

Title: Environmental Impacts—Lake Ecosystems

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Abstract

The North Sea region contains a vast number of lakes; from shallow, highly eutrophic water bodies in agricultural areas to deep, oligotrophic systems in pristine high-latitude or high-altitude areas. These freshwaters and the biota they contain are highly vulnerable to climate change. As largely closed systems, lakes are ideally suited to studying climate-induced effects via changes in ice cover, hydrology and temperature, as well as via biological communities (phenology, species and size distribution, food-web dynamics, life-history traits, growth and respiration, nutrient dynamics and ecosystem metabolism). This chapter focuses on change in natural lakes and on parameters for which their climate-driven responses have major impacts on ecosystem properties such as productivity, community composition, metabolism and biodiversity. It also points to the importance of addressing different temporal scales and variability in driving and response variables along with threshold-driven responses to environmental forces. Exceedance of critical thresholds may result in abrupt changes in particular elements of an ecosystem. Modelling climate-driven physical responses like ice-cover duration, stratification periods and thermal profiles in lakes have shown major advances, and the chapter provide recent achievements in this field for northern lakes. Finally, there is a tentative summary of the level of certainty for key climatic impacts on freshwater ecosystems. Wherever possible, data and examples are drawn from the North Sea region.

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10.1 Introduction

Freshwaters and freshwater biota are highly vulnerable to climate change (IPCC 2013). The various impacts and threats differ substantially between biomes and among geographical regions, and even within geographical regions hydrological factors and catchment properties will be major determinants of the responses in freshwater ecosystems to climate change. Effects on freshwater resources in agricultural or densely populated catchments for example will differ from those in pristine boreal or alpine catchments. In the North Sea region, water scarcity per se is not seen as the most immediate threat of climate change, with the exception of during summer in some areas. Strong flooding events may pose greater challenges. The North Sea region contains a vast number of aquatic systems, including shallow, highly eutrophic water bodies in agricultural areas; systems highly influenced by the input of terrestrially derived, coloured dissolved organic matter in coniferous areas; and large, deep and oligotrophic systems in pristine, sub-alpine areas. Clearly, the review presented in this chapter cannot cover every aspect related to climate and surface waters in the North Sea region; hence a focus on natural lakes and parameters where there is empirical support for climate change effects, as well as on systems for which long-term data sets exist and for which their responses have major impacts on ecosystem properties such as productivity, community composition and biodiversity. Hydrological effects, wetland effects and past climate effects inferred from paleolimnological surveys are covered elsewhere in this report, although there is no doubt that hydrology will also have strong bearings on water chemistry (e.g. by dilution through increased precipitation) and biota (changed fluxes in key elements like nitrogen, phosphorus, carbon, silicon, iron and calcium), dissolved organic matter and pollutants.

Monitoring the impacts of climate change poses challenges because of the many responses within an ecosystem and the spatial variation within the landscape. A substantial body of research demonstrates the sensitivity of freshwater ecosystems to climate forcing and shows that physical, chemical, and biological lake properties respond rapidly to changes in this forcing (Rosenzweig 2007; Adrian et al. 2009; MacKay et al. 2009; Tranvik et al. 2009; IPCC 2013). Fast turnover times from the scale of organisms to entire lake ecosystems are the prerequisite for these rapid changes. Studies of lake ecosystems have provided some of the earliest indications of the impact of current climate change on ecosystem structure and function (Adrian et al. 1995; Magnuson et al. 2000; Verburg et al. 2003) and the conse-

quences for ecosystem services (O'Reilly et al. 2003). Some climate-related signals are highly visible and easily measured in lakes. For instance climate-driven fluctuations in lake level have been observed on a regional-scale across North America (Williamson et al. 2009), and shifts in the timing of ice formation and melt reflect climate warming at a global scale (Magnuson et al. 2000). Other signals may be more complex and difficult to detect in lakes, but may be equally sensitive to climate or more informative regarding impacts on ecosystem services. Long-term historical records and reconstructions from sediment cores have yielded insight into less visible climate-related changes, thus increasing understanding of the mechanisms driving these changes. In particular, paleolimnological records have been critical for reconstructing the climate record over recent geological periods, making it possible to interpret current climate change and predict its future impacts.

Lake ecosystems are excellent sentinels for current climate change. In this context a sentinel is a lake ecosystem that provides indicators of climate change either directly or indirectly through the influence of climate on the catchment (Fig. 10.1; Carpenter et al. 2007; Adrian et al. 2009; Williamson et al. 2009). The indicators are measurable response variables, such as water temperature, dissolved organic carbon, or phytoplankton composition. Lakes are particularly good sentinels for current climate change for several reasons: they are well-defined ecosystems and studied in a sustained fashion; they respond directly to climate change and incorporate the effects of climate change within the catchment; they integrate responses over time, which can filter out random noise; and they are distributed worldwide and so cover many different geographic locations and climatic regions. However, the large range in lake morphology, geographic location, and catchment characteristics means that broad statements about the ability of lakes to capture the impacts of the current, rapidly changing climate must be made with caution. On the other hand, this also means that there are many different types of sensors in the landscape ranging from small shallow turbid lakes to large, deep, clear lakes that may capture, or provide sentinel information on different aspects of climate change, including temperature and precipitation-related components.

This chapter focuses on both the direct and indirect (e.g. via the catchment) effects of climate change, as well as on internal physical, chemical and biological processes and on the role of temporal scale. Wherever possible, data and examples are drawn from the North Sea region, but for important phenomena where North Sea studies are not available, information is 'borrowed' from other parts of the world.

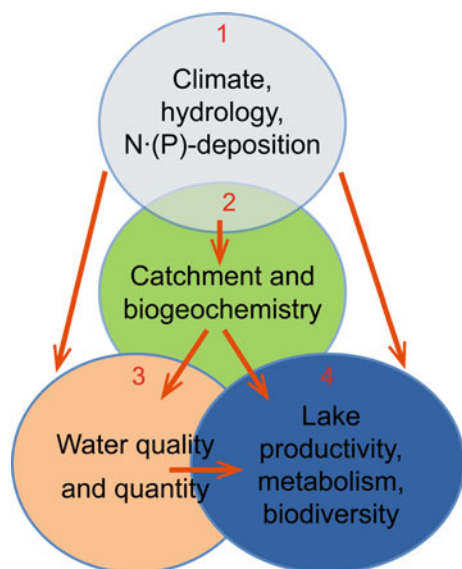


Fig. 10.1 Water and its context: lakes respond to climatic forcing, atmospheric deposition and the properties of their catchments. 1 Atmospheric forcing via temperature, precipitation and deposition of key constituents like nitrogen. 2 The catchment responds to climatic drivers and atmospheric inputs via vegetation and soil processes. 3 This determines the inputs of organic matter, nutrients and key elements determining parameters like retention time, transparency, pH and temperature. 4 The biota respond in terms of phenology, productivity, metabolism, community composition, diversity and food web interactions, to the direct forcing (1), catchment properties (2) and water properties (3)

10.2 Climate Warming and Impacts on Lake Physics

Data-based studies on the impact of climate change on lake temperature began in the early 1990s with the seminal studies of Magnuson et al. (1990) and Schindler et al. (1990). The former demonstrated that near-surface lake temperatures in Wisconsin fluctuate coherently in response to regional climatic forcing, while the latter demonstrated that lake temperatures in the Canadian Experimental Lakes Area were undergoing a long-term increase. Since the 1990s, an increasing number of studies have demonstrated that near-surface lake temperatures can fluctuate coherently over several hundred kilometres (e.g. Benson et al. 2000; Livingstone and Padišák 2007; Livingstone et al. 2010a), and that individual lakes in many parts of the world have been undergoing long-term warming at all depths. Lake warming has been demonstrated in Europe (e.g. Livingstone 2003; Salmaso 2005), North America (e.g. Arhonditsis et al. 2004; Coats et al. 2006; Austin and Colman 2008), East Africa (e.g. O'Reilly et al. 2003; Verburg et al. 2003), Siberia (Hampton et al. 2008) and Antarctica (Quayle et al. 2002). A recent study based on satellite thermal infrared images from 1985 onwards (Schneider and Hook 2010) confirmed that lake

surface temperatures have been undergoing a long-term increase over large areas of the northern hemisphere. In an extensive world wide survey of lake's summer surface temperatures O'Reilly et al. (2015) found an average warming trend of 0.34 °C per decade for the period 1985 until 2009.

Modelling studies on strictly dimictic lakes, which are ice-covered in winter and mix twice per year, suggest that surface temperatures will increase faster than deep-water temperatures as a result of climate change (Robertson and Ragotzkie 1990; Hondzo and Stefan 1993). In monomictic lakes, which mix once per year, the divergence between surface and deep-water temperatures is likely to be less strong as a result of heat carry-over in winter (Peeters et al. 2002). However, even in such lakes historical data show that near-surface water temperatures are increasing faster than deep-water temperatures, which implies an increase in thermal stability leading to an increase in the duration of stratification in summer and a corresponding decrease in the duration of homothermy in winter and spring (Livingstone 2003).

At high latitudes or high altitudes, where lakes are generally ice-covered for many months of the year, the more frequent occurrence of mild winters associated with climate warming will imply a general decrease in the duration of ice cover and a corresponding increase in the duration of summer stratification. Since the mid-19th century, there has been a general long-term decrease in the duration of ice cover in northern hemisphere lakes at a mean rate of about 1.2 days per decade (Magnuson et al. 2000), with the rate for individual lakes ranging from 0.9 to 1.7 days per decade (Benson et al. 2012). This decline seems to be accelerating: over the last 30 years, the equivalent is 1.6–4.3 days per decade (Benson et al. 2012). In regions with relatively brief or mild winters, where lakes are ice-covered for a comparatively short period—for instance in southern Sweden, Denmark and northern Germany—increasingly milder winters are likely to result in ice cover becoming intermittent or even disappearing (Livingstone and Adrian 2009; Weyhenmeyer et al. 2011). The disappearance of ice cover from a deep lake, implying a shift in mixing regime from dimixis to monomixis (Boehrer and Schultze 2008; Livingstone 2008), is likely to cause a change in its physical response to further climate warming, as mixing will no longer necessarily occur at the temperature of maximum density (4 °C) before ice-on and after ice-off. However, mixing can still occur at temperatures higher than 4 °C. Deep lakes that are already monomictic will experience individual years in which some form of stratification persists throughout the year, reducing the intensity of mixing and inhibiting deep-water renewal. Thus some deep monomictic lakes may show a tendency towards becoming oligomictic; i.e. will not mix fully every year. Shallow polymictic lakes, which lose their winter ice cover, are likely to undergo permanent mixing during winter.

10.2.1 Lake Water Temperature

Research on lakes within the North Sea region has demonstrated the occurrence of many of the phenomena mentioned in the previous section. In the UK—at the western boundary of the region, where the influence of the North Atlantic is at its greatest—research has focused on the English Lake District, where several decades of data are available from some of the larger lakes. Here, water temperatures both near the surface and in the deep water have been shown to respond coherently to climatic forcing throughout the year (George et al. 2000), with a clear long-term increase recorded in both near-surface temperatures (George et al. 2007a) and deep-water temperatures (Dokulil et al. 2006). Long-term increases in surface water temperatures have also been recorded in lakes in Sweden, at the region's eastern boundary (Adrian et al. 2009), and in northern Germany, at its southern boundary (Adrian et al. 2006, 2009; Wilhelm et al. 2006). It is thus likely that long-term increases in lake temperature are occurring throughout the North Sea region.

It has become evident that the climatic forcing acting on lakes in the North Sea region is extremely large-scale in nature, with the climate prevailing over the North Atlantic playing a major role in determining the physical behaviour of the lakes. Interannual fluctuations in thermal stratification in the lakes of the English Lake District, for instance, are related to north-south displacements of the Gulf Stream, with the early summer thermocline tending to be shallower and more well-defined when the Gulf Stream has its most northern direction (George and Taylor 1995). This effect appears to be related to the effect of the Gulf Stream on wind speed (George et al. 2007b). However, an even more potent determinant of physical lake behaviour is the climate mode known as the North Atlantic Oscillation (NAO), which governs winter weather in western, northern and central Europe to a very large degree (Hurrell 1995; Hurrell et al. 2003) and which is known to play an important role in determining the behaviour of lakes in this region (Straile et al. 2003). This climate mode, which can be considered a regional manifestation of the Arctic Oscillation (AO) (Thompson and Wallace 1998), is associated with interannual fluctuations in the meridional surface air pressure gradient in the north-east Atlantic (between about 35°N and 65°N). A positive NAO index implies a large meridional air pressure gradient, which results in the strong zonal transport of warm, moist maritime air from the North Atlantic towards north-west Europe. In winter, this implies predominantly mild, wet weather in the North Sea region. When the NAO index is negative, however, the eastward transport of warm, moist air from the North Atlantic is much weaker, implying predominantly cold, dry weather in the North Sea region. In lakes throughout northern and central Europe, surface water

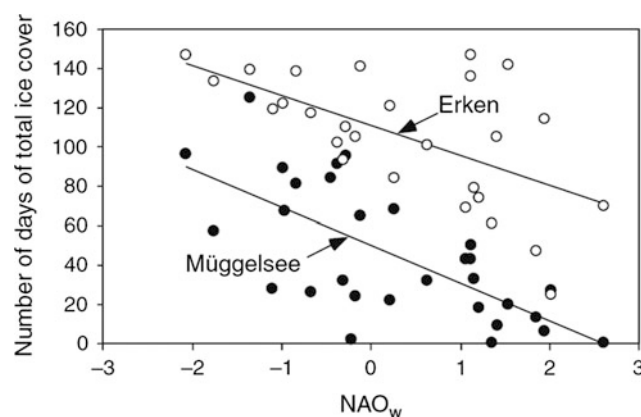


Fig. 10.2 Dependence of the number of days of total ice cover on Lake Erken (southern Sweden) and Müggelsee (northern Germany) on the winter NAO index (NAO_w) of Hurrell (1995), based on data from winter 1976/77 to winter 2005/06. Interannual variability in NAO_w explains 35 % of the interannual variability of the duration of ice cover for Lake Erken and 47 % for Müggelsee. The linear regressions (regression lines illustrated) are significant at $p < 0.01$ (from Livingstone et al. 2010b)

temperatures, near-bottom temperatures and the duration of ice cover (Fig. 10.2) are correlated to some extent with the winter NAO index (Blenckner et al. 2007).

In the English Lake District, lake surface temperatures in winter are tightly correlated with the winter NAO index (George et al. 2000, 2004b, 2007a) as, but to a lesser extent, are deep-water temperatures (George et al. 2004b), with the highest correlations being observed in the shallower lakes (George et al. 2004b). Mean annual water temperature of Lake Veluwe, a shallow lake in the Netherlands, is correlated with the winter NAO index (Scheffer et al. 2001), as are the surface water temperatures of Vänern, Vättern, and Mälaren, the three largest lakes in Sweden, in spring (Weyhenmeyer 2004). However, in Mälaren, a morphometrically complex lake with many sub-basins, the significance of the correlation varies substantially among the different sub-basins, suggesting that local lake characteristics can modify the effect of large-scale climatic forcing even on surface water temperature, which apart from the timing of ice-off is probably the lake variable least affected by internal lake processes. In Müggelsee, a well-studied, shallow, polymictic lake in northern Germany, several studies have demonstrated the effect of the winter NAO on lake temperatures (Gerten and Adrian 2000, 2001; Straile and Adrian 2000).

In a comparative study of Müggelsee and two neighbouring lakes, Gerten and Adrian (2001) showed that the winter NAO leaves a signal at all depths in lake temperature, but that the temporal persistence of this signal can differ substantially from lake to lake. Near the surface, the NAO signal is in general confined to late winter and early spring. In the deeper water, however, the persistence of the NAO

signal depends on the morphometry and mixing characteristics of the lake. The NAO signal persists only through spring in shallow, polymictic Müggelsee, but throughout much of the following summer in the shallow, dimictic Heiligensee, and throughout the whole of summer and autumn in the much deeper, dimictic Stechlinsee. Thus, although an NAO signal is likely to be present to some extent in the temperature of all lakes within the North Sea region, individual lake characteristics are certain to result in a large degree of variability in the strength and persistence of this signal.

In the context of the NAO, one other phenomenon should be mentioned: the late 1980s climate regime shift. In the late 1980s, an abrupt regime shift occurred in the atmospheric, oceanic, terrestrial, limnological and cryospheric systems in many regions of the world. Evidence suggests that this large-scale regime shift involved abrupt changes in the AO and NAO (Alheit et al. 2005; Rodionov and Overland 2005; Lo and Hsu 2010), had a substantial impact on air temperature in northern Europe (Lo and Hsu 2010), and affected fish populations in the North Sea (Reid et al. 2001; Alheit et al. 2005). It is not surprising therefore that a regime shift in lake temperature in the late 1980s was also detected in Müggelsee (Gerten and Adrian 2000, 2001), and it can be fairly confidently hypothesised that a similar regime shift, at least in lake surface temperatures, is likely to have occurred in many lakes within the North Sea region.

In summer, a more regional approach to determining the effects of climatic forcing on lakes is necessary owing to the smaller spatial scales of the weather systems involved. In the case of the UK, the Lamb synoptic weather classification system (Lamb 1950) has proven useful. For both Windermere, the largest lake in the English Lake District, and Lough Feeagh, a lake located near the west coast of Ireland, the highest lake surface temperatures were recorded during a westerly circulation type in winter (corresponding to a positive NAO index), but a southerly circulation type in summer (George et al. 2007b).

On a multi-annual time scale, large-scale regional coherence is greater in winter than in summer. However, on shorter time scales the opposite appears to be the case. Short-term, high-resolution surface temperature measurements in Scottish Highland lochs (Livingstone and Kernan 2009) show a high degree of regional coherence in daily means from late spring to autumn, but much lower coherence in winter and early spring. Short-term regional coherence is high in summer because the surface mixed layer is thin and surface temperatures respond sensitively to climate forcing, and is high in autumn because surface temperatures are dominated by convective cooling, which is governed by regionally coherent air temperature. Short-term coherence is comparatively low in winter because fluctuations in lake surface temperature are small and may be buffered by partial

ice cover, and is low in early spring because the lochs warm up and stratify at different times during the season depending on their altitude and distance from the maritime influence of the Atlantic. This latter effect may be important on the western boundary of the North Sea region, because the ameliorating influence of the Atlantic Ocean acts to increase winter surface temperatures, and hence to reduce the duration of inverse stratification or circulation.

Based on observed air temperature and physical lake characteristics, George et al. (2007b) were able to model well the surface temperatures of the lakes of the English Lake District. Using a regional climate model (RCM) driven by the SRES A2 scenario, they also projected lake surface temperatures in the 2050s. This showed increases of up to 1.1 °C in winter and up to 2.2 °C in summer, with the greatest increase in winter occurring in the shallowest lake, and the greatest increase in summer occurring in the lake with the shallowest thermocline.

10.2.2 Lake Ice Phenology

It is likely that the phenology of ice cover on the lakes of the North Sea region will follow the global trend; with ice-on occurring later, ice-off occurring earlier, and a general reduction apparent in the duration of ice cover (Magnuson et al. 2000; Benson et al. 2012). However, several factors will modify this general trend. Because of the approximately sinusoidal form of the air temperature curve, the dates on which the air temperature falls below and rises above 0 °C, which are crucial for the timing of ice-on and ice-off, respectively, are not linear functions of air temperature. Instead, they are arc cosine functions of air temperature, which implies that the sensitivity of the timing of ice-on, the timing of ice-off, and the duration of ice cover are greater in warmer regions than in colder regions, and so will increase as the climate warms (Weyhenmeyer et al. 2004a, 2011; Jensen et al. 2007; Livingstone and Adrian 2009). Thus, in the North Sea region, the impact of climate warming on lake ice phenology will be disproportionately large in those areas where winters are mild or variable and the duration of ice cover on lakes is already short (i.e. the UK, northern France, Belgium, Netherland, Luxemburg, northern Germany and southern Scandinavia) compared to those areas where winters are consistently cold and the duration of ice cover is much longer (i.e. northern Scandinavia). This is despite the IPCC (Intergovernmental Panel on Climate Change) projections implying that climate warming in winter in northern Scandinavia will be stronger than in the rest of the region (Christensen et al. 2007). In Sweden, several decades of historical data confirm that the timing of ice-off on lakes in the south of the country, where winters are relatively mild, has been responding significantly more sensitively to

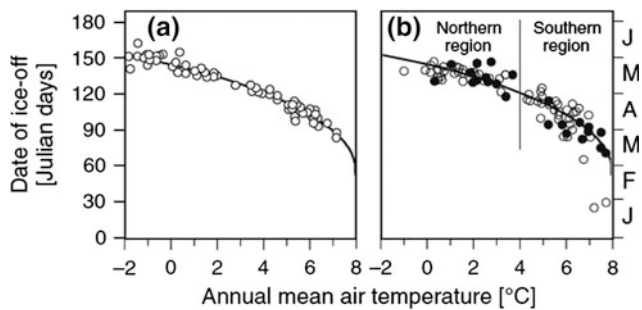


Fig. 10.3 **a** Dependence of the median date of ice-off on annual mean air temperature (1961–1990) for 70 lakes in Sweden. **b** Temporal variation in the relationship between the median date of ice-off and annual mean air temperature for 14 lakes in a northern region of Sweden (61–67°N) and 14 lakes in a southern region of Sweden (56–60°N) for the periods 1961–1990 (*white*) and 1991–2002 (*black*), showing that the form of the relationship is strongly dependent on latitude but not on the time period chosen. Annual mean air temperatures are calculated from July to June, and the curves illustrated are based on the arc cosine model of Weyhenmeyer et al. (2004a) (Livingstone et al. 2010b; after Weyhenmeyer et al. 2004a)

interannual fluctuations in mean winter air temperature than the timing of ice-off on lakes in the north of the country, where winters are longer and more severe (Fig. 10.3; Weyhenmeyer et al. 2004a).

A further study of ice phenology on 54 Swedish lakes during the 30-year IPCC reference period 1961–1990 showed a statistically significant ($p < 0.05$) trend towards earlier ice-off in 47 lakes, with the shift towards earlier ice-off varying between 1 and 29 days (Weyhenmeyer et al. 2005). Again, the shift towards earlier ice-off was stronger in the milder, southern part of Sweden than in the colder, northern part. During the IPCC reference period, the mean air temperature of the northern hemisphere increased by 0.4 °C. This resulted in a shift in the timing of ice-off by ~ 70 days in southern Sweden, but only ~ 10 days in northern Sweden. Applying the arc cosine model suggests that interannual variability in the duration of lake ice cover will be far greater in southern Scandinavia, Scotland and northern Germany than in northern Scandinavia (Weyhenmeyer et al. 2011). A more sophisticated probability model applied to Müggelsee, which now shows extremely variable, intermittent ice cover, predicts that the percentage of ice-free winters for this lake will increase from $\sim 2\%$ now to over 60% by the end of the 21st century (Livingstone and Adrian 2009).

As for winter lake surface temperatures, the duration of ice cover on lakes in the North Sea region also appears to be strongly related to the NAO. In the case of Müggelsee, 47% of the interannual variability of the duration of ice cover can be explained statistically ($p < 0.01$) in terms of the interannual variability of the winter NAO index, while for Lake Erken, in east-central Sweden, the equivalent value is 35% (Fig. 10.2). Even in the UK, where total lake ice cover does

not occur frequently, there is evidence that the number of days of partial ice cover is strongly linked to the winter NAO (George et al. 2004a; George 2007).

As well as the duration of ice cover, the timing of both ice-on and ice-off also appear to be determined to some degree by the NAO. For lakes in Sweden, the timing of ice-off is strongly related to the winter NAO while the timing of ice-on shows a weaker relationship to the autumn NAO (Blenckner et al. 2004). These results agree with those of similar studies showing that the winter NAO is an important determinant of ice phenology in the neighbouring Baltic region (Livingstone 2000; Yoo and d’Odorico 2002; Blenckner et al. 2004; George et al. 2004a). As in the case of lake water temperatures, there is evidence to suggest that the late 1980s climate regime shift may have resulted in an abrupt shift in lake ice phenology in the North Sea region: a study of Swedish lakes showed an abrupt shift in 1988/1989 that was substantial in southern Sweden but not in northern Sweden, again emphasising the relative sensitivity of ice phenology in warmer regions to external climatic forcing (Temnerud and Weyhenmeyer 2008).

10.3 Catchment–Lake Interactions

While lakes are commonly seen as closed entities, which is partly true in terms of populations with low or no immigration or emigration, lakes are strongly influenced by catchment properties such as the proportions of forest, bogs, and arable land that serve as major determinants of element fluxes (and water) to lakes. This is however modified by anthropogenic impacts. For example, acidifying elements such as nitrogen (N) and sulphur (S) will modify the catchment export of ions, dissolved organic matter (DOM) and nutrients, and deforestation or afforestation will also have a major impact on the flux of elements to lakes. This is especially striking for nitrogen, where alpine or otherwise sparsely vegetated catchments may have very low N-retention, while forested catchments may retain almost all nitrate (NO₃) and ammonium (NH₄) inputs during the growing season (Hessen 1999).

Different catchment properties have vastly different effects on lakes, even within the North Sea region, and these properties and effects will also be differently modified by climate drivers (Fig. 10.1). Although large, deep and oligotrophic lakes are common in alpine areas of the North Sea drainage basin, the North Sea region is dominated by two major types of lake system and it is these that will be most affected by climate change. These are the boreal lakes generally found in forested, less impacted, catchments with limited input of bioavailable nutrients but high loads of humic substances of terrestrial origin. The other lake type occurs in agricultural areas with higher nutrient loads. Both

Fig. 10.4 Export of coloured dissolved organic carbon (DOC) from wetlands, bogs and forest via rivers (Photo D.O. Hessen)



categories of lake/catchment encompass a wide range of size, volume, renewal rates, productivity and community composition.

While catchment responses to climate affect downstream rivers, lakes and ecosystems, hydrology (runoff) also plays a major role both in mobilising and diluting dissolved matter and key elements (such as nitrogen, phosphorus, iron, silicon and calcium). Hydrology also affects the water renewal rate, which has major impacts on the physical, chemical and biological properties of waters. These aspects are less well studied and there is a need for ‘bridging the gap’ between hydrology and especially aquatic biology.

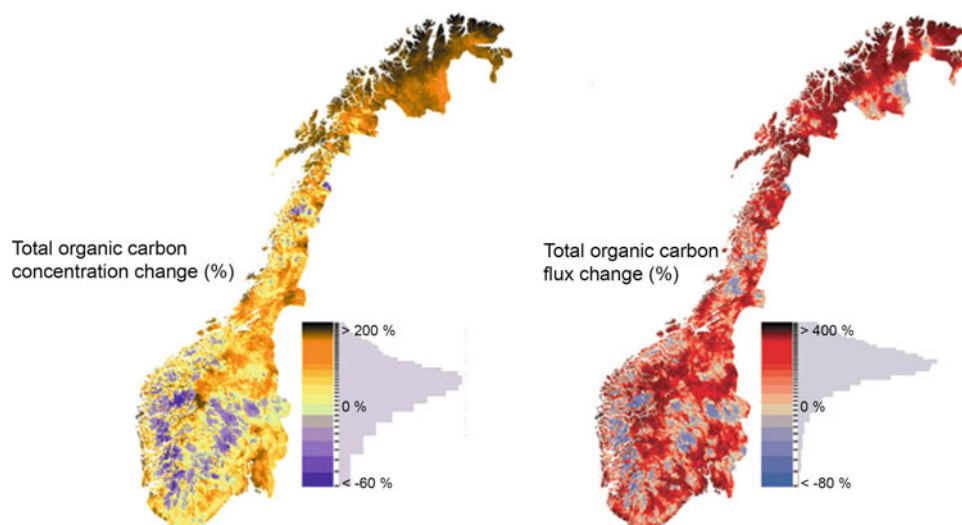
10.3.1 Boreal Lakes

Rising temperatures and changes in precipitation patterns and amounts will have direct effects on lake ecosystems as well as indirect effects via impacts within the terrestrial catchments (Schindler 2001; Kernan et al. 2010). Atmospheric deposition of nitrogen and sulphur will add to these climate-related impacts on ecosystems (Wright et al. 2010). The well-documented increase in dissolved organic matter in boreal lake ecosystems is one of the most obvious indirect effects (Monteith et al. 2007). This ‘browning’ is mainly due to coloured dissolved organic carbon (DOC) which absorbs light and so affects lake production at all trophic levels (Karlsson et al. 2009; Xenopoulos et al. 2009) as well as species composition (Watkins et al. 2001). The export of DOC from wetlands, bogs and forest via rivers (Fig. 10.4) to lakes and coastal

areas is projected to increase, causing reduced primary and secondary production due to light limitation.

Changes in temperature and precipitation drive seasonal and interannual variations in the export of DOC and nutrients by affecting soil organic matter mineralisation and the production of DOC and mineral nitrogen species (Kalbitz et al. 2000; Hobbie et al. 2002a, b), as well as hydrology within the catchment. On a longer timescale, climate change can allow forests to expand into areas at present under heathland and alpine vegetation (Hofgaard 1997), thereby affecting nutrient retention, nutrient export and soil organic matter pools and quality (Kammer et al. 2009). A major climatic response expected in boreal, coniferous areas is an increase in the concentrations of terrestrially derived DOM and DOC. For a large dataset of boreal lakes (1041 Swedish lakes along a 13° latitudinal gradient), Weyhenmeyer and Karlsson (2009) demonstrated a nonlinear response of DOC to increasing temperature, with the number of days above 0 °C as the major predictor. Analysis of a correspondingly large dataset of boreal Norwegian watersheds within the North Sea region, indicates that even a moderate (2 °C average, downscaled Hadley scenario) increase in temperature with associated increase in precipitation and vegetation density has the potential to increase DOC export substantially (Fig. 10.5; Larsen et al. 2011a, b). For other North Sea regions, especially the UK, reduced deposition of acidifying compounds (notably sulphur) has also been shown to affect DOC concentrations (Evans et al. 2006), although the Nordic studies strongly suggest that climatic drivers like temperature and/or precipitation are the key drivers of rising DOC concentrations in lakes.

Fig. 10.5 Projected change in total organic carbon concentrations and catchment fluxes at a new steady state based on a downscaled 2 °C increase (Hadley model) (Larsen et al. 2011b)



The ecosystem responses to elevated DOC export may be profound, and may also act in concert with elevated N-deposition and N-export to lakes, which also may increase as a result of elevated N-deposition due to increased precipitation (de Wit et al. 2008; de Wit and Wright 2008; Hessen et al. 2009). This in turn is likely to affect productivity and autotroph community composition; a large survey of US and Scandinavian lakes suggested a transition from N-limitation to P-limitation in many freshwater systems as a result of chronic, elevated N-deposition (Elser et al. 2009).

An increase in allochthonous carbon may fuel microbial production and serve as an alternative food resource for zooplankton (Hessen 1998; Jansson et al. 2007). Changes in water colour and loading of organic carbon may also affect the relative roles of the benthic and pelagic parts of the lake ecosystem, in favour of the pelagic (Ask et al. 2009; Karlsson et al. 2009). However, increased DOC loads are expected to have negative impacts on overall lake productivity. Recent studies from boreal catchments suggest that P-loads especially will decrease in most areas due to increased terrestrial uptake, intensifying P-limitation and in concert with increased light limitation will reduce the overall productivity of boreal freshwaters (Weyhenmeyer et al. 2007; Jones et al. 2012; Thrane et al. 2014). Since DOM may also be a source of phosphorus in pristine catchments, a unimodal response in fish yield over DOC was found for a large number of boreal, Norwegian lakes (Finstad et al. 2014), where an initial stimulus of DOC-associated phosphorus was superseded by light limitation at higher DOC-concentrations.

Hansson et al. (2012) studied how a combination of warming and increased lake colour affects spring plankton phenology and trophic interactions in a mesocosm experiment. Elevated temperature was crossed with increased water colour. Overall, they found temperature to have a

stronger effect on phytoplankton and zooplankton abundance than humic substances, but importantly also found synergistic effects between the two stressors. Thermal properties will also be affected by changes in ice cover and basin morphometry (MyLake-model, Saloranta and Andersen 2007), and temperature and reduced nutrients may both induce smaller algal cell size (Daufresne et al. 2009; Hessen et al. 2013) and community changes.

10.3.2 Lakes in Agricultural Areas

While changes in DOC may be the main climatic response in boreal lakes, they will also be affected by changes in nitrogen, phosphorus and silicon loads. The nutrient impact is far more severe in urban or agricultural lakes, however, and such lakes are also more susceptible to catchment erosion promoted by extreme rainfall as well as reduced periods of snow cover or frozen ground in winter. Land use and agricultural practices such as harvesting and fertiliser applications largely determine loads of nutrients and particulate matter to these lakes, but climatic factors, not least precipitation patterns, will add to these effects. Typically the nitrogen load from agricultural areas is expected to increase, but with a seasonal shift to increased N-export in winter, reflecting both land-use practices and climatic change (Jeppesen et al. 2011).

Phosphorus loads will also increase due to higher winter precipitation and erosion, but again the effects of land-use practices will be superimposed on the effects of climate change. The net impact on lake productivity is unclear, not least because increased turbidity has such a profound impact on lake productivity and stability (Mooij et al. 2005; Jeppesen et al. 2011). Specific ecosystem responses in lakes in agricultural areas are addressed in the following sections.

10.4 Ecosystem Dynamics

Climate change is expected to alter community structure and ecosystem functioning within lakes worldwide as well as within the North Sea region. Changes may occur in phenology, species and size distribution, food-web dynamics, life-history traits, growth and respiration, nutrient dynamics and ecosystem metabolism. Temperature-induced changes of this type are expected to interact with the increased nutrient flows resulting from enhanced precipitation and runoff (Blenckner et al. 2007; Jeppesen et al. 2010a; Moss et al. 2011).

10.4.1 Trophic Structure and Function

10.4.1.1 Fish

Several studies indicate that fish community assemblages, size structure and dynamics will change with global warming. A long-term study of 24 European lakes revealed a decline in the abundance of cold-stenothermal fish species, particularly in shallow lakes, and an increase in the abundance of eurythermal fish species, even in deep, stratified lakes (Jeppesen et al. 2012). This occurred despite a reduction in nutrient loading in most of the case studies, supposedly favouring fish in cold-water and low-nutrient lakes. The cold-stenothermic Arctic charr *Salvelinus alpinus* has been particularly affected, showing a clear decline in Lake Elliðavatn in Iceland, Lake Windermere in the UK (Winfield et al. 2010), Lake Vättern in Sweden (Jeppesen et al. 2012), and Scandinavian hydroelectric reservoirs (Milbrink et al. 2011).

Other cold-water-adapted species such as coregonids and smelt *Osmerus eperlanus* are affected at the southern border of their distribution. The harvest of whitefish *Coregonus* spp. has declined substantially in Lake Vättern in Sweden and Lake Peipsi in Estonia (Kangur et al. 2007; Jeppesen et al. 2012). In the UK and Ireland, a decline in the coregonid pollan *Coregonus autumnalis* in recent decades has been attributed to changes in temperature (Harrod et al. 2002). A drastic reduction in the population of smelt has occurred in shallow Lake Peipsi as shown from commercial fishing, with the decline particularly strong in years with heat waves (Kangur et al. 2007; Jeppesen et al. 2012). In contrast, the abundance of eurythermal species, including the thermo-tolerant carp *Cyprinus carpio* (Lehtonen 1996; Jeppesen et al. 2012) is rising in several lakes in the North Sea region (Jeppesen et al. 2012).

It is well-established that high-latitude fish species are not only often larger but also often grow more slowly, mature

later, have longer life spans and allocate more energy to reproduction than populations at lower latitudes (Blanck and Lamouroux 2007). Even within species such differences can be seen along a latitudinal gradient (Blanck and Lamouroux 2007) and within North Temperate lakes (Jeppesen et al. 2010b). Thus, changes in life history and size can be expected with warming, and may in fact already have occurred (Daufresne et al. 2009; Jeppesen et al. 2010b, 2012).

10.4.1.2 Plankton

Changes in fish community structure are likely to have cascading effects in lakes, most implying increased predation on larger zooplankton which in turn means less grazing on phytoplankton and so higher algal biomass per unit of available phosphorus (Lehtonen and Lappalainen 1995; Gyllström et al. 2005; Balayla et al. 2010; Ruuhijärvi et al. 2010; Jeppesen et al. 2010a, b; Meerhoff et al. 2012). Decreasing body size has been suggested as a universal biological response to global warming (Gardner et al. 2011; Hessen et al. 2013). However, there is no consensus about the underlying causality.

The predatory effect due to fish that prefer large zooplankton prey could be reversed or partially reversed if the prevailing or additional predators are invertebrates that prefer small prey. In this case, stronger predation at higher temperature would lead to a stronger removal of small species. A shift towards smaller species can also result from stronger resource competition under higher temperatures and competitive advantage for smaller species. Stronger invertebrate predation at higher temperatures has been suggested, particularly for primary producers, because heterotrophic metabolic rates increase faster with rising temperature than photosynthesis (Yvon-Durocher et al. 2011).

Further evidence of warming-induced changes in plankton size structure comes from mesocosm studies that mimic British shallow lakes. In these mesocosms, warming increased the steepness of the plankton community size spectrum by increasing the prevalence of small organisms, primarily within the phytoplankton assemblage. Mean and maximum size of phytoplankton was reduced by about an order of magnitude. The observed shifts in phytoplankton size structure were reflected in changes in phytoplankton community composition, while zooplankton taxonomic composition remained unaffected by warming (Yvon-Durocher et al. 2011). See Sect. 10.6 for more information on responses of lake plankton communities in the context of global warming. Weak changes in the species composition of benthic macroinvertebrates following shifts towards warmer water temperatures were found in Swedish lakes (Burgmer et al. 2007).

10.4.1.3 Cyanobacteria Biomass

Higher phytoplankton biomass, particularly higher biomass of cyanobacteria during summer may be expected as a direct response to enhanced water temperatures and as an indirect response to prolonged stratification. Prolonged stratification causes an increase in internal P-loading (Jensen and Andersen 1992; Søndergaard et al. 2003; Wilhelm and Adrian 2008; Wagner and Adrian 2009b), boosting the decomposition of organic matter and thus oxygen depletion at the water-sediment interface, which further exacerbates the P-release from the sediment (Søndergaard et al. 2003). In polymictic lakes, for example, climate warming extended the periods of stratification, and this lengthening of stratified periods led to more frequent and/or stronger internal nutrient pulses between stratified and mixed periods which again promoted cyanobacteria proliferation during summer (Wilhelm and Adrian 2008; Wagner and Adrian 2009b). In dimictic lakes, on the other hand, longer periods of summer stratification may cause longer periods of nutrient limitation in the epilimnion along with higher water temperature and stronger nutrient pulses during the autumn overturn (Adrian et al. 1995; Huisman et al. 2004; Mooij et al. 2005; Elliott et al. 2006; Jöhnk et al. 2008). Immediate access to the hypolimnetic nutrient pools will be limited to migrating species such as buoyant cyanobacteria species, which are often capable of N-fixation (Reynolds 1984; Paerl 1988). Thus, in addition to causing an increase in algal biomass (particularly for cyanobacteria), climate warming may also lead to a change in ecosystem functionality such as a predominance of species capable of N-fixation (Wagner and Adrian 2009b; Huber et al. 2012).

10.4.1.4 Microbial Loop

How the microbial community and microbial processes are affected by global warming has only been studied in a few large-scale experiments. In mesocosm studies in Denmark the abundance of picoalgae, bacteria and heterotrophic nanoflagellates showed no direct response to experimental warming (Christoffersen et al. 2006). However, experimental warming modified the effects of nutrient addition (Christoffersen et al. 2006; Özen et al. 2013), indicating that interactive effects may be significant in the future given the expected increase in nutrient loading to shallow lakes worldwide (Jeppesen et al. 2009, 2010b; Moss et al. 2011). Increased DOM levels will alter the balance between phytoplankton and heterotrophic bacteria, and thus shift systems (further) towards net heterotrophy (see also Sect. 10.4.4).

10.4.1.5 Macrophytes

Owing to the climate-induced increase in eutrophication there is an increased likelihood of losing submerged

macrophytes and thereby shifting shallow lakes from benthic- to pelagic-dominated systems with a consequent reduction in biodiversity. Indications of such developments are based on long-term data of Danish (Jeppesen et al. 2003) and Dutch shallow lakes (van Donk et al. 2003) as well as modelling studies (Mooij et al. 2007, 2009). Moreover, a dominance of filamentous green algae rather than phytoplankton seems possible under elevated temperatures (Trochine et al. 2011). Space-for-time approaches indicate that macrophyte cover will decrease in lakes with fewer days of ice cover, unless nutrient levels also decline (Kosten et al. 2009). Netten et al. (2011) predicted that milder winters may cause submerged macrophytes with an evergreen overwintering strategy as well as free-floating macrophytes, to outcompete submerged macrophytes that die back in winter. Neophytes such as the free-floating species *Salvinia natans* and the submerged species *Vallisneria spiralis* have been shown to be successful under elevated temperatures at the expense of native submerged macrophytes (Netten et al. 2010; Hussner et al. 2014). Mormul et al. (2012) tested the effects of elevated temperature (3 °C) on native and non-native aquatic plant production in mesocosms in combination with 'browning' (increased DOC), a potentially important change in the northern hemisphere and found browning to be more important for species invasion than warming. Climate change is likely to have a direct effect if non-native species respond positively to climate change and an indirect effect through species interactions, for example, because browning impairs the growth of native macrophytes and reduces biotic resistance to invasion.

Native competitors of the invasive *Elodea canadensis* were less successful in browner waters indicating a reduced resistance to invasion. Warming of mesocosms in the UK by 3 °C also significantly altered the proportions of three macrophyte species due to a higher growth rate and higher relative abundance of the neophyte *Lagarosiphon major* (McKee et al. 2002). A subsequent trial with temperatures 4 °C higher and higher nutrient concentrations resulted in a dominance of floating duckweed *Lemna* spp. which severely reduced oxygen availability and resulted in a fish kill (Moss 2010). In general, however, there are few long-term studies on the effect of climate change on macrophyte species distribution and invasions, coverage and subsequent effects on other trophic levels in aquatic ecosystems.

For large areas of northern Europe, mass occurrences ('nuisance growth') of the macrophyte *Juncus bulbosus* have been recorded (Moe et al. 2013). The reasons for this phenomenon are still unclear, but nuisance growth has been linked with hydrology, carbon dioxide and elevated N-deposition (Moe et al. 2013).

10.4.2 Phenology

The most prominent examples of climate-induced changes in lakes are changes in phenology. Coherent changes in ice phenology (see Sect. 10.2.2), and changes in spring and early summer plankton phenology in the North Sea region in recent years have been attributed to climate change (Adrian et al. 1999; Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Straile 2002) as synchronised by large-scale climatic signals such as the NAO (for a review see Blenckner et al. 2007; Gerten and Adrian 2002a; Straile et al. 2003). While indirect temperature effects such as early ice-off, which improves underwater light conditions have brought forward the start of algal bloom development in spring, direct temperature effects caused changes in the timing of rotifer and daphnid spring maxima (Gerten and Adrian 2000; Adrian et al. 2006; Straile et al. 2012) cascading into an earlier clear water phase (Straile 2002). For zooplankton, phenological shifts were most immediate for fast-growing species such as cladocerans and rotifers (but see Seebens et al. 2007), whereas longer-lived plankton such as copepods showed a lag in response. Copepods responded to altered day-length-specific water temperature affecting the timing of the emergence of resting stages in spring (Gerten and Adrian 2002b; Adrian et al. 2006). In addition, warming-induced accelerated ontogenetic development may enable the development of additional generations within a year as has been shown for copepod species (Gerten and Adrian 2002b; Schindler et al. 2005; Adrian et al. 2006; Winder et al. 2009).

10.4.3 Metabolism

Recent research suggests that global warming tends to shift the metabolic regime of entire lakes toward a dominance of respiration (Allen et al. 2005). This fundamental difference in temperature response between autotrophic and heterotrophic processes may have major implications for biological communities and for ecosystems in general. However, different members of a food web react differently to temperature, for example while cell-division rates may increase with temperature, as may grazing rates and metabolic demands of zooplankton. Thus, the net effect of warming on metabolism is not straightforward also because metabolic rates differ at the species level. As a result, how a changing climate interacts with increased nutrient supply to alter ecosystem metabolism is more uncertain than the change in trophic structure. Although evidence suggests that processes such as deoxygenation, decomposition and denitrification are influenced both by nutrients and by warming, interactions are complex and variable and there are discrepancies in study

results about the end result for system components as well as for systems as a whole.

Mesocosm studies in the UK indicated that gross primary production and respiration increase with warming, while results for net production and carbon storage differ. Two experiments (Moss 2010; Yvon-Durocher et al. 2010) showed a marked increase (18–35 %) in the ratio of diurnal community respiration rates and gross photosynthesis for a warming of up to 4 °C. If extrapolated to the large number of shallow northern lakes, this could have immense implications for positive feedbacks in the Earth's future carbon cycle (Moss 2010). However, these UK experiments were all of short duration (less than one year) and may only have described the transient state after warming, which may lead to overestimation of the net release of carbon. Long-term mesocosm experiments will provide more reliable indications about the net effect of warming on ecosystem metabolism (Jeppesen et al. 2010a; Liboriussen et al. 2011), complemented by long-term research and modelling of whole lake ecosystems (Trolle et al. 2012).

10.4.4 Greenhouse Gases and Heterotrophy

Ecosystems not only respond as recipients of climatic change, but also provide feedbacks, not least via greenhouse gases such as carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O). As previously mentioned, the input of organic carbon to lakes through run-off from the catchment has increased in the North Sea region, inducing changes in water colour (Hongve et al. 2004; Erlandsson et al. 2008) (see also Sect. 10.3). Recovery of soils from acidification and changed hydrological conditions are believed to be important factors determining this development (Monteith et al. 2007). On a somewhat longer perspective, climate effects on hydrology and vegetation density may also promote a substantial browning of boreal surface waters (Larsen et al. 2011a, b).

Autotrophs and heterotrophic bacteria compete for the same essential elements, but utilise different energy sources. While DOC is a major energy source for heterotrophic bacteria, it is also an important absorbent in the photosynthetically active part of the spectrum. DOC thus has negative impacts on primary producers both by competing for photons and by stimulating their major nutrient competitors. Increased levels of terrestrially-derived DOC in concert with reduced availability of inorganic phosphorus in lakes may shift systems further towards net heterotrophy and thus a net CO₂ release (Sobek et al. 2003; Larsen et al. 2011c).

Increased loads of DOM in boreal lakes would also promote anoxia in the deeper water layers, which promotes

CH₄ production and its net flux to the atmosphere (Juutinen et al. 2009). Increased N-deposition in concert with elevated export of DOM may promote export of N₂O (Hong et al. 2015). For lakes in agricultural systems, increased productivity due to increased nutrient inputs from the catchment may promote the net efflux of CH₄ and N₂O (Juutinen et al. 2009; Hong et al. 2015), while the net impact of the CO₂-balance will also depend on lake morphometry and stratification and so is harder to predict.

10.5 Biodiversity

Climate conditions are as important for freshwater biodiversity as for terrestrial and marine biodiversity, and consistently explain a major proportion of the geographic variation in species richness of different freshwater taxa such as amphibians, fish, mammals, crayfish and waterbirds (Tisseuil et al. 2013). Even so, other geographic patterns such as the latitudinal gradient in biodiversity is not as strong in freshwater as it is in the marine or terrestrial realms (Hillebrand 2004). However, these geographic trends (often measured at global to regional scales) cannot easily be transferred into predictions on temporal shifts in biodiversity at regional to local scales under climate change. Freshwater systems are particularly vulnerable to climate change for several reasons: owing to the isolated nature of freshwater habitats embedded in a terrestrial matrix; because climate change has direct influences on local temperatures and temperature-associated factors (such as oxygen saturation); and because many freshwater systems already absorb other anthropogenic stressors such as nutrient loading or an altered hydrological regime (Woodward et al. 2010). This section addresses these issues by reviewing existing information on biodiversity shifts in the North Sea region (Sect. 10.5.1) and deriving more general predictions from theoretical and experimental literature identifying research needs in the North Sea region (Sect. 10.5.2).

10.5.1 Shifts in Biodiversity

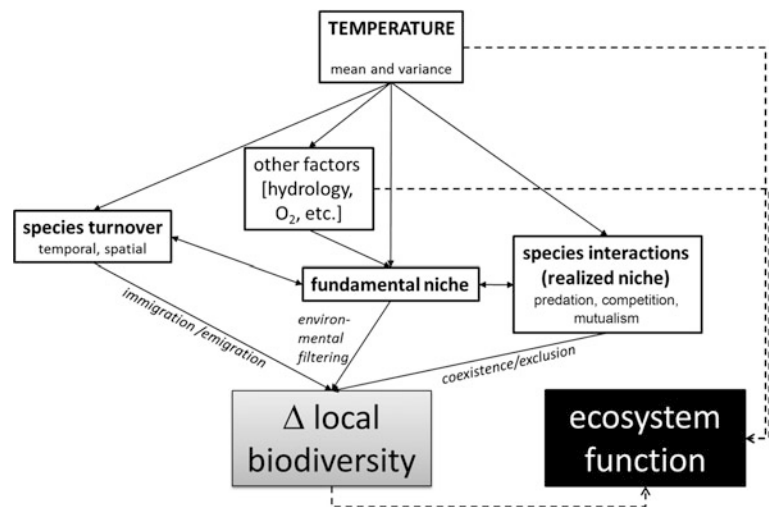
Predicting shifts in freshwater biodiversity in the North Sea region is difficult, because few studies have been explicitly conducted in lentic or lotic water bodies in this region. Predictions concerning future biodiversity are often derived from bioclimatic envelope models, which project future range shifts based on the current distribution of species (Parmesan and Yohe 2003). These models typically predict a northward (and often eastward) shift in ranges, such that warm-adapted species expand their ranges, and the ranges of cold-adapted species narrow.

Although changes in marine biodiversity in the North Sea region have frequently been predicted using this approach (Beaugrand et al. 2002), studies for freshwater systems in this region are rare. The species richness of macroinvertebrates across running waters in Europe has been predicted to decline in the southern North Sea countries (UK, Germany, Netherlands, Denmark), but to increase in the North (Norway) (Domisch et al. 2013). Changes in distribution and diversity have already been observed in some freshwater groups, such as odonates in the UK (Hickling et al. 2005). Other diversity shifts caused by local, climate-related range retractions have been reported for fishes in Iceland (Jeppesen et al. 2010b) and crustaceans in Norway (Lindholm et al. 2012). Correspondingly, analyses of long-term monitoring data on community composition revealed shifts in macroinvertebrate assemblages associated with ambient temperatures in Greenland, Iceland, Norway, Denmark and Sweden (Burgmer et al. 2007; Friberg et al. 2013). However, few long-term monitoring data sets still exist for freshwater systems within the North Sea region.

Thus it seems clear that specialised communities in colder regions around the North Sea have a high potential for reduced biodiversity. Macroinvertebrates in glacier-fed river systems will be characterised by lower local species richness and lower beta-diversity if warming leads to glacier retreat (Jacobsen et al. 2012). In boreal regions of northern Europe, the riparian zones of running waters are predicted to be affected by additive or interactive combinations of higher temperature, increased annual discharge but less seasonal variation in runoff, changes in groundwater supply, and altered ice regimes (Nilsson et al. 2013). Potential consequences for biodiversity can be negative or positive. Negative consequences are likely if the riparian zone narrows, such as by hydrologic changes, and thus species richness locally declines. In contrast, higher temperatures might allow invasion of exotic species leading to higher local species richness. Other types of change include altered disturbance regimes (e.g. altered freezing and thawing regimes during winter), which could foster a more dynamic and species-rich riparian vegetation, but also a more specific and species-poor assemblage of stress-tolerant species.

Floodplain systems around the North Sea coast have been massively altered by human regulation of flow regimes and inundation (Tockner et al. 2010). At the same time, they harbour a diverse fauna and flora shaped by the interaction of different climatic, hydrological and biological drivers as well as by the interaction between aquatic and terrestrial ecosystems with respect to the exchange of water, nutrients and organisms. Climate-induced shifts in flow regime are thus of primary importance for biodiversity. European-scale modelling scenarios predict that North Sea region floodplains will experience moderately higher flow levels

Fig. 10.6 Schematic representation of pathways leading to altered local biodiversity and thus ecosystem function. Main pathways include changes in species pools (species turnover) and on the fundamental as well as realised niches of species



(contrasting with predictions for other regions, such as the Mediterranean floodplains) (Schneider et al. 2013). Consequences for biodiversity remain largely unknown.

Climate-driven changes in biodiversity are very likely to interact with changes associated with other anthropogenic pressures, such as eutrophication (Moss et al. 2009). Some synergistic effects have been found in UK mesocosm studies (Feuchtmayr et al. 2009). For example, warming promoted increased phosphorus concentrations and the frequency of severe benthic anoxia in the mesocosms, with the potential to exacerbate existing eutrophication problems (McKee et al. 2003).

10.5.2 Predictions, Theory and Experimental Studies

Although functional aspects of ecosystem impacts (biomass, productivity, element cycling) under climate change can be predicted with some accuracy (see previous sections), information on shifts in freshwater biodiversity in the North Sea region remains vague (Moss et al. 2009). This is due not only to the scarcity of studies themselves, but also to the focus on larger spatial scales (i.e. regional climate-envelope models on range shifts), which makes predictions for local ecosystems difficult. Information from ecological theory and experiments can help to fill this gap by identifying potential changes in freshwater biodiversity and associated pathways (Fig. 10.6). Local attributes may also be superimposed on large-scale patterns. In an analysis of global lake zooplankton data, Shurin et al. (2010) found increased biodiversity in lakes showing greater temperature variation on different time scales (intra- and interannual). A recent review argued strongly for including temperature variability in climate-change experiments (Thompson et al. 2013).

The survival of a species can be directly impaired if temperatures are shifted beyond the fundamental thermal niche, leading to local extinction (Fig. 10.6). Temperature also affects the fundamental niche of a species with respect to other conditions, which are often directly related to temperature (e.g. oxygen saturation, hydrological regimes, solute concentrations). Indirect consequences of temperature change can be seen in freshwaters from around the North Sea, for example with respect to stratification regimes (Wagner and Adrian 2011) or oxygenation (Wilhelm and Adrian 2008). These changes alter the environmental filtering of colonising species, such that local diversity can increase or decrease depending on the number of species that are precluded or enabled to establish viable populations.

The meta-community context (Leibold et al. 2004) reflects the interplay of dispersal and local processes and will become an important tool to predict future changes in aquatic biodiversity. This is even more likely given that much of the regional biodiversity in aquatic systems is contributed by ponds and shallow lakes as these have high beta-diversity due to their often isolated nature (Scheffer et al. 2006) and provide important ecosystem services such as carbon storage due to their high number (Giller et al. 2004; Downing et al. 2006; Tranvik et al. 2009).

At the same time, there is high potential for small isolated systems to lose species with global climate change (Burgmer and Hillebrand 2011) and spatial dynamics are important for maintaining biodiversity in these systems. Meta-community dynamics can also provide spatial insurance for freshwater ecosystems (Loreau et al. 2003). In a meta-community mesocosm study, colonisation from a regional species pool and higher biodiversity positively affected the recovery of the pond ecosystems from heat stress (Thompson and Shurin 2012).

Changes in species turnover with time reflect changes in biodiversity dynamics, i.e. local immigration and extinction.

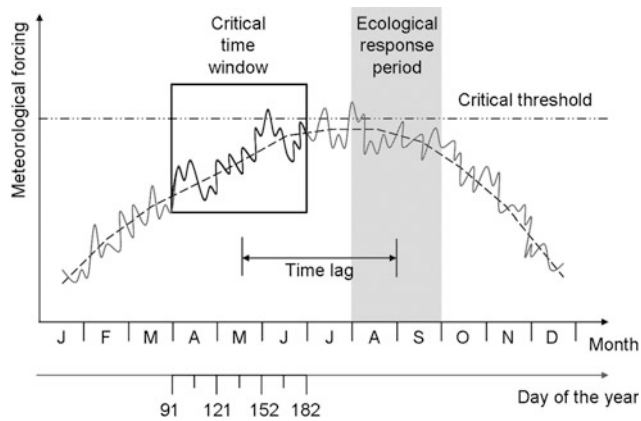


Fig. 10.7 Timing of ecosystem responses to meteorological forcing. Ecological responses are often triggered by changes in critical time windows. The triggering mechanism frequently involves the crossing of critical thresholds in forcing variables (*dashed-dotted line*), and responses tend to occur with a time lag. In this conceptual sketch, analysis at the monthly timescale (*dashed line*) would not be sufficient to detect threshold exceedance, in contrast to analysis at the daily timescale (*solid line*) (Adrian et al. 2012)

Most experiments suggest a more rapid turnover of species at higher temperatures reflecting an acceleration of colonisation–extinction dynamics. In the thermal effluent of a nuclear power plant, higher temperatures resulted in a faster turnover of species composition but without affecting species richness (Hillebrand et al. 2010). Laboratory experiments also indicated faster change in species composition with increasing temperature (Hillebrand et al. 2012). Analysing temporal turnover in community composition could thus be a better means of identifying climate-induced changes in biodiversity than simple univariate measures of biodiversity such as richness or evenness (Angeler and Johnson 2012). Especially because even major changes such as a shift in dominance between functional groups (e.g. from diatoms to cyanobacteria in phytoplankton) might occur without a change in species richness (Wagner and Adrian 2011).

Temperature also modifies species interactions and their consequences for biodiversity (Fig. 10.6). Increased temperatures are often associated with higher rates of consumption (Hillebrand et al. 2009), which can lead to either lower biodiversity (higher mortality) or higher biodiversity (more consumer-mediated coexistence). Competitive interactions are also strengthened by higher temperatures, leading to more rapid exclusion of inferior species—an effect which was shown to depend on consumer presence (Burgmer and Hillebrand 2011). Not only can the strength of interactions be altered by temperature, but also the temporal match of the interacting species through changes in phenology (Berger

et al. 2010). Information on temperature-dependent changes in mutualistic interactions in freshwaters is currently missing.

Both experiments and models indicate that warming-induced shifts in biodiversity have functional consequences for ecosystems (Fig. 10.6), among others with respect to primary production, resource use efficiency and temporal stability of ecosystem functions (Hillebrand et al. 2012; Schabhuettl et al. 2013). In a long-term freshwater phytoplankton experiment, temperature-induced reductions in species richness were associated with lower biomass production, and higher extinction rates were associated with higher variability in biomass production (Burgmer and Hillebrand 2011). Similar strong relationships between diversity and resource use efficiency are found in freshwater field data from the UK and Scandinavia (Ptacnik et al. 2008).

10.6 Importance of Temporal Scale

Responses to climate change in lake ecosystems operate on various temporal scales. Physical forces such as variation in temperature and mixing regimes span sub-daily to monthly time scales. Organisms differ in their generation time from daily to yearly time scales (Adrian et al. 2009). Thus, to understand the impacts of single climatic forcing events in the context of longer term dynamics it is necessary to consider not only sufficiently long periods (several decades) but also to consider appropriate small temporal scales within the yearly cycle. For example, ecological variables may respond to meteorological forcing only during short critical time windows, or to short-lived exceedance of ecologically-relevant critical thresholds. Thus, annual, seasonal or monthly climate data may not be enough to capture the thermal dynamics to which organisms actually respond (Fig. 10.7; Adrian et al. 2012).

Members of the grassroots organisation GLEON (Global Lake Observatory Network; www.gleon.org) or the European project NETLAKE (Networking Lake Observatories in Europe; www.cost.eu/domains_actions/essem/Actions/ES1201) established an international network of automatic stations in lakes to address dynamics of ecosystem properties at sub-hourly scales.

The following sections focus on the role of temporal scale in climate impact research and provide examples of responses at small (sub-daily) to large (decadal) temporal scales, the role of critical time windows, and the significance of exceeding critical thresholds for lakes within the North Sea region (which also applies for lakes throughout the North Temperate Zone).

10.6.1 Critical Temporal Scales

The importance of addressing critical temporal scales in climate impact research has been documented for various lakes in the North Sea region (see Adrian et al. 2012; Sect. 10.2). A closer look at sub-hourly measurements showed that the rate of increase in the daily minima (night-time water temperature) exceeded that of the daily maxima (daytime water temperature) (Wilhelm et al. 2006). The consequences of this day-night asymmetry for the biota are unclear, but may contribute to some of the unexplained changes observed in ecosystem dynamics over time. Day-to-day variation in respiration seems to be common in lakes worldwide, including those in the North Sea region (Solomon et al. 2013). Daily variation in gross primary production explained 5–85 % of the daily variation in respiration. Solomon et al. (2013) found respiration to be closely coupled to gross primary production at a diurnal-scale in oligotrophic and dystrophic lakes, but more weakly coupled in mesotrophic and eutrophic lakes.

Known changes in the thermal regime of lakes in the North Sea region (Sect. 10.2) operate over a broad range of temporal scales, and are closely related to lake morphometry: on sub-daily (Wilhelm and Adrian 2008) to weekly scales in polymictic lakes (Wagner and Adrian 2009b), and on weekly to monthly scales in monomictic or dimictic lakes (Gerten and Adrian 2000; Livingstone 2003). While variation in the timing of spring overturn affects underwater light conditions and thus the start of algal growth (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Peeters et al. 2007), variation in the timing of summer stratification affects water temperature and internal nutrient loading and subsequent plankton development and species composition in productive lakes (Wilhelm and Adrian 2008; Wagner and Adrian 2011). Differences in water temperature between mixed and stratified periods can be up to 5 °C within days or a just few weeks in summer, favouring thermophilic copepod species for example (Wagner and Adrian 2011).

Changes in phenology in abiotic and biotic variables (see Sect. 10.4.2) operate on time scales of weeks (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Straile et al. 2003). Thus, in terms of their duration, seasons should be defined by cardinal events within the lake itself, rather than by fixed calendar dates. Important markers successfully used to define phenology-adjusted seasons in lakes include temperature thresholds, ice-off dates, the timing of the clear-water phase, and periods of stable thermal stratification (Rolinski et al. 2007; Wagner and Adrian 2009a; Huber et al. 2010).

Wagner et al. (2012) proposed a seasonal classification scheme tuned to specific hydrographic-sensitive phases for dimictic lakes across a latitudinal gradient: inverse stratification (winter), spring overturn, early stratification and the

summer stagnation period. They estimated a mean latitudinal shift of 2.2 days per degree of latitude for the start of these sensitive phases. After accounting for latitudinal time shifts, mean water temperatures during the defined hydrographic cycles were similar in lakes spanning the gradient between 47° and 54°N. Adjusting seasons in this way thus enhances the probability of identifying the major driving forces in climate impacts on lake ecosystems.

10.6.2 Critical Time Windows

Responses to warming trends are often expressed in terms of average changes in temperature on seasonal or annual scales, however species exhibiting short generation times such as planktonic organisms respond only during specific time windows within a season. Shatwell et al. (2008) showed how short time windows can open for cyanobacteria in warm springs in an otherwise diatom-dominated season. They argued that if cyanobacteria attain a critical biomass during that critical time window they can dominate the phytoplankton during summer. In terms of zooplankton, the abundance of cyclopoid (Gerten and Adrian 2002b; Seebens et al. 2009) and calanoid copepods (Seebens et al. 2007) in summer and autumn are determined by conditions in spring—probably related to temperature-induced changes in the emergence of resting stages (Adrian et al. 2006) or short time windows of high food availability which increases offspring survival (Seebens et al. 2009).

Temperature-driven changes in the timing of food availability and of predation by young-of-the-year fish during critical time windows in spring/early summer determined the mid-summer decline in daphnids (Benndorf et al. 2001). More specifically, water temperatures in narrow time windows either before (2.2 weeks) or after the typical clear-water phase (3.2 weeks) affected the start-up populations of summer crustacean zooplankton and explained some of their contrasting success during three hot summers characterised by more or less the same average summer water temperature (Huber et al. 2010).

10.6.3 Critical Thresholds

Threshold-driven responses to environmental forces have gained attention in ecology because of their seeming unpredictability and their potentially large effects at all levels of ecosystems. The crossing of critical thresholds may result in abrupt changes in particular elements of an ecosystem (Andersen et al. 2009; Scharfenberger et al. 2013) or entire ecosystems—the famous example being the alternative stable states of clear versus turbid lakes (Scheffer and

Carpenter 2003). Abrupt changes within ecosystems are already known under warming trends experienced in the recent past for a number of variables spanning abiotic and biotic components, such as nutrients or algal blooms (Wagner and Adrian 2009a; for review see Adrian et al. 2009, 2012). The underlying forces are often unclear, but may involve competition for common resources and the crossing of critical thresholds in the abundance of conspecifics (Scharfenberger et al. 2013) or multiple overlapping environmental forces (Huber et al. 2008).

Critical thresholds are known to have been exceeded within lake ecosystems (Hargeby et al. 2004). For example, Peeters et al. (2007) quantified the exceedance of critical thresholds in spring for several meteorological variables to determine early or late onset of phytoplankton growth in Lake Constance (Germany). In a recent model, Straile et al. (2012) used water temperature phenology as a predictor for *Daphnia* seasonal dynamics in North Temperate lakes. The day of the year when surface water temperatures reached a threshold of 13 °C explained 49 % of the variability of the timing of the spring *Daphnia* maximum in two German lakes (Lake Constance, Müggelsee) and in Lake Washington (USA). The *Daphnia* phenology model also performed well for predicting the timing of the *Daphnia* maxima in 49 lakes within the northern hemisphere—many located in the North Sea region (Straile et al. 2012). Early spawning of zebra mussel *Dreissena polymorpha* in Müggelsee was related to early attainment of the same critical water temperature threshold of 13 °C, known to initiate the first spawning event of the year (Wilhelm and Adrian 2007).

Exceeding direct and indirect temperature thresholds (length of thermal stratification) has been shown to trigger processes such as the onset and magnitude of cyanobacteria blooms (Wagner and Adrian 2009a; Huber et al. 2012). Stratification periods of more than three weeks caused a switch from a dominance of non-N-fixing cyanobacteria to a dominance of N-fixing cyanobacteria species, thus affecting not only biomass of cyanobacteria but also ecosystem functioning (Wagner and Adrian 2009a). In addition to warming-related changes in species composition (Adrian et al. 2009), habitat shifts northward toward temperate-zone lakes over the last few decades have been observed for *Cylindrospermopsis raciborskii*, an invasive freshwater cyanobacterium, originating in the tropics (Padisak 1997). Observations of *Cylindrospermopsis raciborskii* in pelagic populations were found to be temperature-mediated. Filaments emerged in the pelagic habitat when water temperature rose above 15–17 °C in two north German lakes (Wiedner et al. 2007).

10.6.4 Extreme Events

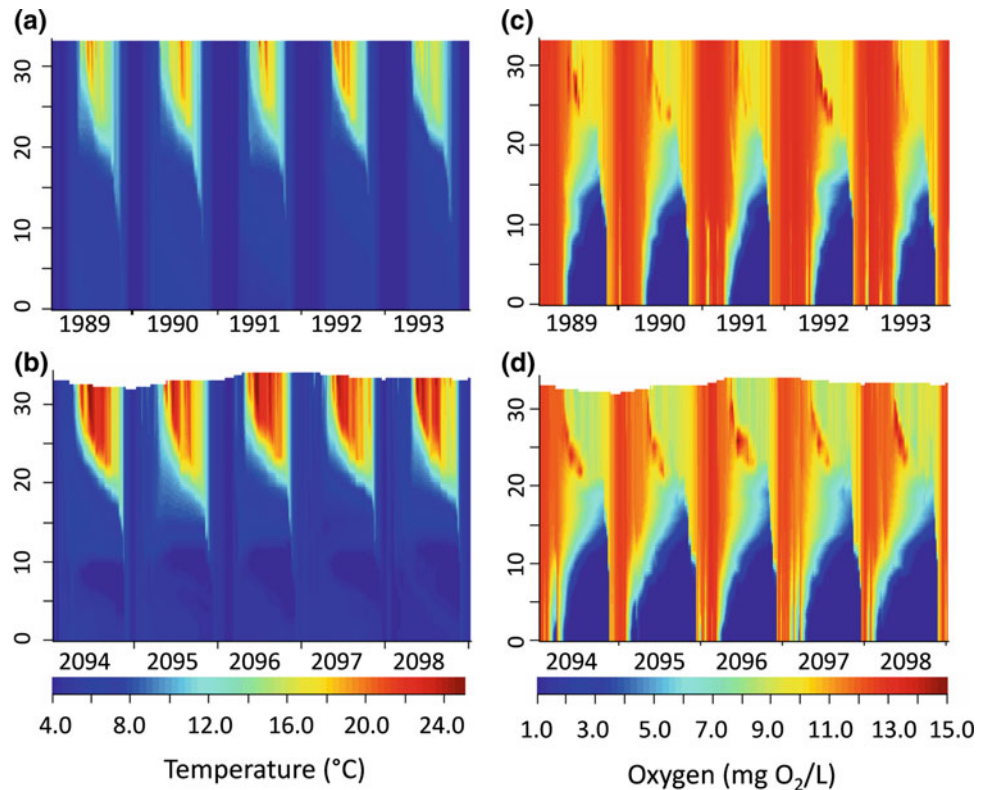
Extreme events, which are expected to become more frequent in the future, are often ecologically more relevant than fluctuations in mean climate. For lakes, extreme events principally refer to exceptionally mild winters, summer heat waves, or extreme storms or heavy rainfall events. For example, an extreme event for a lake that typically freezes in winter would be if the lake did not freeze at all. Based on regional climate model forecasts, Livingstone and Adrian (2009) predicted that the percentage of ice-free winters for a lake in northern Germany would increase from about 2 % at present to over 60 % by the end of the century; see Sect. 10.2.2 for more detail on the frequency of extremely late freeze-up, early break-up and short ice duration. These extremes affect thermal stratification patterns and underwater light conditions, with implications for oxygen conditions and phytoplankton development (see Sect. 10.4.2).

Central Europe has recently experienced extreme heat waves, most notably that of summer 2003. Mean air temperature in summer that year exceeded the long-term average by around 3 °C over much of Europe (Schär et al. 2004). Although heat waves are likely to promote cyanobacteria blooms (Jöhnk et al. 2008), water temperatures above average to the same extent in Müggelsee (Germany) in two recent summers (2003 and 2006) resulted in very different situations: a cyanobacteria bloom in 2006 but a record low cyanobacteria biomass in 2003. This difference was due to the thermal stratification pattern being critically intense only in 2006 (Huber et al. 2012).

Summer fish kills and a change in fish community structure have been attributed to summer temperature extremes in combination with eutrophication in shallow Lake Peipsi (Estonia/Russia) related to a decline in near-bottom oxygen conditions and a decrease in water transparency (Kangur et al. 2013). An extreme rainy period in 2000 caused a strong increase in chemical loading, particularly for organic carbon, in Lake Mälaren (the third largest lake in Sweden) followed by an increase in water colour by a factor of 3.4 and a doubling of spring cryptophyte biomass. This increase in algal mass required changes in the treatment of raw water from Lake Mälaren for the drinking water supply of Stockholm city (Weyhenmeyer et al. 2004b). Extreme summer rain events have also altered CO₂ and CH₄ fluxes in southern Finish lakes, with the systems switching from being a net sink to a net source of CO₂ to the atmosphere (Ojala et al. 2011).

Episodic events of extreme wind speed or rain events exceeding two standard deviations of the seasonal means

Fig. 10.8 Simulated water temperature for the deep Lake Ravn, Denmark, for current climate (represented by 1989–1993) (a) and future climate (represented by 2094–2098) (b), and simulated oxygen concentration for current climate (c) and future climate (d). Simulations were performed using DYRESM-CAEDYM. Future climate forcing was derived by the Danish Meteorological Institute using the regional HIRHAM model and the SRES A2 scenario for Denmark. Y-axis represent water level (m) (D. Trolle, original)



have strong but complex impacts on thermal structure and stability, DOC loading and underwater PAR (photosynthetically active radiation) levels in northern European lakes—the magnitude and direction of change depending on the location of the lake and catchment characteristics (Jennings et al. 2012). A comprehensive summary as to how extreme weather events affect freshwater ecosystems is provided by the British Ecological Society (BES 2013).

10.6.5 Regime Shifts

While ecosystems may be buffered against single short-lived critical threshold exceedance events, gradual changes over longer periods may cause lake ecosystems to switch abruptly from one state to another. The most likely and widespread climate warming-induced shift in lakes will be shifts in thermal regime (see Sect. 10.2). Climate change alters heat redistribution over time (within the annual cycle) and space (vertically within the water column), and eventually leads to transitions in the seasonal mixing regime of a lake much in the sense of scenarios described by regime shift theory (Scheffer and Carpenter 2003).

On the basis of existing climate scenarios, Kirillin (2010) predicted a shift from a dimictic to a monomictic regime in the majority of European dimictic lakes by the end of the 21st century, with the loss of ice cover in the cold season

meaning that winter stratification in these lakes would completely disappear. In summer, climate warming has an opposite, stabilising effect that may eventually lead to the mixing regime shifting to a dimictic regime in hitherto polymictic lakes. The ecological consequences of this type of regime shift may be even more far-reaching than for di-/monomictic transitions, because the abrupt detachment of the nutrient-rich hypolimnion from the euphotic layer is likely to trigger stronger competition between autotrophic species resulting in changes in phytoplankton species composition and ecosystem functionality (Wilhelm and Adrian 2008; Wagner and Adrian 2009a, b, 2011).

10.7 Modelling

Predicting the fate of freshwater ecosystem processes under climate change is non-trivial, because many physical, chemical and biological processes interact, and may be affected on different spatial and temporal scales by climate forcing. In attempting to account for these complex interactions, mechanistic numerical models continue to play a greater role in hypothesis testing (system understanding) and for predicting the future state of ecosystems given the projections of future climatic forcing according to climate models (Trolle et al. 2012). Thus, the ability to link—and equally importantly to quantify—complex interactions

between physical, chemical and biological processes makes models one of the most important tools of modern science, and for the past decade, models have been used extensively, aiming to establish the potential effects of future climate on freshwater ecosystems (Mooij et al. 2007; Trolle et al. 2011; Elliott 2012).

10.7.1 Linking Physical and Ecological Dynamics

A widely accepted effect of increased climate warming on lakes is increased stability of the water column, which is readily quantified by hydrodynamic models (see Fig. 10.8). Increased stability can cause prolonged periods of stratification, with subsequent effects on biogeochemical cycling, for example by increasing the duration of anoxia in bottom waters and thereby the potential for release of iron-bound phosphorus.

Climate warming is also expected to result in decreased duration and thickness of ice cover on lakes, and models such as MyLake have recently been applied to provide quantitative estimates of such decreases.

Models with a strong focus on food-web dynamics, such as PCLake (Janse 1997) have also been used to quantify the effects of warming in facilitating lake ecosystems to shift from a clear, macrophyte-dominated state to a turbid, phytoplankton-dominated state, under different combinations of warming scenarios and external nutrient load scenarios (Fig. 10.9). Modelling exercises of this type are readily undertaken using a standard desktop computer, in contrast to testing such scenarios in experimental mesocosm studies, for example, which is extremely time consuming and expensive.

One of the key messages from the model study by Mooij et al. (2007) shown in Fig. 10.9 was that the critical loading of phosphorus to a lake, at which a shift from a clear to a turbid state occurs, is likely to decrease as warming continues. This effectively means, that according to the model, external loading will need to be reduced in the future, if lakes are to retain the ecological quality of present day.

10.7.2 Predictions Versus Observations

Modelling studies of the long-term effects of climate change on northern hemisphere temperate lakes (e.g. Elliott et al. 2005; Mooij et al. 2007; Trolle et al. 2011) generally imply that overall phytoplankton biomass is likely to increase, and that cyanobacteria will become a more dominant feature of the phytoplankton species composition. This is in line with

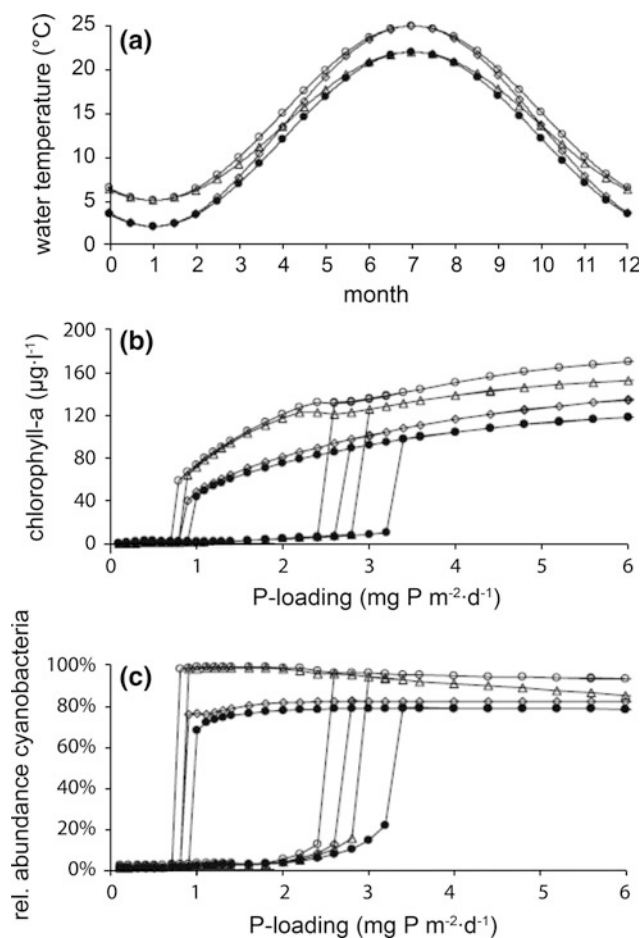


Fig. 10.9 Three scenarios with elevated temperatures (a) simulated using PCLake adapted for shallow Dutch lakes, and evaluated for average summer chlorophyll-a concentration (b) and the percentage of cyanobacteria relative to total phytoplankton biomass (c). The simulations include four scenarios: a control (*closed circles*), an all year round temperature increase of 3 °C (*open circles*), an increase in summer maximum temperature of 3 °C but no change in the winter minimum (*open diamonds*), and an increase in winter minimum temperature of 3 °C, but no change in the summer maximum (*open triangles*) (adapted from Mooij et al. 2007)

empirical observations from time series (Jöhnk et al. 2008; Wagner and Adrian 2009a, b; Posch et al. 2012) and with cross-system analyses (Jeppesen et al. 2009; Kosten et al. 2012). However, the effects may be even more severe than suggested by models, as current models do not fully account for structural changes in the lake ecosystems that could occur due to warming. As stated in Sect. 10.4.1 the composition of fish stocks could change towards smaller and faster reproducing fish, implying more predation on zooplankton and so less grazing on phytoplankton (Jeppesen et al. 2010a; Meerhoff et al. 2012). Such changes have yet to be included in dynamic models.

Table 10.1 Level of certainty for key climatic impacts on freshwater ecosystems

Parameter	Comment
<i>High certainty</i>	
Lake temperature	Several time series, strong modelling tools
Ice development	Several time series, strong modelling tools, satellite data
Phenology	Several time series, modelling tools for autotrophs
Water level, runoff, retention	Strong hydrological modelling tools
Thermal regime	Extension of stable stratification periods, good modelling tools
Oxygen depletion	Several time series, linked with hydrology and trophic state
<i>Medium certainty</i>	
DOC concentration	Long-term data, good modelling tools
Concentrations of key elements	Some data, closely linked with hydrology
Primary production	Contrasting effects of DOC and nutrient inputs. Local differences
Autotroph community composition	Prevalence of cyanobacteria. Local differences
Deterioration of trophic state	Warming acts like eutrophication; linked with hydrology and trophic state
Range expansion of invasive species	Northwards distribution of species
Loss of cold cold-stenothermic fish species	Several time series; results from fish harvest
<i>Low certainty</i>	
Secondary production	Hard to arrive at general conclusions. Taxon- and locality-specific differences
Heterotroph community composition	Taxon- and locality-specific differences. Secondary impacts of autotrophs
Diversity	Limited data availability, taxon- and locality-specific differences; changes in ecosystem function
Food-web responses	Accumulated uncertainty from all other responses
Greenhouse gases (carbon dioxide, methane, nitrous oxide)	Lakes as carbon sink or source, large-scale enclosure experiments
Water clarity	Progress expected with new satellite data

10.7.3 Linking Landscape Activities and Nutrient Losses

A recent trend is to assemble multidisciplinary modelling teams with expertise both in hydrological and ecological modelling. Coupling hydrological and ecological models (Norton et al. 2012; Nielsen et al. 2013) enables a direct and quantitative link between land use activities and surface water quality. For example, Norton et al. (2012) used a farm-scale nutrient budget model (PLANET; Planning Land Applications of Nutrients for Efficiency) combined with a generic nutrient runoff model (GWLF; Generalized Watershed Loading Function) to estimate nutrient losses to Loweswater, a small lake in northwest England. The simulated nutrient losses were subsequently used as input to an ecological model for the lake, PROTECH (Phytoplankton Responses To Environmental CHange). This model-chain has been used to forecast the abundance of different phytoplankton types within the lake in response to a range of catchment management measures. Ongoing research projects are currently expanding such model chains to include the effects of future climate on both hydrology and aquatic ecosystems.

10.8 Conclusion

Freshwater systems, and notably lakes, are well suited to trace climate-induced effects both directly via changes in ice cover, hydrology and temperature, but also indirectly via biotic communities since they represent closed bodies (aquatic islands in the landscape). Moreover, they also offer strong tools as ‘sentinels’ by integrating changes at the catchment scale that elsewhere would be hard to detect (Adrian et al. 2009). The North Sea region has a wide range of freshwaters that reflect changes related directly and indirectly to climate forcing. This includes a number of long-term monitoring sites, and experimental studies offer insights into climate change in freshwaters—and subsequent impacts on downstream coastal recipients. The major impacts on lakes, both those known to date and those predicted to occur, can be addressed with different levels of certainty (tentatively summarised in Table 10.1). The level of certainty falls substantially, once higher trophic levels and the complexity of trophic interactions are included. Nevertheless, this summary may be used to identify systems and parameters that are already well suited for addressing climate responses, those that need further attention, and those that

are likely to need addressing at local scales and where general statements and predictions are hard to achieve.

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