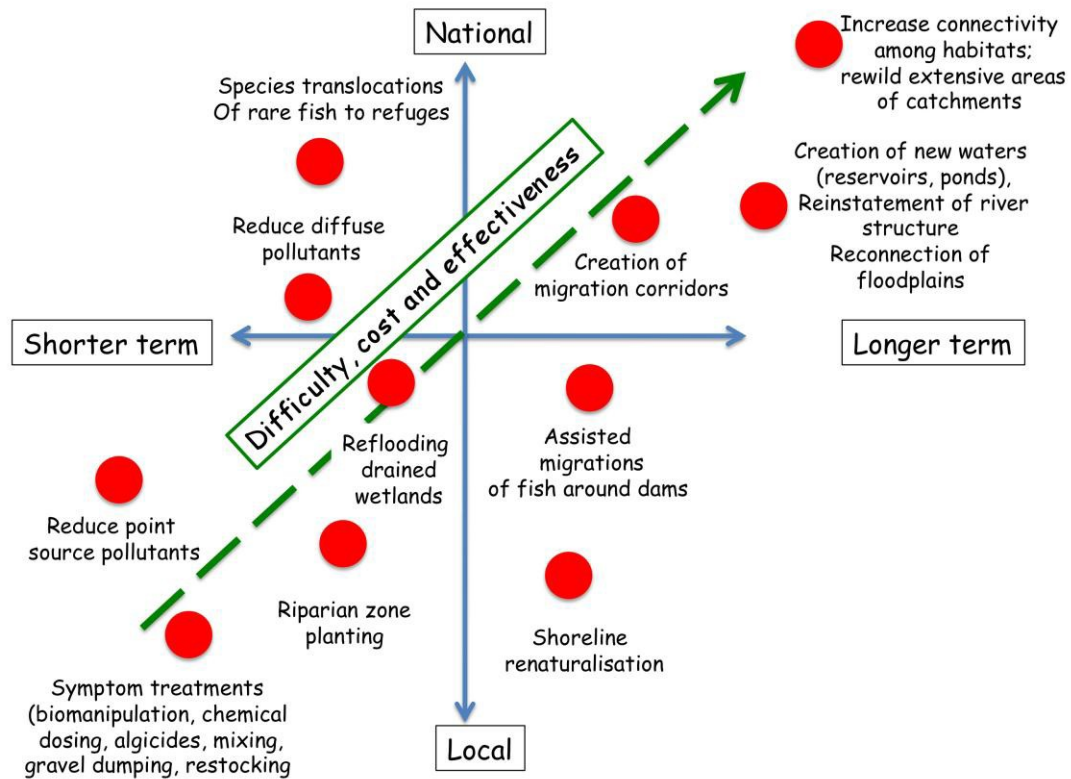


Fig.10 Approaches to the rehabilitation of the freshwater system in the face of many current human impacts. All approaches are, at least indirectly, in the interests of adaptation to climate change, but some of those to the upper right, particularly extension of wetlands through rewilding and increased connectivity of the hydrological systems, may, if extensive enough, contribute to mitigation through increased carbon storage . Greatly modified from an idea by Muir et al. (2012).

There is a variety of tools for treating damage to freshwaters but mostly they counteract symptoms and not the ultimate causes that are nested in society's organisation, aspirations and philosophy, nor even the proximate causes linked with catchment management as opposed to lake and river management. Two approaches at present specifically address the symptoms of warming. The first is establishment of riparian woodland to cool stream waters by shading (Wilby et al., 2010; Imholt et al., 2012) and the second is establishment of new communities of coregonids at higher or more northerly locations.

Future adaptation must involve substantial catchment management. Solutions that regulate fertiliser use, remove nutrients at all wastewater treatment works, create large buffer areas (not just narrow zones) for diffuse nutrients, and re-establish river channel structure and functioning floodplains, are likely to be most effective. It is desirable that water be retained on floodplains and in forests in the uplands to regulate water flow and flooding intensity. It is sensible to reduce eutrophication problems for they are costly and deleterious for biodiversity, and exacerbated by

warming. Establishment of more generous environmental flows on rivers below reservoir dams or power plants offers some protection to animal communities in droughts, when small southern rivers may come close to drying up in the future. But re-establishing freshwater habitats that provide renewed regulatory services will be very difficult without zoning and rewilding. Multiple use is a convenient idea but often means multiple mediocrity and is currently failing our freshwater systems. Fig. 10 notionally summarises the costs and ambition of potential approaches for the future.

Le Quéré et al. (2012) point out that that of around 9 Gt C yr⁻¹ released into the atmosphere, around 4 Gt accumulate and are not absorbed into sinks. Current sinks on land and in the ocean accommodate about 2.5 Gt each. If emissions are not reduced very substantially, to mitigate climate change, there will need to be about a doubling of the current land sink by restoration of forests and wetlands at the expense of about a third of current agricultural land (Moss, 2014). This can only be achieved by radical changes in world societies, and measures that fall at the upper right on Fig.10 and beyond.

8. References

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