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Abstract

This report focuses on potential effects of climate change on ecological reference conditions and on ecological responses to nutrient pressures in lakes, especially threshold-type and non-linear responses. Reference conditions and thresholds responses are both fundamental for national ecological classification systems according to the European Water Framework Directive (WFD), for defining reference values and management targets (Good/Moderate class boundary) respectively. Effects of climate change on these components therefore have important implications for assessment of ecological status and management of lakes.

We have addressed the effects of climate change on lakes by an extensive literature review, as well as by analysing palaeolimnological datasets, large-scale European datasets and long-term time series for four individual lakes in Norway, Estonia and Germany (case studies). The climatic changes considered include increased temperature, increased precipitation (and consequently increased content of organic matter) and reduced precipitation (and consequently reduced water levels and increased salinity). The literature review describes effects of climate change on reference conditions for each biological quality element (BQE; phytoplankton, macrophytes, macroinvertebrates and fish); of these phytoplankton and fish tend to be most sensitive to climate change.

Results from new palaeolimnological analyses suggest that nutrients are the dominant driver of diatom compositional change, and there is insufficient evidence to suggest how reference conditions should be modified in light of climate change. Nonetheless further work is required to explore the relationship between diatoms and climate change in more detail. Analysis of chlorophyll a (chl-a) in European reference lakes suggest that under future climatic conditions, increased temperature in combination with increased TP (due to increased winter precipitation) will lead to increased chl-a concentrations, although the effects will vary with the lake type (notably the humic level). Large-scale analysis of cyanobacteria in North-European lakes, considering both lake typology and climatic variables, suggest that the risk of exceeding regulatory thresholds for cyanobacteria will increase with future higher temperature, but also that this tendency to some degree might be compensated by increased precipitation. The four case studies provide more detailed examples of interactions between climatic factors and nutrient pressures on plankton communities, and demonstrate some of the complexity involved in ecological responses to climate change in lakes. Finally, the report provides a set of recommendations for river basin management, considering impacts of climate change on reference conditions and ecological thresholds, and the implications for WFD-based classification systems.

Abbreviations

BN: Bayesian network
chl-a: chlorophyll a
CPT: conditional probability table
BQE: biological quality element
DOC: dissolved organic carbon
DOM: dissolved organic matter
EEA: European Environment Agency
EC: European Commission
EQR: ecological quality ratio
G/M: Good/Moderate
GAM: generalised additive model
GLM: generalised linear model
N: nitrogen
nEQR: normalised ecological quality ratio
P: phosphorus
RBMP: river basin management plan
TN: total nitrogen
TOC: total organic carbon
TP: total phosphorus
WFD: Water Framework Directive
WWTP: wastewater treatment plant

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1. Introduction

European lakes have long been subject to land use and pollution driven impacts such as eutrophication, acidification, toxic pollution, accelerated catchment erosion, water level change, salinisation and invasion by non-native species. Impacts have ranged from low-level contamination by long-distance transported air pollutants in remote areas to complete ecosystem transformation in agricultural and heavily populated regions. Lakes in Europe now face additional pressures from climate change, directly and through interaction with these other stressors. In the future, however, the effects of climate change are expected to become more prominent, with a temperature increase of about 0.2 °C per decade projected for the next two decades for a range of emission scenarios. An important objective of the REFRESH project therefore is to identify reference conditions and ecological thresholds in aquatic ecosystems facing climate change.

Climate change challenges the currently static concept of the reference state as defined by the European Water Framework Directive (WFD) (EC 2000). Under climate change, reference conditions become dynamic, as identified by the Euro-limpacs project (Johnson et al. 2010), and the definition of good ecological status becomes uncertain, e.g. in cases where flow regimes in streams become sufficiently altered for biological elements typical of good status to be endangered. Here we build upon the results from Euro-limpacs and examine how reference conditions for lakes might change following climate change and how the concept of a dynamic reference state can be built into WFD methodologies. Here, to avoid confusion, we will use the term "reference condition" to mean the natural conditions in reference lakes (which may be modified climate change), and the term "reference values" to mean the specific value set in the national classification systems (which are legally binding and should not be modified, until the revision of assessment methods in the next six-year River Basin Management planning cycle).

A critical concern in the management of freshwater ecosystems is the attempt to prevent water bodies from crossing key thresholds, where systems may change abruptly and involve a switch to regimes that are difficult to restore. Although ecological thresholds for some ecosystems and pressures have been well studied, e.g. lakes suffering from eutrophication or acidification, there is much less knowledge about how climate change may cause such thresholds to be crossed, or even cause thresholds to move. The most pressing challenge is to identify thresholds in structure, function and biodiversity for the effects of temperature, low water levels (including impacts on salinity), and organic matter in combination with nutrient pressures.

This report focuses on the potential impact of climate change on reference conditions and ecological thresholds, which are fundamental to ecological assessment of water body status in the WFD. In this review the term ‘reference condition’ follows the definition in the WFD as the condition expected in the absence of significant anthropogenic influence. Central to the WFD is the measurement of ecological quality (including chemical, hydromorphological and biological quality) as judged by the degree to which present day conditions deviate from those at reference condition. Ecological status is divided into five classes: high, good, moderate, poor and bad. EU member states are required to restore lakes to ‘good ecological status’ (or ‘good ecological potential’ in the case of heavily modified and artificial water bodies), defined as minimal deviation from the reference condition. Hence, the way the reference value is defined is of critical importance. The boundaries between status classes, in particular the good/moderate boundary (i.e., the management target), should preferably be defined by discontinuities (thresholds) in the relationships between the pressure gradient and the biological response metric (Schmedtje et al. 2009). Potential impacts of climate change on such pressure-response relationships are therefore particularly important, because they may affect the fundament underlying the good/moderate class boundary, which is a critical component of ecological classification systems (as illustrated in section 2.3.1)

Lake status is assessed with four Biological Quality Elements (BQEs) - phytoplankton, aquatic flora (phytobenthos and macrophytes), benthic invertebrates and fish (Lyche-Solheim et al. 2013). These are organism groups which integrate the effects of various stressors such as nutrient enrichment, acidification, hypoxia or habitat degradation. For each BQE certain parameters are required by the WFD being biomass, taxonomic composition and bloom metrics for phytoplankton; taxonomic composition and abundance for macrophytes; taxonomic composition, abundance and diversity for benthic invertebrates; and taxonomic composition, abundance and age structure for fish. To provide a common scale of ecological quality, biological assessment results need to be expressed using a numerical scale between zero and one, known as the ‘Ecological Quality Ratio’ (EQR), whereby an EQR value of one represents reference value and high ecological status, and values close to zero represent bad ecological status. The fact that EQR uses reference condition as an anchor point for the classification means that great emphasis is placed on an accurate determination of the reference value.

Reference values of different BQEs should be set based on objective criteria, preferably by measuring ecological status in unimpacted sites with agreed pressure criteria for what is unimpacted (EC 2009). However, few European lakes can be considered to be in a ‘pristine’ state and finding minimally disturbed reference sites in Europe and elsewhere is challenging (Poikāne et al. 2010, Bennion et al. 2011, Brucet et al. 2013b). The WFD identifies a number of approaches that can be used for establishing reference values for lakes including historical data, expert judgement, spatial state schemes, mathematical modelling and palaeolimnology (Wallin et al. 2005). While historical and palaeoecological methods have been used by several member states for some biological groups (Leira et al. 2006, Bennion & Simpson 2011), it is more usually the minimally disturbed conditions observed in a region that are used to define reference conditions (Johnson et al. 2010). Brucet et al. (2013b) found that reference conditions were estimated for about half of the lake methods using near-natural reference sites (i.e. pristine or minimally disturbed sites selected using pressure data), complemented with other approaches, such as historical data, modelling and expert judgment. Overall about 40% of the methods used more subjective approaches to establish reference values (e.g. selecting near-natural reference sites without any pressure criteria or a ‘least disturbed conditions’ approach) or no information was available. An added complication is that a site might be considered as being in reference condition for one biological community but not another, for example morphological pressure may affect macrophyte but not phytoplankton assemblages. Some of the methods for lakes employ a type-specific approach where sites are grouped based on their environmental similarities (e.g. similar alkalinity and depth class) and a reference value is defined for that lake type whereas others employ a site-specific approach where the reference community for each site is directly predicted from environmental variables (Logez & Pont 2013).

In all of the above approaches, it is assumed that the reference condition is relatively stable so that the observed deviations and the respective ecological status consistently reflect the effects of anthropogenic disturbances. However, given the projected changes in climate across Europe, the assumption of stable and consistent reference conditions is increasingly unlikely to be met. Temperature and precipitation are two major components of hydrosystem functioning which are strongly affected by climatic changes. Indeed climate change will make it increasingly difficult to find true reference lakes (Moss 2007, 2008). Clearly, therefore, climate change must be considered in future implementation of the WFD (Nõges et al. 2009b). The

WFD does not classify climate change as an anthropogenic pressure per se but there is growing recognition that the objectives and programmes of measures within the WFD are potentially climate-sensitive (Wilby et al. 2006, Wilby et al. 2010, Quevauviller 2011, Quevauviller et al. 2012). The EC currently states "it is not expected that, within the timeframe of WFD implementation (i.e. up to 2027) and within the metrics used for status assessment, a climate change signal will be statistically distinguishable from the effects of other human pressures at a level requiring reclassification of sites" (EC 2009). They concede, nonetheless, that climate change could impact status assessment in the relatively short term and influence the water body type and/or reference conditions in some cases. With its six yearly river basin management planning cycles the WFD is well suited to review definitions of reference values and class boundaries and to handle the long-term implications of climate change.

In this report we have addressed the effects of climate change on reference conditions and threshold relationships in lakes by an extensive literature review, as well as by analysing palaeolimnological datasets, large-scale European datasets and long-term time series for individual lakes (case studies). We then give recommendations on how this knowledge can be incorporated into future river basin management (classification systems, monitoring and restoration measures) needed to achieve the objectives of the WFD under a future climate.

2. Literature review of reference conditions and thresholds

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2.1. Background

This review examines the implications of climate change for ecological reference conditions and thresholds. It incorporates outputs from the earlier EU projects, Euro-limpacs and WISER, as well as results from the REFRESH project. Reference is made to relevant peer reviewed literature, EU project deliverables and EU reports. In their paper on the key messages from the WISER project, Hering et al. (2013) highlighted that phytoplankton and fish were the two BQEs likely to be most affected by climate change in lakes. The aquatic flora was identified as being affected to a lesser extent by climate change and great uncertainty still surrounds the impacts of climate on macroinvertebrates in lakes. Therefore, this review will focus more on the implications of climate change for reference conditions and effects of nutrient pressures for phytoplankton and fish than for the other BQEs, as well as on general considerations for setting reference values and class boundaries for lakes under a changing climate. The review has followed the common approach for REFRESH literature reviews as described by Sandin et al. (2011).

2.2. Climate change in Europe and general effect on lakes

Global average temperatures in 2100 are projected to be between 1.8-4.0 °C higher than the 1980-2000 average and sea levels are projected to rise 0.18-0.59 m by 2100 (IPCC 2007). In Europe, average temperature for the last decade increased 1.3°C above the pre-industrial level and it is projected to increase between 2.5 °C and 4 °C by 2100, even greater than the global predictions (EEA 2012). Additionally, more frequent and intense extreme weather events are expected and indeed parts of Europe have experienced severe floods, droughts and heat waves in recent decades. However, climate change will not be uniform across Europe. Future warming in northern regions is likely to be greatest in winter, while in the Mediterranean region it is expected to be greatest in summer. In mountain areas, temperature rise has been larger than the European average. For instance, the Alps have undergone an increase in temperature twice the rate of average warming of the Northern hemisphere (EEA 2009). Annual precipitation is very likely to increase in most of northern Europe and to decrease in southern parts, while in central Europe the major change is projected to be in the seasonality of precipitation with a likely increase in winter precipitation and a decrease in summer. Extremes of daily precipitation are likely to increase in the North. In southern and Central Europe several models indicate fewer precipitation days and longer dry spells.

Changes in temperature and precipitation are already impacting on water quality and quantity (Battarbee et al. 2008), and are projected to impact still further in future. Most notably, during the last century, the water temperature of European rivers and lakes increased by 1-3 °C (EEA 2007). Effects on ice cover duration have also been observed, with a mean increase in rate of 12 days per century starting from the 19th century to the present. The direct and indirect effects of climate change on lakes have been the subject of numerous studies (e.g. George 2010, Kernan et al. 2010, Jeppesen et al. 2012a, Jeppesen et al. 2013b) and can briefly be summarised as follows (adapted after Hering et al. 2010b).

In cold and temperate ecoregions:

- Shorter ice cover period and earlier snowmelt especially in cold ecoregions with effects on the production and biodiversity of phytoplankton and the occurrence of winter fish kills
- Earlier onset and prolongation of summer stratification leading to changes in mixing processes
- Increasing dissolved organic carbon (DOC) and total organic carbon (TOC) concentrations especially in cold ecoregions and an associated increase in water colour (a process known as “brownification”).
- Higher external, and in some cases internal, nutrient loading to lakes e.g. Nitrogen loading from land to streams is expected to increase in North European temperate lakes due to higher winter rainfall and changes in cropping patterns (Jeppesen et al. 2011a)
- Compositional changes in phytoplankton (e.g. a shift from diatoms to cryptophytes to cyanobacteria dominance) and earlier occurrence of spring blooms
- Changes in macrophytes in temperate ecoregions with inter-annual variation in water temperature leading to deeper macrophyte colonisation and increase in plant biomass
- Compositional changes in zooplankton especially in temperate ecoregions (e.g. higher *Daphnia* biomass leading to earlier phytoplankton suppression)
- Changes in cold water fish with higher temperatures resulting in disappearance of cold water species from littoral areas in spring and summer
- Spread of alien fish, macrophyte and macroinvertebrate species especially in temperate ecoregions
- Effect on food webs as cyprinid planktivorous fish are supported by higher temperatures so large zooplankton are suppressed and grazing intensity on phytoplankton is reduced
- Alterations to habitats and distribution of aquatic organisms with some species moving northwards in Europe and possible extinction of some aquatic species.
- Increased bioavailability of persistent organic pollutants in high mountain regions due to higher volatility and atmospheric deposition of these compounds with significant effects on aquatic communities.

In warm ecoregions, additional effects include:

- Decreased water volumes, or drought, owing to increased temperatures and decreased precipitation
- Oxygen depletion as higher temperatures stimulate phytoplankton growth
- Salinity and nutrient increases as a result of greater evapotranspiration and reduced inflow.

While climate change is a global phenomenon and all lake types will be affected, some water bodies may be more sensitive than others. In a literature review for the REFRESH project dedicated to lake vulnerability, Angeler & Johnson (2012) showed that ecosystems at high latitudes, especially subarctic and arctic lakes, streams, ponds and wetlands, are particularly sensitive to climate change due to the combined impacts of modified ice cover regimes, increasing water temperature, thawing permafrost, and changes to hydrological processes and water balance. They concluded that the impact of global change on northern freshwaters is likely twice as much as the global average and may be having dramatic effects on the abiotic and biotic characteristics of these freshwater ecosystems.

Livingstone et al. (2010), reviewing the effect of morphometric differences of lakes on their sensitivity, showed that deep lakes tend to exhibit a more persistent physical response to climatic forcing than shallow lakes. The deep waters of lakes which are chemically stratified also tend to respond less sensitively to climatic forcing than the deep waters of lakes which are not. Large lakes, especially those with a convoluted coastline and multiple basins such as the Swedish lakes Mälaren, Vättern and Vänern, can be exposed simultaneously to several different local weather regimes, to which they exhibit an internally heterogeneous response. Lake morphometry also influences the distribution of heat with larger wind exposed surface contributing to the dominance of convective wind mixing among the mechanisms of heat transfer (Nõges et al. 2011). Analysis carried out in the UK (George et al. 2010) showed that shallower lakes were more sensitive to the observed variations in the number of northerly days since they lose proportionately more of the heat stored during the summer. In temperate regions, the highest surface water temperatures in winter are recorded in deep lakes that retain heat and the lowest in shallower lakes that lose more heat to the atmosphere (Dokulil et al. 2010).

The effect of the projected increases in the winter rainfall on the residence time of lakes depends on lake size, catchment area and geographic location. George et al. (2010) showed that the most sensitive sites in Britain and Ireland will be small lakes located in the ‘wet’ west and the least sensitive sites large lakes situated in the ’dry’ east. Pettersson et al. (2010) demonstrated the importance of physical characteristics of individual lakes for controlling P cycling in lakes. Lakes with a short retention time were typically more sensitive than lakes with a long retention time whilst the internal dynamics of phosphorus was very different in isothermal and thermally stratified lakes.

Even some of Europe’s most remote mountain lake systems are showing signs of climate change effects. Catalan et al. (2009b) assessed the ecological status of European mountain lakes in terms of climate forcing, chemical environment, species distribution and pollution threats and concluded that climate warming already affects most of the study lake districts and there are considerable uncertainties as to how this will modify current conditions in these systems.

Climate change has the potential, therefore, to alter a number of the biological, chemical, hydrological and quantitative parameters used by the WFD to assess ecological status (Wilby et al. 2006). Perhaps one of the most concerning impacts of climate change is that warming will exacerbate the symptoms of eutrophication (Jeppesen et al. 2010b), suggesting that nutrient reduction efforts will need to be strengthened if restoration targets are to be met.

2.3. Climate change effects on reference conditions

2.3.1. Shifting baselines

As outlined in section 1, the WFD requires the degree of degradation to be assessed against a reference value. It is now recognised, however, that climate change may limit the use of the reference value as the baseline for defining restoration targets, as the future status of the ecosystem will differ from that at the present under a 'do nothing' scenario (Malve et al. 2012, Verdonschot et al. 2013), e.g. as species become eliminated or migrate into cooler habitats. While this does not invalidate the reference condition concept, there is a need to re-define the reference as boundary conditions change and, if necessary, adjust restoration targets so that they are achievable under changing climatic conditions (Wilby 2004, Battarbee et al. 2005, Wilby et al. 2006, Wilby et al. 2010), e.g. it will not be possible to restore winter ice-cover under a warmer climate or freshwater conditions after inundation following a rise in sea-level. Wilby (2004) points out that changes in ecological communities at reference sites will render the initial set of environmental standards obsolete unless there is a system for regularly reviewing ecological objectives.

In the last few years, the concept of 'shifting baselines' has appeared in the literature (Andersen et al. 2009, Duarte et al. 2009, Nõges et al. 2009b, Johnson et al. 2010, Bennion et al. 2011, Battarbee et al. 2014), highlighting the fact that reference conditions are not only dynamic but subject to directional change where the baseline is continually changing. This is illustrated in Figure 1 taken from Bennion et al. (2011). The diagram illustrates in this case the use of the historically defined reference, not as a target for recovery, but as the starting point for modelling the probable future impacts of climate change on the reference condition (cf. Battarbee et al. 2008). It shows not only the need to reduce all pressures to reach a reference-based recovery target, but also the need to re-define the reference as boundary conditions change.

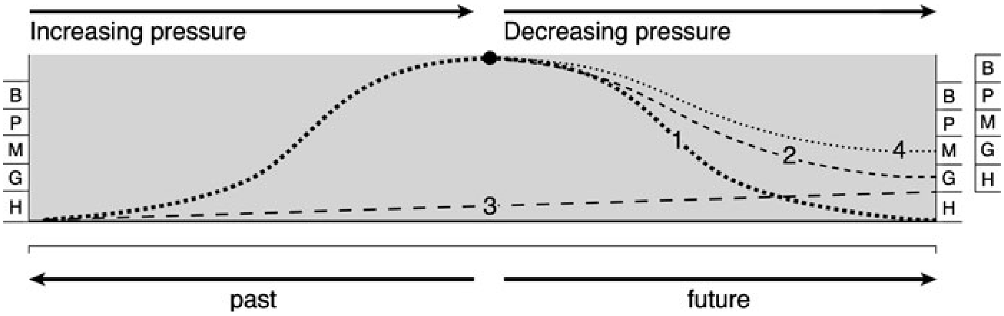


Figure 1. Conceptual diagram to show the potential impact of climate change on reference conditions and its implication for the WFD: 1. Ideal return trajectory to the palaeo-defined reference value; 2. Response trajectory to measures designed to achieve 'good' ecological status by a specified time; 3. Shift in reference baseline as a result of climate change; 4. Altered trajectory caused by the reduced effectiveness of the measures taken as a result of climate change. In this example climate change prevents restoration to 'good' status. Options are either to intensify the measures taken or to shift the recovery target and re-classify the 'good/ moderate' boundary as indicated by the right hand panel (based on Battarbee et al. 2005). H, G, M, P, B refer to the high, good, moderate, poor and bad categories of the WFD.

In line with the scientific literature, the concept of 'shifting baselines' due to climate change has also been addressed in EU science-policy documents related to the WFD (Nõges et al.

2009b, Reyjol et al. 2010). The ECOSTAT working group report on 'Climate change impacts on reference conditions and ecological boundary settings' (Nõges et al. 2009b) aimed to provide guidance on how to consider climate change in the context of River Basin Management Plans, especially in relation to reference conditions and ecological quality classification of the water bodies. They developed a conceptual model considering three potential scenarios (Figure 2).

(1) If the pressure-response curves are linear and quality class boundaries are set on statistical principles (fixed percentile values based of a set of reference sites), a change in reference value directly translates into a change in the absolute boundaries with the ecological quality ratio (EQR) remaining the same (Figure 2a).

(2) If boundaries are set as absolute values based on certain thresholds or discontinuities of the pressure-response curves (Schmedtje et al. 2009), a shift in reference value may not change the boundary values, but the EQRs (and the interpretation of the normative definitions) need to be changed, because the reference value has moved closer to the threshold (Figure 2b). It cannot be excluded, however, that the changes induced by future climate change will be severe enough to push the reference value over the threshold.

(3) If boundaries are set according to thresholds of the pressure-response curves, climate change combined with the pressure may shift directly the threshold point in addition to or independently from the reference value (Figure 2c). Surpassing these thresholds may cause an irreversible system shift to a new state with undesirable consequences to water quality. Maintaining good water quality in these conditions requires following of more stringent management and protection standards according to corrected pressure EQR values. Class boundaries for the biological metric remain unchanged.

The ECOSTAT document only makes reference to management implications of scenario (c) and recognises that "*surpassing the threshold point due to the combination of climate change and pressure may cause an irreversible system shift to a new state with undesirable consequences for water quality. Maintaining good water quality in these conditions requires more stringent management and protection standards.*" In the science-policy report from Reyjol et al. (2010), where contributions by scientific experts and water managers were gathered into different chapters, one of the 10 priority issues refers to the links between global changes and ecosystem functioning and assessment tools. Section 2.7 highlights the need for predicting the ways and degree by which reference conditions are affected by global stressors, on how biological quality metrics may be affected and the consequences for ecological assessments and the success of EU River Basin Management Plans.

2.3.2. Lake recovery trajectories

Although there is little direct evidence that climate change has altered baselines so that new system equilibria have resulted, independent of the effects of existing pressures, several studies have demonstrated that as the driver or pressure is reduced, the recovery of ecosystems may not follow a similar pathway to return to the initial state that prevailed before the pressure increase. In terms of lake management, therefore, recovery may not simply be the reversal of the degradation pathway and the reference value may perhaps never be achievable in some lakes. This may be due to lag or hysteresis effects, ecological constraints or the influence of other confounding pressures such as nitrogen deposition. But there is increasing evidence to demonstrate that climate is a key factor influencing the success of restoration efforts and, therefore, the value of the reference condition concept in determining management targets.

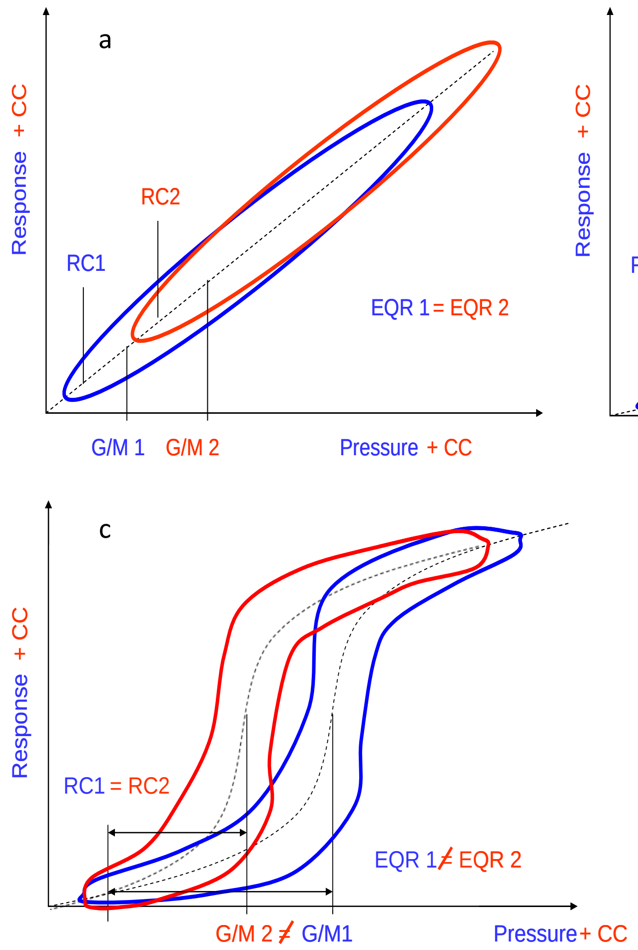


Figure 2. Conceptual model showing climate-induced shift in reference conditions (RC) (and thereby reference values), and the different consequences on setting the management target (the Good/Moderate boundary). (a) The pressure-response curve is linear and a change in RC directly translates into a change in the boundaries with the ecological quality ratio (EQR) remaining the same. (b) The pressure-response curve is nonlinear and a shift in RC may not change the boundary values but the EQRs need to be changed. (c) The pressure-response curve is nonlinear and a shift of the threshold (G/M boundary) changes the EQR in addition to or independently from the RC. (From Nõges et al. 2009b).

As part of the WISER project Bennion et al. (2012b) employed palaeoecological techniques to examine the degree of impact and recovery in thirteen European lakes that have been subject to eutrophication and subsequent reduction in nutrient loading. Eleven sites showed progressive deviation from the reference sample (core bottom) prior to nutrient reduction. The shifts in diatom composition following reduction in nutrient loading were more equivocal, with a clear reversal towards the reference flora only in four deep lakes and one shallow lake. The compositional changes were gradual suggesting that ecological recovery may take several years to decades. In the remaining deep lakes, alternative nutrient sources seemed to explain the lack of apparent recovery. In three shallow lakes the diatom assemblages did not track back along the enrichment pathway following remediation but were replaced by a community associated with lower productivity. Hence, ecosystem recovery was not simply a reversal of the degradation process. The present assemblages remain different from those of the preenrichment samples in all sites. For two of the lakes, more detailed studies revealed that climate change may be confounding recovery. For example, palaeolimnological analysis of the sediment record of Loch Leven, a large shallow lake, concluded that on a decadal-centennial scale, the nutrient enrichment signal overshadows the potential impact of climate as a control on the diatom community (Bennion et al. 2012a). However, at an inter-annual scale, changes in species composition occurred that may be attributed to climatic controls (Bennion et al. 2012a). The Bennion et al. (2012b) data support the findings of recovery studies carried out in coastal and riverine systems in that ecosystem recovery is shown not simply to be a reversal of the degradation process; for example Duarte et al. (2009) examined four coastal systems demonstrating that they failed to return to the reference status upon nutrient reduction.

In an analysis of nutrient and climate impacts on seven European lakes as part of Eurolimpacs, Battarbee et al. (2012) attributed limited recovery to continuing high nutrient concentrations related to an increase in diffuse nutrient loading or to internal P recycling, but there was some evidence that climate change may be playing a role in offsetting recovery at some sites. If this is the case, then lake ecosystems suffering from eutrophication may not necessarily return to their pre-eutrophication reference status despite the measures that have been taken to reduce external nutrient loading. Lakes Mjøsa and Piburger See experienced significant changes in the diatom assemblages of the sediments towards pre-eutrophication floras of the lakes. However in Mjøsa, not all the pre-eutrophication taxa have reappeared, and the lake remains on the borderline between oligotrophic and mesotrophic, either because nitrate concentrations remain high or because water temperature has increased (Hobæk et al. 2012). In Piburger See, several diatom taxa (i.e. *Asterionella formosa* and some *Cyclotella* species) have appeared in the lake that have not occurred previously. This appears to be related to an increase in productivity linked to climate change rather than to nutrient loading, as nutrient loads have now been reduced to baseline levels and internal P recycling is limited. Both TP and chl-a levels are now increasing despite the reduction in external loading (Thies et al. 2012).

Battarbee et al. (2012) combined palaeo- and observational evidence for ecosystem change to construct a conceptual diagram of the past, present and potential future trajectories of European lake systems experiencing nutrient pollution and climate change (Figure 3). From a starting point (a) that represents relatively oligotrophic reference conditions, the palaeo-record provides evidence for the progressive increase in nutrient loading that has taken place giving rise to increasing primary productivity. Measures taken to reduce nutrient loading are represented by point (b). Evidence indicates that nutrient enrichment remains the dominant influence on the trophic status of the study lakes, and arrows (d) and (e) represent the dominant trajectories expected. In some lakes, e.g. Mjøsa, there has been an immediate decrease in production with the recovery trajectory (arrow d) heading directly towards the reference point a. In other cases, especially shallow lakes such as Loch Leven and Esthwaite Water, the response has been limited with little reduction in production despite significant decrease in external loading. At such sites, recovery is delayed by internal P recycling despite the reduction in loading, but may be expected eventually to head back towards the reference (arrow e). However, there is also evidence that climate change may be offsetting some of the recovery expected from a reduction in nutrient loading at some sites. These lakes follow a deflected trajectory away from the reference (arrows f and g) and towards a new endpoint (c), for example Piburger See appears to be following the trajectory represented by arrow (g).

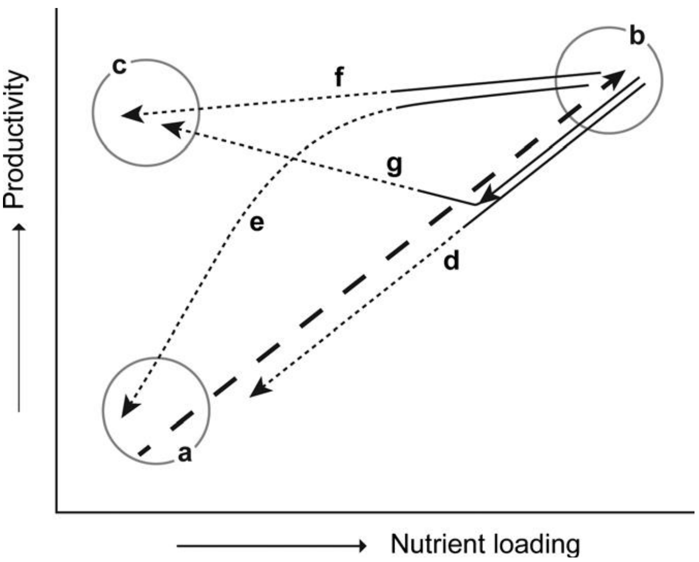


Figure 3. Conceptual diagram using a combination of palaeolimnological data (dashed line), contemporary long-term monitoring data (solid lines) and future conjecture (dotted lines) to show idealised changes in the past, present and future relationship between nutrient loading and productivity for European lakes recovering from eutrophication. Point (a) indicates the reference state and the target endpoint following restoration; point (b) indicates the point of intervention to reduce nutrient loading; and (c) indicates a more probable potential endpoint in cases where recovery to the past reference (a) is prevented by the enriching effects of climate change. Arrows (d, f, e and g) are explained in the text. (From Battarbee et al. 2012)

There is also evidence that recovery pathways of lakes recovering from acidification might be influenced by climate change. Studies of the recovery of boreal lake ecosystems from acidification observed changes in phytoplankton and littoral invertebrate assemblages indicative of decreasing acidity (Stendera & Johnson 2008). However, other changes unrelated to changes in acid deposition occurred including a decline in the richness of sublittoral and profundal invertebrate assemblages which may have resulted from climate-related change acting on habitat quality, such as ambient oxygen concentrations and temperature.

Battarbee et al. (2014) used lake sediment records to track the degree of recovery from acidification at a set of UK lakes. Their study demonstrated that recovery varies amongst sites but in all cases its extent is limited when compared with the pre-acidification reference. In most cases the recovery, although usually slight, is characterised by a decline in acid tolerant taxa and a return towards pre-acidification taxa. In a few cases, however, the floristic composition of recent samples is different from those that occurred during and before the acidification phase. The reasons for this are not yet clear but it is possible that nutrient enrichment from atmospheric N deposition and/or climate change is beginning to play a role in driving water quality as acidity decreases. Most sites have experienced a change in climate over the monitoring period. Based on evidence for Lochnagar, surface waters of lakes across the UK Acid Water Monitoring Network are now likely to be up to 1°C warmer than in the early 19th century, potentially influencing both the thermal structure of the water column and the rate of important biogeochemical and ecological processes in the lakes and their catchments. Recovery from acidification may also be compromised through an increase in acid pulses as a result of more extreme precipitation events or remobilisation of catchment nitrogen. The extent to which climate change is responsible for the observed change in diatom assemblages in the study lakes over the last 20 years is unknown and it is difficult to disentangle the warming effects of climate change from the effects of N enrichment as both pressures are likely to cause symptoms of eutrophication (Moss et al. 2011). However, at sites such as Lochnagar and

Burnmoor Tarn where planktonic diatoms are now more abundant than in the pre-acidification period, increasing surface-water temperature may be playing a role. The increase in *Cyclotella* taxa at Burnmoor Tarn is consistent with changes that have taken place at other sites where climate change is believed to be responsible (Catalan et al. 2002, Rühland et al. 2008).

Battarbee et al. (2014) conclude that factors such as increased temperature and the influence of nitrate as a nutrient might lead to the development of entirely new ecosystems where communities in future are characterised by less acid-tolerant flora and fauna as acidity decreases, not necessarily by a faithful progression towards the return of pre-acidification taxa. Such a return may also be inhibited by modifications to within-lake habitat structures and food-webs that have taken place during the acidification process that are not only difficult to reverse but are also likely to be further modified by external pressures if water temperatures continue to rise. At one of the UK study sites, Round Loch of Glenhead, Helliwell & Simpson (2010) combined output from the MAGIC model with the analogue technique to investigate the influence of future changes in deposition and climate on biogeochemical processes and water quality. The results demonstrate that pre-acidification restoration targets will not be achieved by simply reducing acid deposition, and climate change will further confound the beneficial effects of deposition reductions. Similarly in a study of recovery of the Imandra Lakes in the Russian Arctic, Moiseenko et al. (2009) detected subtle signs of recovery due to a decrease in toxic metals and nutrient loading but the biota were slow to respond. They suggest that this Arctic ecosystem will not experience full recovery under a warmer climate and eurybiontic taxa are likely to predominate.

2.3.3. Shifting lake types

Within the WFD, water bodies are placed into types using a set of obligatory (e.g., topographic, geological, physical, hydrological) and optional (e.g., water depth, mixing characteristic, nutrient status) descriptors, a number of which are climate sensitive and thus are subject to variation under climate change (e.g. mean water depth, mixing characteristics, air temperature range, background nutrient status, water level fluctuation) (from Wilby et al. 2006). Lakes do not easily fall into groups or types as in nature they form a continuum, hence some lakes lie on type boundaries and it is possible that such sites could change type as a consequence of gradual climate change (Nõges et al. 2007, Nõges et al. 2009a). Nõges et al. (2007) state that one of the most probable changes is to lake mixing type. For example, in a warmer climate cold monomictic lakes may stratify in summer and become dimictic, previously dimictic lakes may become warm monomictic lakes with the disappearance of ice-cover, and some deep lakes may change from holomictic to meromictic as higher stability of the water column prevents full mixing. Morphometry of water bodies may also change due to for example the decline in lake area caused by draining or a shift from permanent to temporary water bodies due to a decrease in precipitation and increase evaporation in the future climate scenarios for warm regions.

Over longer timescales it is possible that some sites could shift between different categories of water bodies, such as a lake to transitional water category as sea levels rise. In arid and semi-arid climates, warmer temperatures may also lead to a decrease in water level and an increase in salinity in lakes (e.g. Quintana et al. 2006, Beklioğlu et al. 2011). During prolonged periods of drought, salt accumulates each year and may ultimately cause a shift to oligosaline or mesosaline lakes (Jeppesen et al. 2009, Beklioğlu et al. 2011). In the most extreme circumstances, drought will transform permanent water bodies into temporary systems (Beklioğlu et al. 2007), with strong consequences for the biota, ecological quality and the provision of ecosystem services.

Fortunately, the WFD allows for the characterisation process to be iterative as there is scope to capture changes within the six-yearly characterisation cycle. The European Commission (2009) recognises the potential for lake types to shift with climate change and recommends that these water bodies should be transferred to the appropriate type and the corresponding reference values applied to them. The need to define site-specific reference values instead of type-specific ones may become increasingly important as each site responds in its own way to climate change. Uncertainties introduced by applying broad types may increase (cf. Nõges et al. 2009a).

2.3.4. Novel ecosystems

Hobbs et al. (2009) present the concept of "novel ecosystems" arising from global change in which the species composition and/or function have been completely transformed from the historic system. They suggest that these systems will require a refocusing of conservation and restoration practices away from existing or historical assemblages. They also introduce the notion of a "hybrid system" being one that retains characteristics of the historic system but whose composition or function now lies outside the historic range of variability, e.g. where most of the measurable traits of the ecosystem (i.e. nutrient load, hydrology, species diversity, etc.) are the same but most of the species have changed. They argue that owing to the arrival of invasive species a suitable goal for some systems is their retention in a hybrid state, where some non-native species are accepted as part of the system. They conclude that under climate and land use change a dynamic and flexible approach to conservation and restoration is required that considers a range of approaches to deal with an increasingly uncertain future.

If lake hydromorphology or catchment soils have been irreversibly changed or if, in future, climate change fundamentally alters the baseline, re-assembling species-based assemblages may then be impossible. In line with the thinking of Hobbs et al. (2009), Bennion et al. (2011) suggest that restoring past lake habitats and ecological processes and functions may be more appropriate. An alternative to site-specific reference conditions is to use reference assemblages from more than one site, similar in type to the lake of interest. This is nicely illustrated by the palaeolimnological study of Battarbee et al. (2011b) who examined diatom assemblages from a set of low alkalinity lakes to identify reference communities. However, even within the low alkalinity typology they observed considerable variation in reference assemblages from naturally acidified systems dominated by benthic taxa to circumneutral sites where planktonic diatoms were more abundant. By grouping sites into clusters it was possible to derive reference assemblage characteristics of a type of lake rather than a specific site, which matches more closely the use of metrics in the WFD. The Euro-limpacs project showed that the biological response to climate change, at species level, will be less predictable than the response of water chemistry or hydrology. There is great uncertainty, therefore, in predictions of how species in reference sites will be affected. Another approach is to use habitat structure and functional process to determine reference conditions rather than species composition. This can be applied in a palaeolimnological approach by the use of contemporary ecological training sets representing functional attributes and habitat characteristics of different organism groups (Sayer et al. 2010, Bennion et al. 2011).

2.3.5. Management implications of altered reference conditions

It should not be forgotten that, even in the absence of climate change, a number of factors will change over time that could affect achievement of objectives over the long term. With direct reference to the WFD, Wilby et al. (2006) state that reference sites are themselves subject to natural variability, cycles and succession, hence they recommend a periodic review of reference conditions to accommodate slow changes arising from ecological succession and climate change, or their explicit linkage to slowly varying natural drivers such as the NAO. They point out that long term data are necessary in order to assess the response of aquatic systems to natural variability. The need for periodic review is also outlined by Nõges & Nõges (2014) in their ’Guidelines for the development of adaptation, mitigation and restoration strategies (for lakes)’, where they state that restoration targets will need to be evaluated periodically, accepting that some changes have become permanent. Indeed, Article 5(2) of the WFD requires that characterisation and determination of reference values is reviewed (and if necessary updated) at least 13 years after entry into force and every six years thereafter. Therefore, the WFD does not assume that type-specific reference conditions will remain static, and the cyclical review, together with 'climate change' proofing of the reference conditions for individual quality elements, can be used to achieve good integration of climate change in the WFD (EEA 2007). Nonetheless accommodating climate change in methodological assessments used to establish type-specific reference conditions is a major challenge (EEA 2007). How does a metric cope with new species that appear as a result of climate change? EEA (2007) argues that the wording of Annex II of the WFD implies that where climate change introduces a high degree of variability in a quality element there is scope to exclude that element. In our view, this would be a last resort.

The recent guidance document produced by the European Commission on ‘River basin management in a changing climate’ (EC 2009) recognises the need to assess and monitor the impact of climate change on reference sites. The report advocates a “sufficiently robust long-term monitoring network of reference sites [...] linked to meteorological data” as the only direct way of detecting responses of water bodies to climate change impacts. They consider long term coherent changes in the status of reference water bodies over large geographical areas to be proof of changing reference conditions. The report stresses the need to establish the causes of the change and to decide whether the site still constitutes a reference site or not. The document states that climate trends are expected to play a minor role in early WFD river basin management cycles and that natural variability in annual and seasonal climate will be far more significant. Their main message is that “reference [values] and default objectives should not be changed due to climate change projections over the timescales of initial WFD implementation (up to 2027) unless there is overwhelming evidence to do so”. For the upcoming WFD cycles in 2015, 2021 and 2027, the European Commission (2009) suggests the following actions are taken where monitoring data show strong evidence that conditions at reference sites are changing:

- In order to achieve better distinction between climate change pressures and other human pressures, maintain robust long-term, concurrent meteorological, water quality and biological monitoring to improve evidence of causative links between climate variability and local ecological status. Maintain monitoring programmes at sites with a long history of monitoring in order to give the longest possible time series.
- Use homogeneous climate indices (for instance the NAO, Central England Temperatures or England and Wales Precipitation series) to contextualise biological samples taken under different conditions (i.e., hot-dry, cool-wet, etc.). Use palaeoenvironmental reconstructions and other proxy evidence to represent the full range of conditions experienced at reference sites over multiple decades.
- Undertake periodic reviews of conditions and pressures at reference sites to assess whether the site can still be used as a reference site.
- Prioritise to distinguish climate change impacts from those caused by other anthropogenic pressures.

- Be aware of the challenges associated with attribution of environmental changes to anthropogenic climate change and avoid over-interpretation of observed trends.
- Focus on how climate variability and change will work alongside pressures from human activities and use the degraded water status because of these various pressures as the starting point for planning of measures.

The following section will examine the potential impacts of climate change on reference conditions for the biological elements relevant to lakes.

2.4. Climate change effects on reference conditions for different BQEs

2.4.1. Climate change impacts on phytoplankton

The phytoplankton parameters that the WFD requires include phytoplankton abundance, composition and bloom frequency and intensity (European Union 2000). There is an increasing body of evidence that all of these parameters are impacted by climate change with implications, therefore, for establishing reference conditions for phytoplankton.

Several studies have shown how interannual variability in NAO affects lake plankton assemblages by affecting temperature, ice cover and timing of spring algal blooms (Johnson et al. 2010). Predicted future changes in temperature and precipitation are also likely to impact on phytoplankton. Increased temperature and changes in flow have both been shown to have a strong influence on phytoplankton abundance and composition especially in terms of boosting the dominance of cyanobacteria. For example, in an application of the PROTECH model to Esthwaite Water, a relatively shallow English lake, Elliot (2010) predicted that with increasing temperature and decreasing flow cyanobacteria abundance increased, comprised a higher proportion of the phytoplankton and had a longer duration. A similar outcome was reported by Kosten et al. (2012) based on a study of 143 shallow lakes along a latitudinal transect ranging from subarctic Europe to southern South America. They showed that the percentage of the total phytoplankton biovolume attributable to cyanobacteria increases steeply with temperature. Their results also revealed that the percent cyanobacteria is greater in lakes with high rates of light absorption, indicating a synergistic effect of nutrients and climate (see also section 2.6.3).

Similar synergistic effects have been reported by Gallina et al. (2013) in a study from six deep, warm, monomictic, peri-Alpine lakes. Interestingly, they found differences in cyanobacteria composition mainly due to air and water temperatures and nutrients (P, N), and to the duration of the stratification period (e.g. Oscillatoriales were related to higher water temperatures and longer stratification period whereas Chroococcales were related to higher temperature and nutrient input). Previously, the same author observed that extreme warm air temperatures increased cyanobacteria biomass in the epilimnion, whereas cold temperatures had the opposite effect (Gallina et al. 2011). However, they did not observe any differences between the responses of toxic and non-toxic cyanobacteria to temperature. Also in deep lakes, the population dynamics of cyanobacteria in response to climate change may present different patterns depending on behavioural traits of species, as observed in Lake Mondsee, an alpine oligo-mesotrophic lake in Austria (Dokulil & Teubner 2012). In contrast to other phytoplankton species, the biomass of the cyanoprokaryote *Planktothrix rubescens*, a species inhabiting mainly the metalimnion, increased only during the spring-early summer transition and not with a lengthening of the summer thermal stratification. These results suggest that certain cyanobacterial blooms in deep lakes present different dynamics from the total phytoplankton, adding more complexity to the management of algal blooms in deep stratified lakes.

In some lakes, especially those in cold temperate ecoregions, climate change is expected to bring about increases in DOC and hence a brownification of waters. In a mesocosm experiment to investigate the dual effects of temperature and water colour on cyanobacterial bloom formation and toxicity, Ekvall et al. (2013) showed that total cyanobacterial biomass mostly remained unaffected. However, bloom incidence of the invasive flagellate algae *Gonyostomum semen* were found to increase with water colour and pH in 124 boreal lakes (Trigal et al. 2013). The distribution of this species was mainly explained by temperature and the length of the growing season. This suggests that the co-occurrence of higher temperatures and brownification effects due to climate change may lead to the spread of particular species. In such an event there are important implications for reference conditions based on phytoplankton composition.

Evidence of climate change impacts on the algal composition of unimpacted (reference) lakes is provided by Rühland et al. (2008) who presented a synthesis of over 200 diatom-based paleolimnological records from non-acidified/non-enriched lakes. Their study reveals remarkably similar taxon-specific shifts across the Northern Hemisphere since the 19th century, namely significant increases in the relative abundances of planktonic *Cyclotella* taxa and sharp declines in both *Aulacoseira* taxa and benthic *Fragilaria* taxa. They demonstrate that this trend is not limited to Arctic and alpine environments, but that lakes at temperate latitudes are now showing similar ecological changes. They conclude that their data provides clear evidence that unparalleled warming over the last few decades resulted in substantial increases in the length of the ice-free period that likely triggered a reorganization of diatom community composition. The duration of the ice-free period is clearly an important driver and has been shown to be related to the phytoplankton species richness and biomass in Sweden (Weyhenmeyer et al. 2013), partly because of correlations between nutrients, latitude and temperature but also a direct result of a shorter growing season. When the ice-free period increased above a threshold of 170 days, the phytoplankton seasonal succession changed from one to two peaks a year, with a consequent increase in species richness.

Within the Eurolimpacs project long term data combined with palaeolimnological records were employed to examine diatom response to nutrients and climate in seven European lakes (Battarbee et al. 2012). In deep lakes Mjøsa (Norway) and Piburger See (Austria) significant changes in the diatom assemblages of the sediments towards pre- eutrophication reference floras of the lakes were observed following nutrient reduction. However in Mjøsa, not all the pre-eutrophication taxa have reappeared and an increase in water temperature was offered as one explanation (Hobæk et al. 2012). In Piburger See, several diatom taxa namely *Asterionella formosa* and some *Cyclotella* species (cf. Rühland et al. 2008) have appeared in the lake that have not occurred previously, again possibly due to climate change (Thies et al. 2012). At two of the shallow lakes, a climate influence on the diatom assemblages was also observed. At Loch Leven, Scotland, there were several changes in species composition in the recent fossil record that may be attributed to climatic controls. Most notably from 1996–2005 there was a higher abundance of *A. granulata, A. granulata var. angustissima* and *A. ambigua* relative to *A. subarctica*. The former generally bloom in late summer to early autumn, and are known to tolerate warmer waters than *A. subarctica* which tends to peak in late winter to early spring. In a similar study by Dong et al. (2012) of diatoms in Esthwaite Water, England, the presence of *Aulacoseira granulata* and *Aulacoseira granulata var. angustissma* also seemed to coincide with warmer temperatures.

The three strongest metrics for phytoplankton, recommended for assessing ecological status of European lakes in relation to nutrient pressures, are the phytoplankton trophic index (PTI), chl-a and cyanobacterial biovolume (Carvalho et al. 2013b). Composition metrics, such as the size-structured and trait-based indices, or diversity and evenness metrics may in fact not just represent impacts of eutrophication, but may indicate the impacts of other stressors, including climate change which affects flushing rates and water column stability. One of the key phytoplankton metrics that has been developed across Europe is the PTI, which is based on species composition (Ptacnik et al. 2009, Phillips et al. 2013). The metric is significantly related to total phosphorus concentrations, but is also sensitive to alkalinity, lake size and climatic variables. Ordination analysis showed that temperature had a strong influence on phytoplankton community structure in addition to nutrient status, most likely due to its impact on length of the growing season. Rainfall also had a significant influence on PTI, which may reflect flushing rate.

In order to derive these metrics, phytoplankton indicator taxa for reference conditions for each lake type have been identified. For example, Järvinen et al. (2013) identified phytoplankton indicator taxa for reference conditions in Northern and Central European lowland lakes. Reference lakes were selected based on low pressure from catchment land-use, low population density and the absence of point sources. Reference lakes had low phytoplankton biomass and taxa richness compared to non-reference lakes. In low alkalinity lakes of Northern Europe, the reference communities had high biomass proportions of chrysophytes and low proportions of cyanobacteria. In Central European high alkalinity stratified lakes, the reference communities have access to more nutrients and bicarbonate and thus differ from those in the north by having less chrysophytes and more pennate diatom taxa (e.g. *Asterionella formosa*, *Fragilaria*). One characteristic of the reference communities is the absence of many taxa typically found in non-reference lakes. The implications of the growing body of evidence on climate change impacts on phytoplankton are that these taxa lists may change in future. Clearly it will be important to monitor the phytoplankton communities in a set of reference lakes to assess the nature and degree of any change.

Focusing on deep lakes, Shimoda et al. (2011) reviewed lake ecosystem response to climate change in North temperate areas, including modelling studies. With respect to cyanobacteria dominance in the epilimnion, the modelling predicted the ability of the exogenous TP levels to shape the phytoplankton biomass and the relative percentage of cyanobacteria in response to climate change during the summer stratified period. According to these results, phosphorus limitation may control cyanobacteria biomass in epilimnetic environments of deep lakes, and may thus help mitigate the effects of warmer temperatures.

In shallow lakes there is evidence of climate change effects on phytoplankton populations via changes in temperature and water level. Nõges (T.) et al. (2010e) demonstrated that in Estonian shallow lakes (e.g. Lake Peipsi) increased temperature favours the development of cyanobacteria blooms. Further in their study of Lake Võrtsjärv, a large, shallow Estonian lake, Nõges (P.) et al. (2010b) highlighted the influence of climate-induced water level change on phytoplankton seasonality (see also case study in section 4.5). They observed an inverse relationship between lake mean depth and phytoplankton biomass during summer and autumn related to changing light-limitation. With dropping water levels generally more light becomes available and nutrients take over the control of phytoplankton. At the same time, the influence of wind on turbidity increases at low water levels causing a highly variable underwater light field.

In warm ecoregions of Southern Europe, the projected extension of hypolimnetic anoxia and higher bottom water temperatures are likely to enhance internal nutrient loading and potentially alter phytoplankton populations. A study by Nõges (P.) et al (2011) showed that the impact was more pronounced in lakes with lower trophy. In contrast to cool temperate lakes, Jeppesen et al. (2011a) suggest that external nitrogen loading is expected to decline in warm temperate and arid climates. However, they point out that in warm arid lakes high N concentrations exist despite reduced external loading due to increased evapotranspiration leading to higher nutrient concentrations in the remaining water. The high concentrations may also reflect a low oxygen induced reduction of nitrification. They conclude that the critical N as well as P loading for good ecological state in lakes likely has to be lower in a future warmer climate in Mediterranean lakes as well as in north temperate lakes.

In Southern European regions, especially those in Mediterranean areas, climate change is expected to increase evaporation and evapotranspiration processes and lead to enhanced salinity. As salinity increases, a shift occurs from dominance of large and more efficient filter-feeding cladoceran species to dominance of copepods and small cladoceran species (Jeppesen et al. 2007, Brucet et al. 2009, Jensen et al. 2010). The reduction in the size and abundance of zooplankton grazers due to enhanced salinity may decrease the capacity of zooplankton to control phytoplankton crops and negatively affect the resilience of lakes to enhanced nutrient loading (Jeppesen et al. 2007, Brucet et al. 2010, Brucet et al. 2012) .

In summary, there is growing evidence that climate change is leading to changes in phytoplankton composition, abundance and the onset and frequency of algal blooms. However the response is complex, varies considerably with lake type and ecoregion and is strongly interlinked with changes in nutrient concentrations. Clearly reference values for phytoplankton will need to be evaluated periodically to assess the extent of shifts in species composition and any increase in biomass.

2.4.2. Climate change impacts on fish

The fish parameters that the WFD requires for lakes include assemblage composition, body size and age structure. In recent decades changes in all of these parameters, principally in response to climate change, have been profound (Jeppesen et al. 2012c, Malve et al. 2012). Temperature, in particular, has been shown to be a major determinant of the taxonomic and functional structure of European fish assemblages (Brucet et al. 2013a). Therefore, global warming will likely affect both the composition and the functional structure of fish assemblages (Brucet et al. 2013a, Logez & Pont 2013). The most striking changes have been a decline in cold-stenothermal species, particularly in shallow lakes, and an increase in eurythermal species, even in deep, stratified lakes, as well as a decrease in the average size of the dominant species (Jeppesen et al. 2012c). These shifts have occurred despite an overall reduction in nutrient loading that should have favoured fish typically living in cold-water, low-nutrient lakes and larger-sized individuals. One of the fish indices developed for assessing the ecological status of European lakes is the fish EUindex, which includes composition and abundance metrics that reflect the eutrophication pressure in lakes (Argillier et al. 2013). Clearly such an index will be affected by the climate-induced changes to fish populations reported above and discussed in more detail below.

One of the most comprehensive studies of climate change impacts on fish reviewed published and long-term fish data series from 24 European lakes along a north–south gradient from Sweden to Spain (Jeppesen et al. 2012c). This study revealed complex changes in fish assemblage structure with climate change owing to direct effects of temperature and indirect effects operating through eutrophication, water level changes, stratification and salinisation. In association with an annual temperature increase of about 0.15-0.3 °C per decade, the authors showed that marked and rapid changes have occurred in either fish assemblage composition, body size and/or age structure during recent decades. They noted a shift towards higher dominance of eurythermal species (e.g. common bream, common carp, pike-perch, shad) in both deep and shallow lakes and a decline in the abundance of cold-stenothermal species with Arctic charr having been particularly affected. Introduced species such as roach have taken advantage of higher temperatures after years of low population densities, e.g. Lake Windermere, UK. The study highlights the fact that eutrophication can amplify the effect of temperature extremes, for example cyanobacteria and fish kills have co-occurred in hot summers with calm weather in Lake Peipsi, Estonia. The review suggests that climate change is creating novel fish assemblages and it seems highly unlikely, therefore, that a return towards reference fish assemblages can be achieved in a warmer climate. The study concludes that it will be difficult to achieve good ecological status required by the WFD in European lakes facing climate warming and suggests that reducing nutrient loads to lakes even further than planned at present and to regulate fisheries accordingly may at least go some way to counteracting the effect of warming.

Brucet et al. (2013b) explored the key factors controlling fish diversity in European lakes at a macroecological scale (>1700 lakes). They showed that temperature, related to geographical factors, was a strong predictor of most components of fish diversity. This study highlights the importance of temperature in determining broad-scale patterns of fish diversity in European lakes and suggests that global warming is likely to impact on fish metrics based on diversity and size structure indices. Furthermore, the temperature-related effects on fish density (due to both latitudinal or altitudinal differences) may act independently of lake trophic status since, for a similar total phosphorus concentration, they found generally a greater number of fish in warm than in cold lakes.

Logez & Pont (2013) looked specifically at the impact of global warming on functional fish-based metrics and the potential shift in reference conditions that may arise. While the study was based on rivers there are some interesting observations that are equally applicable to lakes. The study shows that traits based on species intolerance are expected to be most negatively affected by climate change, namely species intolerant to habitat degradation, species with high oxygen needs, rheophilic (preferring to live in high-flow conditions) and eurytopic (broad tolerance to flow conditions) species. The authors argue that for metrics that encompass these traits, reference values will have to be changed because they will become poorly adapted to future climate. They propose that reference values could be modified by including climatic conditions in the computation of the predicted metric values in the absence of pressure. They call for caution to be exercised when using the intolerance-based metrics, especially where a huge disappearance of cold-intolerant species has occurred, as these metrics may no longer reflect the faunal specificity of the regional fauna. Their study also draws attention to the fact that the effects of climate change vary by ecoregion, suggesting that for some ecoregions the current tools will more rapidly become inadequate, although the authors do not specify in which ecoregions this is likely to be the case. Interestingly Logez & Pont (2013) found that the traits related to reproduction were not expected to be greatly affected by climate change with possible explanations being either that only some species will be affected by climate change depending on their thermal preferences or that the same function will be represented by other species with higher thermal preferences but with similar characteristics. They also found that local species richness was not affected by climate change, suggesting replacement of intolerant cold-water species with more eurytopic species.

Logez and Pont (2013) alluded to the fact that the effects of climate change on fish populations will vary by ecoregion. The study of effects of climate and nutrient enrichment on growth rates of rainbow trout (*Oncorhynchus mykiss*) in warm-temperate lakes by Blair et al.

(2013) suggests that effects will also vary by lake type. They showed that in deep oligotrophic and mesotrophic lakes, trout growth rates increased with increasing lake productivity. In contrast, in shallow eutrophic lakes, where fish habitat volume is constrained by temperature and dissolved oxygen, trout growth rates declined with increasing productivity. Their findings suggest that increases in lake productivity and temperatures as a result of climate change are likely to be more detrimental to salmonid habitat quality in shallower, productive lakes than in deeper, oligotrophic lakes. They argue that this information will be valuable to fishery managers when planning future stocking of salmonid fisheries in warm-temperate climates. Their findings also have implications for reference conditions based on fish body size as the suggestion is that climate change will result in reduced body size in shallow lakes and increased body size in deep lakes. Indeed several studies (Blanck & Lamouroux 2007) (Meerhoff et al. 2007, Jeppesen et al. 2010a, Brucet et al. 2013a) found that mean body size of fish at the assemblage level tends to decrease with increasing temperature.

In high mountain lakes, fish populations have been reported to be adversely affected by bioaccumulation of airborne pollutants. Given that the geographical distribution of semi-volatile organochlorines is strongly influenced by air temperatures, future climate change will potentially enhance their physiological effects on fish in mountain lake ecosystems (Jarque et al. 2010) and reduce their potential for resistance to and recovery from toxicant exposure (Moe et al. 2013a).

All of the above studies indicate that climate change is expected to impact on fish assemblages in European lakes in ways that are likely to affect the metrics used in ecological status assessment. The effects vary considerably with lake type. Logez & Pont (2013) highlight the need to maintain a biomonitoring network of undisturbed sites which reflect current reference conditions in order to fully capture the functional changes in European fish assemblages.

2.4.3. Climate change impacts on macrophytes

The macrophyte parameters that the WFD requires for lakes include composition, richness and abundance. Much of the metric development has focused on macrophyte response to eutrophication and, to a lesser extent, hydromorphological pressures and, given that both of these are likely to be impacted by climate change, they will form the focus of this review.

For eutrophication pressure, in many European countries, aquatic plants have been aggregated into categories according to their requirement along a trophic gradient with taxa typically grouped into tolerant and sensitive to eutrophication. For example, in the UK, metrics reflecting the composition (Lake Macrophyte Nutrient Index- LMNI), richness (numbers of hydrophyte taxa and hydrophyte functional groups) and abundance (mean cover, relative algal cover and relative invasive species cover) of the vegetation have been developed to reflect different aspects of the WFD normative definitions (Willby et al. 2010). Recently a number of studies have collated the available national macrophyte datasets and have compared metrics on a European scale (e.g. Penning et al. 2008, Kolada et al. 2011, Lyche-Solheim et al. 2013). As part of the WISER project, Kolada et al. (2011) and Lyche-Solheim et al. (2013) tested the performance of i) the Intercalibration Common Metric for lake macrophytes (ICM_LM), which is based on a lake trophic rank (LTR) score which grades taxa by their response to nutrient enrichment, ii) the Ellenberg Index (EI), which assigns indicator values for nitrogen to each macrophyte taxon, and ii) the maximum growing depth of submerged macrophytes. They showed that the ICM_LM was one of the strongest and most sensitive metrics responding to eutrophication pressure.

It is widely reported that macrophytes are adversely affected by eutrophication with numerous examples worldwide of macrophyte decline and, in some cases, complete plant loss (e.g.

Sand-Jensen et al. 2000). This arises because increased nutrient availability increases phytoplankton in lakes, leading to increased turbidity and impoverished light conditions. Lakes tend to shift from a clear state dominated by submerged macrophytes to a turbid state dominated by phytoplankton (Scheffer 1998). Given that climate change is expected to enhance the effects of eutrophication, it is likely that the risk of loss of submerged macrophytes will increase (Jeppesen et al. 2011a). Multiple regression analysis of late summer data from 800 Danish lakes indicates that warming will lead to a tendency to reduced zooplankton biomass and zooplankton:phytoplankton biomass ratio. Consequently, these changes lead to increased turbidity, which will impoverish the growing conditions of submerged macrophytes (Jeppesen et al. 2013a). This has implications for reference conditions as the frequency and abundance of sensitive species, which are most apparent or only appear in reference lakes, decreases or the species disappears entirely, with increasing eutrophication pressure (Penning et al. 2008).

It is thought that submerged macrophyte dominance gives way to phytoplankton dominance at lower nutrient concentrations in warmer lakes than in colder (Beklioğlu et al. 2007, Mooij et al. 2007), although results of experiments are rather inconclusive. For example in mesocosm experiments in shallow Mediterranean lakes, Romo et al. (2004) reported that macrophytes gave way to phytoplankton dominance at lower nutrient concentrations than in similar studies conducted in North European lakes. However, in some lakes, Scheffer et al. (1992) found that the temperature in early spring had a positive effect on macrophyte coverage. In one of the most comprehensive analyses of macrophyte data from over 500 shallow lakes from different climate zones including North America, South America, and Europe, Kosten et al. (2009) attempted to test the hypothesis that macrophytes disappear at lower nutrient concentrations in warmer climates by exploring the relationship between macrophyte coverage and nutrient levels, lake characteristics and climate variables. Their analysis did indeed show that in warmer regions macrophyte coverage is reduced at lower nutrient levels than in cooler regions. They also found that ice cover duration had an indirect effect on submerged macrophytes by improvement of the light climate. This resulted from partial fish kills under the ice which had cascading effects on periphyton and phytoplankton. This is in line with the findings of Hargeby et al. (2004) who reported a decline of submerged macrophyte coverage in a Swedish lake associated with a decrease in ice cover duration. Importantly their findings suggest that, in regions where climatic warming is projected to lead to fewer frost days, macrophyte cover will decrease unless nutrient levels are reduced. These studies suggest that metrics based on macrophyte abundance are likely to be affected by climate warming and hence reference values may need to be modified under a warmer climate.

One metric that has been proposed for WFD classification is the maximum growing depth of submerged macrophytes (Søndergaard et al. 2013). However, the authors point out that the predicted rise in temperature and changes in precipitation may increase loading of dissolved organic carbon (DOC) from boreal areas and thereby affect water colour (i.e. brownification). This may, therefore, be a factor which will increasingly reduce the depth distribution of submerged macrophytes in the future and clearly has implications for the setting of reference values for maximum growing depth in boreal lakes.

In addition to their use as indicators of eutrophication pressure, macrophytes are one of the key indicators of hydromorphological changes in lakes (Kolada et al. 2011). Aquatic macrophytes are typically found growing in the littoral zone and are therefore sensitive to changes in the water level fluctuation regime. Zonation of macrophytes is typically observed with helophytes growing in the uppermost zone and isoetids, elodeids and charids occupying deeper areas of lakes, and even small changes in the dynamics of water level fluctuation can affect the distribution and the elevation of zones. The literature suggests that the impact of water level change on macrophytes depends on the nature and amplitude of the water level fluctuation. Several studies have found lower diversity of macrophytes in lakes with considerably fluctuating water level (e.g. Rørslett 1985, Rørslett 1989, Nilsson et al. 1997, Hill et al. 1998, Hellsten 2001, 2002). Additionally, morphological changes of the littoral zone, caused for example by dredging or embankments, can significantly disturb the aquatic vegetation. The effects of water level fluctuation are enhanced in lakes covered by ice because the effects of down-dwelling ice are especially harmful for plants sensitive to freezing (e.g. Hellsten 2001).

The impact of hydromorphological change is not always negative, however, as a slight increase in disturbance can create suitable habitats for some aquatic macrophytes (Murphy et al. 1990) and increasing monthly water level fluctuation range has been reported to increase diversity in some cases (e.g. Riis & Hawes 2002). In fact, generally, a lowering of water level will lead to increased diversity as a newly exposed littoral zone or general shallowness allows the sublittoral zone to cover the entire water body (e.g. Toivonen & Nybom 1989, Rørslett 1991). Kolada et al. (2011), in a review of macrophyte metrics for hydromorphological pressure, point out that taxonomic composition is less likely than abundance to be affected by water level increase because most of the species are still present following the increase. They also conclude that the effect of water level fluctuation on zonation patterns depends on the bathymetry of a lake and thus is a lake-specific reaction. Given the complexity of lake response to water level fluctuation, assessing the implications of climate change for reference conditions for macrophytes with respect to hydromorphological pressures is not an easy task.

One of the metrics that has been developed for hydromorphological pressures is a taxonomic composition index for macrophytes based on responses to water level fluctuations in Nordic hydropower reservoirs (Mjelde et al. 2013). This water level drawdown index (WIc) employs macrophyte data from 73 lakes with varying water level fluctuation in Finland, Norway and Sweden and is based on the ratio between sensitive and tolerant macrophyte species. In general, sensitive species are defined as species preferring relatively unimpacted or reference lakes, and have low frequency and abundance if water level fluctuations increase. These species are often absent when winter drawdown exceeds 2.5-3 m. Tolerant species increase in frequency and abundance if water level fluctuations increase and are less frequent in reference lakes. Climate change could potentially bring about alterations to the sensitive species found in reference lakes but the authors do not discuss how warmer temperatures or increased precipitation might affect the metric.

It is likely that the impact of water level fluctuation will be most greatly felt in the warmer Mediterranean regions of Europe where higher summer temperatures and lower rainfall are predicted to result in increased demand for irrigation. Greater evapotranspiration rates and reduced inflows may result in salinity and nutrient increases which could have major ecological consequences. Salinity is a critical factor in Mediterranean shallow lakes that may affect growth of macrophytes and littoral processes (Beklioğlu et al. submitted). A comprehensive study that included both the contemporary plant community and surface sediment remains of aquatic plants collected from 35 shallow lakes showed that conductivity was the most important environmental factor determining macrophyte community (Levİ et al. 2014). It is perhaps in these most vulnerable parts of Europe where reference values for macrophytes, and indeed all biological quality elements, will need to be most thoroughly reviewed in light of climate change. As for the other biological groups, it will be crucial to establish a monitoring network of undisturbed sites which reflect current reference conditions in order to fully capture the changes in European lake macrophyte assemblages.

2.4.4. Climate change impacts on macroinvertebrates

The macroinvertebrate parameters that the WFD requires include taxonomic composition, abundance, diversity and proportion of sensitive taxa. In contrast to the large body of work on macroinvertebrate classification schemes for rivers, macroinvertebrates have been somewhat neglected in the development of assessment systems for lakes and the literature is relatively limited compared to that of the other biological quality elements (Solimini et al. 2006). As benthic invertebrates respond sensitively not only to pollution but also to a number of other factors such as hydrology, temperature, morphology and acidification, it is expected that climate change will impact on the benthic invertebrate fauna of lakes.

A shift in geographic distribution due to higher temperatures has been predicted for aquatic macroinvertebrates (Domisch et al. 2013). Macroinvertebrate traits (e.g. dispersal, thermal tolerance) may determine the colonization success of species in new suitable habitats, their adaptability to the new climatic conditions or the risk of becoming extinct. For instance, for species with aerial dispersal, Hickling et al. (2005) showed how 37 species of non-migratory British dragonflies and damselflies have shifted northwards at their range margins over the past 40 years. In streams, Bonada et al. (2007) noted that the Mediterranean region was characterized by macroinvertebrates with higher dispersion and colonization capabilities than temperate regions, suggesting that species loss in the temperate region, by extinction or northward emigration of taxa, would be compensated by immigration of southern Mediterranean taxa. In a study on macroinvertebrate assemblages in 25 high alpine ponds, Oertli et al. (2008) suggested that global warming would lead to higher local and regional richness through an increase in the number of colonisation events resulting from the northward shift of species. However, they suggested that higher extinction will occur in cold stenothermal species such as Dytiscidae *Hydroporus foveolatus* and *H. nivalis*, Chironomidae *Micropsectra notescens* and *Pseudosmittia oxoniana* and Trichoptera *Acrophylax zerberus*. Such changes in macroinvertebrate community composition due to global warming have implications for reference conditions and the use of taxonomy-based metrics in the current bioassessment tools (i.e. multimetric indices).

Several lake macroinvertebrate studies have examined the dual impacts of climate change and acidification. An analysis of temporal trends in littoral macroinvertebrate community metrics in acidified and circumneutral lakes in southern Sweden revealed the importance of decreasing sulphate concentrations but a weak response to climate variables (Angeler et al. 2011, Verdonschot et al. 2012). Nonetheless, they observed that groups of species within a community were differently affected by sulphate and that temporal dynamics of the same group of macroinvertebrates showed a response to NAO winter index in many lakes. This suggests a potential interaction of acidification and climate change with climate change potentially confounding recovery. More recently, Murphy et al. (unpublished data under revision) examined the recovery from acidification of the macroinvertebrate community of UK freshwaters (including rivers and lakes) over a 20 year period. Only 5 of the 12 lakes showed signs of biological recovery from acidification. The authors attribute this to the limited dispersal capacity of acid-sensitive species and potential ecological interactions, but also to other environmental changes such as climate. A Euro-limpacs study over a 16-year period of reference boreal lakes showed that invertebrate communities did not fluctuate around a long-term mean (Stendera & Johnson 2008). Instead, they showed signs of degradation unrelated to specific stressors. The results imply the influence of one or more underlying large-scale drivers of ecological change. One explanation given for the long-term trends noted in both the reference and acidified lakes is a gradual shift in baseline conditions brought about by the effects of global warming. For example, a shift in spring temperatures caused by warmer winters in the early years of the study might have caused changes in the timing or duration of summer stratification.

Climate change can alter habitat availability in lakes due to reduction in lake surface area, water level fluctuations or salinization, for example. These effects are most profound in warmer ecoregions due to decreased precipitation and increased evaporation although habitat changes also occur in colder regions due to a reduction in winter ice cover. Therefore, changes in the macroinvertebrate community linked to habitat changes are likely to be observed in reference lakes. White et al. (2010) investigated the effects of annual water level fluctuation on the benthic macroinvertebrate community of littoral stony habitats from 16 natural boreal lakes with an average depth of 10 m. Benthic macroinvertebrate richness decreased with reduced lake area, but it increased with lowered water levels, with changes observed with fluctuations of less than 1 m. McGoff et al. (2013) measured beta diversity from 46 lakes across seven European countries along a north–south and east–west gradient, obtaining a positive relationship of beta-diversity with lake area. McGoff & Sandin (2012), when analysing the impact of land use and habitat in 50 lakes from the central plains region of Sweden, observed a stronger response of macroinvertebrates to habitat heterogeneity related to substrate than to trophic status, masking the effects of eutrophication and land use. Focusing on chironomid fossil assemblages, Engels & Cwynar (2011) assessed the influence of water depth on seven shallow and one deep lake from Plymouth Aquifer in Massachusetts (USA). They found thresholds for chironomid composition responding to water depth and also a correlation of depth with species such as *Tanytarsus spp*., indicating the sensitivity of these aquatic communities to water level and their potential use for reconstruction of lake level changes. Therefore, macroinvertebrate communities may strongly respond to habitat changes as a result of climate change in reference lakes, shifting the baseline conditions, but also blurring the response to restoration of other human pressures.

Macroinvertebrate communities in the sublittoral and profundal zone of lakes may be affected by anoxia. Stendera & Johnson (2008) observed a decreasing trend in richness and diversity indices during their 16-year study of reference lakes, related to lower oxygen concentrations in deep water zones. In Mediterranean lakes, Bazzanti et al. (2012) assessed eutrophication effects on macroinvertebrates in different depth zones and concluded that the total number of taxa, and the BMWP and ASPT scores, discriminated among lakes of different trophic category only in the sublittoral/profundal zone. This arose because the latter community is strongly related to effects on oxygen concentration and, thereby, more susceptible to eutrophication. Therefore any direct or indirect effects of climate change on lake oxygen conditions are likely to impact on the macroinvertebrate community. If longer stratification occurs during the summer period due to climate warming, some macroinvertebrate taxa from deeper habitats may be negatively affected and changes in community composition are likely to occur. This effect may be accentuated by increased dissolved organic carbon in Northern ecoregions. Cross-comparison studies along latitudinal gradients, both in freshwater (Meerhoff et al. 2007) and in brackish (Brucet et al. 2012) shallow lakes found that plant-associated macroinvertebrates had much lower richness (at different taxonomic resolution, mostly order level) in the warmer regions (subtropics and Mediterranean) than in comparable temperate lakes, suggesting that warming may reduce the richness of the macrophyte-associated fauna. The same studies traced up to eight times lower densities of plant-associated macroinvertebrates in the warmer systems compared to the temperate ones. Higher risk of drought and large variations in salinity may also reduce macroinvertebrate species richness and abundance in Mediterranean shallow lakes (Boix et al. 2008, Brucet et al. 2012).

The studies cited above highlight the potential effects of climate change on lake macroinvertebrate communities. The responses are complex and will vary from lake type and by ecoregion. Clearly reference values for macroinvertebrates will need to be evaluated periodically to assess the extent of shifts in species composition and diversity. Moreover, it may be that macroinvertebrate indices based on functional traits have more promise (see section 2.4.5).

2.4.5. Climate change impacts on food webs and ecosystem processes and functions

After reviewing the effect of climate change on the different BQEs, in this section we adopt a more holistic perspective, considering the interactive effects that may lead to changes in the trophic structure, processes and functions of lake ecosystems. Woodward et al. (2010) raised the importance of considering species/community interactions to improve our predictive capacity of the biological impacts of climate change. Thus, although this section highlights the complexity of climate change impacts on food webs and hence the difficulty for defining reference values, an improved understanding of these impacts should contribute to more robust predictions.

Results from the WISER project showed a clear change in trophic structure in lakes along climatic gradients from simple, often elongated food-webs in cold climates to truncated webs in warmer systems with a higher degree of omnivory (Malve et al. 2012). With increasing temperature, European lakes are likely to witness significant impacts on phytoplankton, zooplankton, fish and macrophyte populations with implications for ecological status and biological assessments, particularly where there are barriers to migration. In a review on the impact of global warming on shallow lakes, Meerhoff et al. (2012) documented the effects on trophic interactions with increasing temperature based on space-for-time substitution approaches. These cascading effects included higher predation pressure of planktivorous fish on zooplankton (and also, to a lesser extent, macroinvertebrates), with a consequent decrease in large-bodied zooplankton and lower capacity of the system to control phytoplankton blooms (Figure 4). Furthermore, a reduction in mean body size in fish and zooplankton due to warmer temperatures was predicted. The reduction of zooplankton mean body size due to direct effects of temperature may further reduce the grazing pressure on phytoplankton. Such effects have also been reported by Jeppesen et al. (2009, 2011a, 2013a); for example in a multiple regression analysis of late summer data from 800 Danish lakes Jeppesen et al. (2013a) showed that warming will lead to a tendency to reduced zooplankton biomass and zooplankton: phytoplankton biomass ratio. These changes lead to increased turbidity, which in turn impoverishes the growing conditions of submerged macrophytes. In a further study on 37 Danish lakes including shallow and deep lakes, Balayla et al. (2010) observed that in cold years, when fish kills in winter were abundant, zooplankton could reach higher body sizes during summer, thus grazing on phytoplankton was higher. This effect was much more marked in shallow than in deep lakes. Altogether, the evidence suggests that food webs in temperate and cold shallow lakes will be affected by warming.

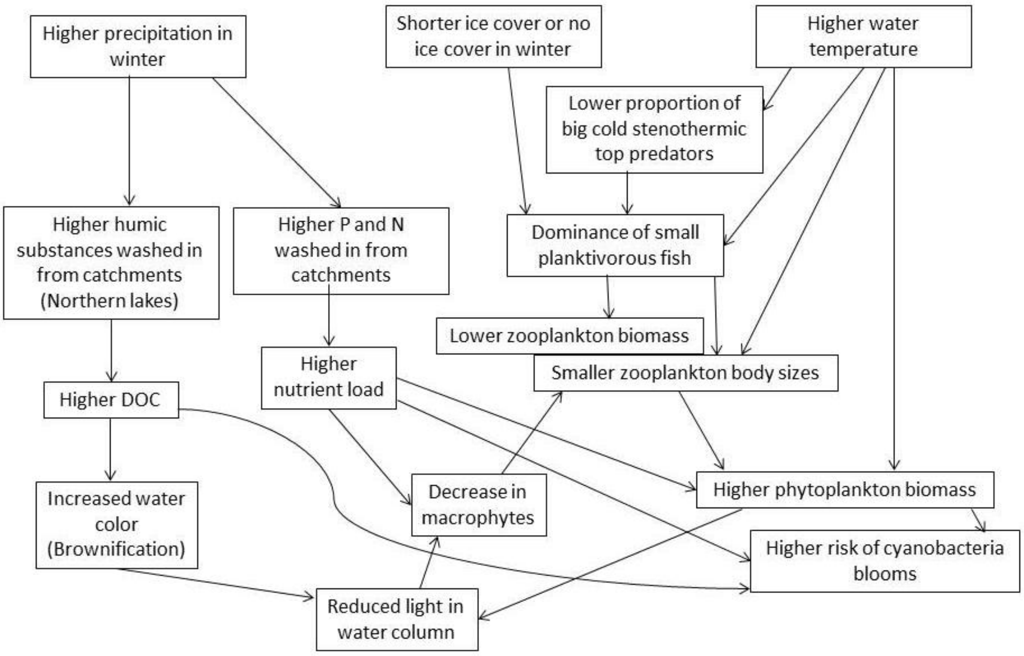


Figure 4. Simplified schema of the principal cascade effects due to climate change predicted in the literature, mainly for shallow lakes in colder ecoregions (adapted and extended from Blenckner et al. 2010).

Similar shifts in the trophic structure of shallow lakes typically occur along a salinity gradient (Jeppesen et al. 1994, Jeppesen et al. 2007, Brucet et al. 2010, Brucet et al. 2012). As salinity increases, a change occurs from dominance of large and more efficient filter-feeding cladoceran species at low salinities to dominance of copepods and small cladoceran species at higher salinities (Jeppesen et al. 2007, Brucet et al. 2009, Jensen et al. 2010). Such a change in species composition along the salinity gradient may weaken the top-down control on phytoplankton at the higher salinities (Jeppesen et al. 2007, Brucet et al. 2010). Moreover, there is also emerging evidence that fish communities may change with increasing salinity (Jeppesen et al. 1994, Brucet et al. 2010, Jensen et al. 2010). Eutrophic and hypertrophic brackish temperate lakes hold a fish community resembling that of warm lakes, that is, with dominance of small planktivorous fish which have more cohorts per year than fish in comparable freshwater lakes and may predate intensively on the zooplankton (Jeppesen et al. 1994, Jeppesen et al. 2007, Brucet et al. 2010, Jensen et al. 2010). This would explain why nutrient-rich brackish lakes remain turbid even at high macrophyte coverage. Indirect effects of climate warming, such as changes in salinity and hydrology, could thus have larger consequences for the trophic structure of shallow lake ecosystems than an increase in nutrients or temperature per se (Brucet et al. 2009, Brucet et al. 2010). Some brackish and saline lagoons might be capable of coping with slight increases in salinity since the organisms dominating these systems can tolerate varying salinities, and well-structured communities can be found at high salinities. However, rising salinity levels, together with increasing temperatures, could have dramatic effects in slightly brackish waters and even more severe impacts on current freshwater lakes.

As mentioned previously the predicted increase in phytoplankton due to climate change may indirectly cause negative impacts on macrophyte communities (Jeppesen et al. 2011a, Jeppesen et al. 2013a, Moss et al. 2013). Because macrophytes can act as refugia for zooplankton, the reduction of macrophytes may enhance fish predation and thereby further increase phytoplankton biomass. These predicted top–down effects as a response to a warmer climate plus an increased nutrient input due to higher precipitation in cold ecoregions, and to increased evapotranspiration and reduced inflow in warmer areas, may result in a higher risk that lakes will shift from a clear to a turbid state and in an increased sensitivity of lakes to algal blooms and eutrophication.

Hansson et al. (2012) tested experimentally the effect of food-chain length on community responses to predicted higher temperatures, but also the synergistic effects with increased water colour (brownification). In agreement with the predictions above, they found that phytoplankton, and thereby algal blooms, will benefit from climate change in three-trophic level systems (i.e. phytoplankton, zooplankton and planktivorous fish), but not in two-trophic-level systems (i.e. phytoplankton and zooplankton). In the in two-trophic-level system, zooplankton grazers will benefit from a warmer climate, especially in synergy with higher humic content. Although brownification alone showed no positive effect on zooplankton, the effect on body size was much higher when combining higher temperature and brownification. Moreover, they observed that both phytoplankton and zooplankton advanced their spring peak abundances similarly in response to temperature increase, in contrast to the consumer/resource mismatch reported in other studies for future climate scenarios (see Hering et al. 2010b). Finally, cyanobacteria (*Microcystis sp.*) benefited from a higher temperature and humic content irrespective of the food-chain composition. In a similar two-trophic-level mesocosm study, Nicolle et al. (2012) did not observe the consumer/resource mismatch but saw an earlier peak in phytoplankton and zooplankton. Also, they obtained a positive effect of brownification on cladocerans and calanoid copepods, leading to higher grazing reduced chl-a concentrations. Other food web effects attributed to brownification are changes in piscivore–prey fish interactions due to a reduced visibility, which may lead to changes in piscivore foraging efficiency and prey escape behaviour (Ranåker et al. 2012). Similar interactive effects may be expected from eutrophication.

In a study of small, oligotrophic high-DOC lakes in southern Sweden, von Einem and Granéli (2010) predicted limitation of phytoplankton by the bottom-up effects of reduced light in the water column due to higher DOC inputs in combination with an increase in epilimnion depth. According to the authors, lakes from this area will experience reduced primary productivity and become more heterotrophic, while fish production will decrease. Forsström et al. (2013) performed a mesocosm experiment to study the responses of the microbial food web to increased allochthonous dissolved organic matter in an oligotrophic subarctic lake in northern Finland. In agreement with von Einem and Granéli (2010), an increase in dissolved organic matter increased the abundance of heterotrophic nanoflagellates (HNF) and decreased primary productivity, indicating a shift towards a more heterotrophic lake. Another bottom-up effect predicted from modelling is related to the increased abundance of toxic cyanobacteria in response to climate change (Mooij et al. 2007, Elliott 2012). Modelling studies have predicted that inedible cyanobacteria could reduce the amount of energy that can flow up to the higher trophic levels, thus having negative impacts upon zooplankton and fish populations.

Alterations of other lake processes and functions as a result of changes in community structure of the different BQE can also be expected with climate change. For instance, fish may directly alter nutrient cycling via excretion, which depends on differences in body mass (i.e. higher excretion rates with decreasing body biomass) but also on interspecific variability (Villéger et al. 2012). Increased proportions of smaller-bodied individuals, as shown by Jeppessen et al. (2010b), or changes in fish community composition with dominance of species having higher excretion rates, may lead to a higher nutrient availability and faster nutrient recycling. The timing of key events such as spawning, hatching and growth phases of the various BQEs are also likely to be altered by climate change causing a mismatch in the food web and resulting in changes to the functioning of the entire ecosystem (Winder & Schindler 2004). In such cases reference values would clearly need to be reviewed (Nõges et al. 2007).

Changes in the macroinvertebrate community may lead to different species trait composition under future climate scenarios that will directly alter ecosystem processes and functions (e.g. organic matter decomposition). In streams, Ferreira et al. (2010) observed reduced performance of detritivores with increasing temperature and thus a direct effect on the processing of organic matter. Although it is generally accepted that biodiversity contributes to the provisioning of ecosystem functions (Cardinale et al. 2006), functional trait approaches (e.g. based on macroinvertebrate traits) may provide a promising approach for adapting baselines to climate change since species traits, defined as a set of physiological, morphological, and ecological attributes, are the main properties by which organisms influence ecosystem processes. Despite its potential, the value of functional traits remains insufficiently explored in freshwater ecosystems (Lecerf & Richardson 2010), and particularly in lakes.

In addition to the impacts of climate change on food webs and ecosystem processes described above, we should also acknowledge the potential of climate change to increase the spread of alien species in reference lakes. Arrival of invasive species is likely to result in marked impacts on ecosystem structure and function in some systems. However, the impact of alien species on reference conditions falls outside of the scope of this review.

In conclusion, here we have evidenced the complexity of climate change effects on ecosystem processes and functions and the difficulty of predicting clear responses at the ecosystem level. Changes in precipitation, ice cover duration and warmer temperatures and the interactions between them will create a diverse range of environmental scenarios resulting in different biological responses in the various ecoregions and lake types. Importantly, climate induced changes in food web length, the predominance of bottom-up or top-down factors, and shifts in species traits need further consideration when defining and modifying reference values in the context of climate change.

2.5. Climate change and ecological thresholds

2.5.1. The role of ecological thresholds in lake management

The role of non-linear dynamics and threshold-type responses in ecosystems have long been recognised (Scheffer et al. 2001). In the most extreme cases of threshold responses, increased pressure can induce a regime shift between alternative stable ecosystem states in lakes, such as a clear-water, macrophyte-dominated state versus a turbid, phytoplankton-dominated (Scheffer & Jeppesen 2007, Carpenter & Lathrop 2008) or between different groups of dominating phytoplankton (Nõges et al. 2010a, Jochimsen et al. 2013). This phenomenon has also been described for other ecosystems including grasslands and corals (reviewed by Andersen et al. 2009). The existence of alternative stable states implies that the ecosystem may display hysteresis: for example, if a certain critical level of nutrient pressure induces a regime shift from a clear-water to a turbid state, then the nutrient pressure must be reduced substantially below this critical level before the lake will return to the clear-water state (see Andersen et al. 2009). The possibility of alternative states and hysteresis clearly have important implications for management of lakes and for planning restoration measures, but in practice it has proved difficult to to identify critical thresholds *sensu stricto* in specific ecosystems and to incorporate the dynamics in management or predictive models (Groffman et al. 2006).

The concept of thresholds has also been used in a much wider sense in the ecological literature: to describe environmental conditions that lead to abrupt or significant changes in ecosystem properties. Thresholds in this sense have been described for a wide range of ecosystems and ecological metrics, e.g. thresholds in environmental variables governing the species assemblages of alpine lakes (Catalan et al. 2009a), and thresholds in acidification pressure affecting sensitive invertebrates in river and lakes (Schartau et al. 2008, Moe et al. 2010b). Moreover, as reported in section 2.6.1, thresholds in responses to eutrophication pressure have been described for sensitive chrysophytes and tolerant cyanobacteria, as well as sensitive macrophytes (Lyche Solheim et al. 2008). Although these more general non-linear relationships are less likely to induce regime shifts or hysteresis, information about such thresholds *sensu lato* may nevertheless be important for ecosystem management. In this document, we will therefore use the threshold concept in this wider sense.

The WFD recognises ecological thresholds as an important factor in ecological classification systems. According to the intercalibration guidance (Schmedtje et al. 2009), WFD class boundaries should preferably be based on thresholds or discontinuities in the relationship between a biological metric and the pressure gradient. If there are distinct discontinuities in the relationship between the biological metric and the gradient of impact represented in a dataset, this discontinuity can be used as either the class boundary or the class centre. For example, a steep decrease of macrophyte abundance can correspond to the Good/Moderate class boundary (Schmedtje et al. 2009).

Recent research suggests that climate change may enhance the probability of crossing ecological thresholds. For example, ten case studies from North America illustrate how changes in climate can lead to rapid, threshold-type responses in terrestrial, freshwater and marine ecosystems (Burkett et al. 2005). Palaeolimnological studies show that many nutrient-poor lakes throughout the Northern Hemisphere have displayed reorganization of diatom community composition, which can best be explained by higher temperature and increased length of the ice-free period (Rühland et al. 2008). Other palaeoecological studies of different ecosystems suggested that "double triggers" (different pressures occurring together) increase the risk of exceeding ecological thresholds (Willis et al. 2010). For example, in the coastline of Madagascar a threshold shift from closed littoral forest to open heathland occurred in response to the combined effects of aridity and sea-level rise, but not in response to either variable alone. Moreover, climatic changes such as increased temperature may interact with and enhance the effect of other pressures, so that a certain biological response is obtained at a lower pressure level. A well-documented example is the synergistic effects of climate change and eutrophication on the risk of cyanobacterial blooms (Paerl & Huisman 2008, Jeppesen et al. 2010b, Kosten et al. 2012). Hence, climate change might also shift an ecological threshold (move the position relative to the pressure gradient), as illustrated in Figure 2c. In spite of the many examples, analysis of effects of climate change effects on ecological thresholds is very demanding, and examples of quantification of such effects are therefore rare (e.g. Law et al. 2009, Scharfenberger et al. 2013).

Following the aim of the REFRESH project, this review focuses mainly on European lowland lakes as those most threatened by projected changes in temperature, water level and nutrient loading. We will mainly address the following climatic changes: (i) increased temperature (all of Europe), (ii) increased precipitation (mainly Northern Europe), and (iii) decreased precipitation (mainly Southern Europe). Climate change may also have more indirect effects on water quality due to human adaptation, e.g. increased land use in parts of Northern Europe (Kattwinkel et al. 2011). Nevertheless, such indirect effects will not be covered here. Although climate change is generally considered to enhance effects of eutrophication in lakes (Jeppesen et al. 2010b, Moss et al. 2011), there are various ecological mechanisms involved. Moreover, the mechanisms may vary with the geographic region and with the lake type. Here we will address effects of climate change on pressure levels (nutrients), on other environmental factors influencing the effect of these pressures, and on ecological mechanisms including food web interactions. The majority of examples will be on effects on phytoplankton, reflecting the emphasis of the relevant literature. However, effects on other BQEs will be included as far as possible; the important role of zooplankton will also be considered (Jeppesen et al. 2011b). The implications for lake management according to the WFD will be highlighted (Moe et al. 2010a, Nõges et al. 2010d, Nõges et al. 2010c).

2.5.2. Definition of thresholds and key questions

The concept of thresholds in lake management has been used in many different ways, from the strict sense in connection with regime shits (Andersen et al. 2009) to the wider sense as non-linear relationship between pressure and response (Lyche Solheim et al. 2008), as well as regulatory thresholds (Carvalho et al. 2013a). In this review we consider all these types of thresholds. Moreover, thresholds can be defined in different parts of the DPSIR (driver-pressure-state-impact-response) framework: in the driver, in the pressure, in the ecological state, etc. Here we consider the in-lake nutrient concentration as the (main) **pressure**, while any factor (climatic or other) affecting the nutrient concentrations can be considered as a **driver**. Ecological state or **impact** is considered mainly for the biological quality elements described in section 2.4, and are typically measured by different biological indicators. In this review we try to draw a clear distinction between the different types of thresholds, and categorise the different types as follows (Figure 5).

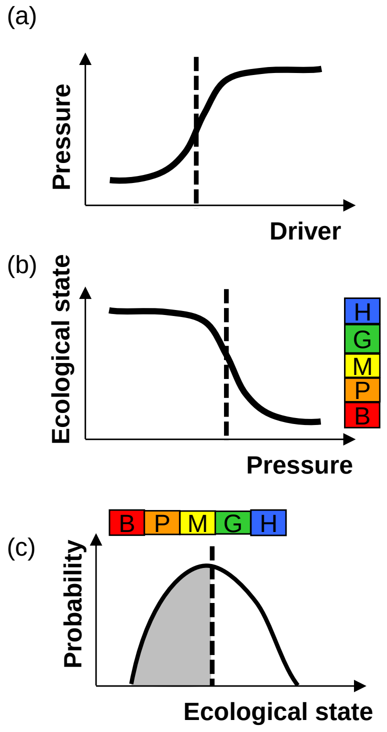


Figure 5. Main types of thresholds addressed in this paper. (**a**) "Environmental threshold": Non-linear relationship between a driver (climatic or other, e.g., precipitation) and a nutrient pressure (e.g., total P concentration). The stippled line indicates a threshold along the driver gradient. (**b**) "Ecological threshold": Non-linear relationship between the nutrient pressure and the ecological state for a given biological metric (e.g., EQR based on amount of cyanobacteria). The stippled line indicates a threshold in the pressure gradient. The column indicates the WFD ecological status classes for the metric (H=high, G=good, M=moderate, P=poor, B=bad). (**c**) "Regulatory threshold": status class boundaries in lake classification systems, e.g., the WFD Good/Moderate boundary (indicated by the stippled line). The shaded area of the probability distribution curve indicates the risk not complying with regulatory threshold.

i) <u>Threshold in driver-pressure relationship (environmental threshold)</u>: a small change in a driver results in a large effect on the pressure (Figure 5a). For example, if P loads to a lake increase, there may be a risk of crossing a threshold to sustained eutrophication with high in-lake P concentrations (Carpenter & Lathrop 2008).

ii) Threshold in pressure-state relationship (ecological threshold): a small change in the pressure results in a large effect on the biological metric (Figure 5b). For example, a small increase in P concentration may result in a high proportion of cyanobacteria (Lyche Solheim et al. 2008).

iii) Regulatory threshold: a threshold value defined by regulatory authorities, e.g. a P concentration, or a biological metric value (Figure 5c). Examples of regulatory thresholds are the WFD status class boundaries set for different biological quality elements (Poikāne 2009), or the World Health Organisation (WHO) 'low health alert' threshold for abundance cyanobacteria (1 mg L^{-1}) (Carvalho et al. 2013a).

The status class boundaries of the WFD-based lake classification systems should in principle be defined based on non-linear relationships between physico-chemical pressures and ecological responses (cf. Figure 5) (EC 2005). In these cases, a regulatory threshold such as a Good/Moderate boundary also represents natural thresholds. For example, this is the case for the G/M boundary set for proportion of cyanobacteria in northern European lakes; (Ptacnik et al. 2008). However, regulatory thresholds may also have been defined based on other criteria and will therefore not always reflect natural thresholds in pressure-response relationships. For example, some metrics display a more linear response to the pressure (e.g., the ASPT metric for response of macroinvertebrates to organic pressure), so that it is not possible to identify a natural threshold in the response. More information about the criteria used for class boundary setting for each individual lake metrics in European countries can be found in the WISER methods database (Birk et al. 2012), under section 3.11 "Boundary setting procedure" (Birk et al. 2010).

In this review we are most interested in the ecological thresholds (Figure 5b), because the ecological status is defined primarily by the biological metrics. Effects of climate change on the pressure may therefore have disproportionally large effects on the ecological state (Figure 6e-h). However, thresholds in driver-pressure relationships (Figure 6a) may also be important in this context. Even if the pressure-response relationships is nonlinear (Figure 6c), a gradual increase in a climatic driver (Figure 6a-b) that has a disproportionally large effect on the pressure (e.g. nutrients), may translate to a large effect also on the ecological state (Figure 6d) (see also Andersen et al. 2009).

This part of the literature review will address the following key questions regarding thresholds and lake management.

For "natural" thresholds (type i and ii):

- What are the environmental or ecological mechanisms resulting in the threshold?
- Are the thresholds quantified (e.g. a value/range of the pressure variable)?
- Are the thresholds currently applied in lake management, or recommended as relevant? (E.g. the response variable as biological indicator, or the thresholds as management targets)
- How are climate-related variables involved in the driver-pressure or pressure-state relationship (which mechanisms)?
- How may climate change affect the pressure level (i.e. affect the probability of exceeding such thresholds)? (cf. Figure 7a)
- How may climate change affect the ecological response level, for a given pressure level (i.e. affect the thresholds / relationships themselves)? (cf. Figure 7c)

For regulatory thresholds (type iii), furthermore, these questions are addressed:

- Is the probability of exceedance of a regulatory threshold quantified?

- How may climate change affect the probability of exceedance of regulatory thresholds (e.g. WFD class boundaries)?

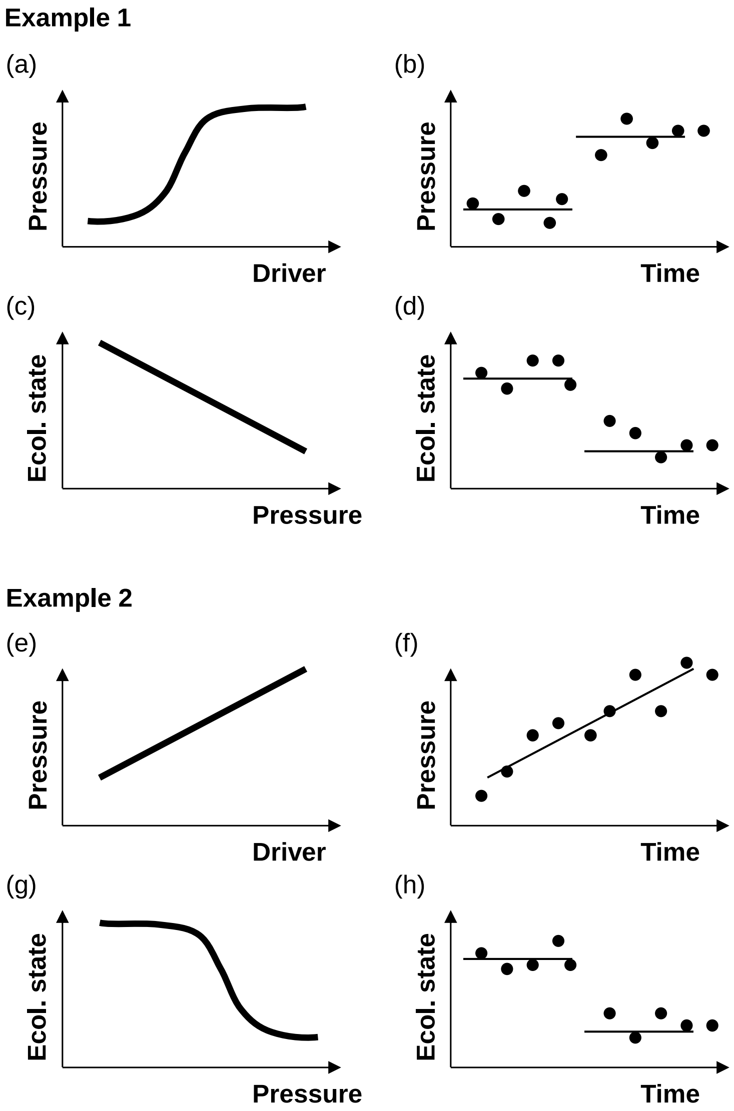


Figure 6. Schematic illustration of thresholds in driver-pressure-state relationships (left panel), and consequences for effects of climate change on pressure and ecological state (right panel). Here, the driver is assumed a variable related to climate change (e.g., more precipitation) that increases over time and that may affects the nutrient pressure of a lake.
Example 1: the driver-pressure relationship has a threshold (a), while the pressure-state relationship is linear (c). As the driver increases gradually over time, the pressure may display an abrupt change (b), and consequently the ecological state may display a similarly abrupt change (d).
Example 2: the driver-pressure relationship is linear (e), while the pressure-state relationship has a threshold (g). As the driver increases gradually over time, the pressure may display a gradual change (f), which may result in an abrupt change in the ecological state (d). Thus, an abrupt change in ecological state over time can result from thresholds both in driver-pressure relationship and in pressure-state relationships. (After Figure 1 in Andersen et al. 2009)

2.5.3. Methods for analysing thresholds

The theoretical framework for describing ecological thresholds and regime shifts in lakes is well developed (Scheffer & Jeppesen 2007). However, there have been relatively few efforts to conduct tests and quantitative inferences on the actual appearances of such phenomena in ecological data, even though a wide range of suitable statistical methods are available (reviewed by Andersen et al. 2009). For description of ecological thresholds in the wider sense (non-linear responses), a number of different methods have been applied.

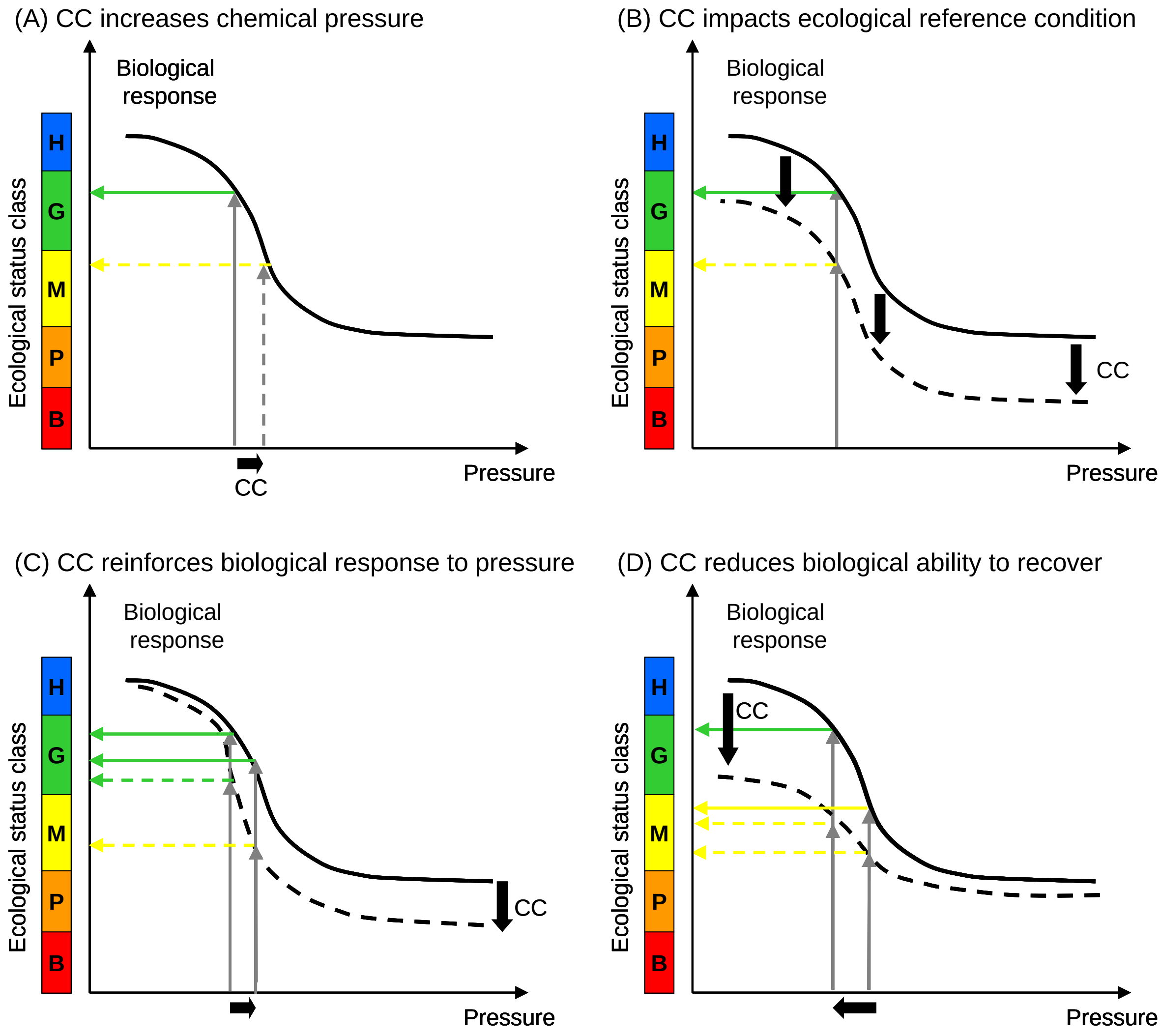


Figure 7. Potential impacts of climate change on components of ecological status classification, for a biological metric (e.g., EQR based on amount of cyanobacteria) which responds to a nutrient pressure. Ecological status classes: H = high, G = good, M = moderate, P = poor, B = bad. Solid curves: present situation; stippled curves: impact of climate change (CC). (A) CC affects the level of local pressures. (B) CC affects the reference condition of the biological element (i.e. the baseline or condition found in sites with minimal impact of other anthropogenic pressures). (C) CC affects the biological element's response to increased local pressures, including thresholds used for defining boundaries between ecological status classes. (D) CC affects the biological element's ability to recover when local pressures are decreased due to measures. (From Moe et al. 2010a).

Analysis of time series from single lakes may reveal abrupt change in an ecological metric over time (Figure 6d, h). When data series on climatic and chemical variables are available, it may also be possible to quantify an underlying nonlinear relationship in either driver-pressure relationships (Figure 6a) or pressure-response relationships (Figure 6g). A wide range of approaches have been used. Steady-state analysis of 30 years of annual P budgets was used to estimate probabilistic thresholds in the relationship between P loading and in-lake P concentrations (i.e., a driver-pressure relationship cf. Figure 6a) of Lake Mendota, USA (Carpenter & Lathrop 2008). Statistical change-point analysis (Killick & Eckley 2013) has been applied for estimating abrupt changes in climatic, chemical and/or biological time series, for example for Lake Mjøsa (Hobæk et al. 2012) (see case study in section 4.2). Another popular statistical method is regression tree analysis, which has been used to estimate thresholds in i.a. climatic and chemical variables with significant effects on ecological responses in individual lakes (e.g. Lake Müggelsee; Huber et al. 2012) (see also case study in section 4.4). Such non-parametric methods are not able to describe the threshold response as a non-linear curve (as in Figure 5a), but will identify the points along the x-axis where the most abrupt change in y-values occur. Other studies have used a combination of different statistical techniques such as breakpoint and trend analysis for both identifying thresholds, and non-linear regression analysis for quantifying the pressure-response relationships (Scharfenberger et al. 2013), and artificial neural networks in combination with regression models (Tan & Beklioglu 2006).

Since long time series are available only for a limited number of lakes, an alternative approach for quantifying thresholds is analysing data from multiple lakes (space-for-time approach). Non-linear regression methods such as GAM (generalised additive models), various GLM (generalised linear models) and quantile regression have been applied for describing non-linear responses in pressure-response relationships for large sets of lakes, e.g. for non-linear effects of eutrophication on different phytoplankton metrics (Ptacnik et al. 2008), effects of acidification on macroinvertebrate metrics (Schartau e*t* al. 2008, Moe et al. 2010b) as well as non-linear pressure-response relationships for macrophytes and fish (Moe et al. 2007, Lyche Solheim et al. 2008). Regression trees have also been applied for large-scale datasets, for estimating breakpoints in nutrient pressures, climatic variables and other explanatory variables, e.g. for effects on fish (Brucet et al. 2013a) and on phytoplankton (see section 4.1). Other methods applied to estimating ecological thresholds in large-scale datasets include clustering based on species composition similarity (Lyche 1990, Catalan et al. 2009a). Results from factorial experiments have also suggested ecological thresholds, e.g. in salinity (Jeppesen et al. 2007). However, factorial experiments with few treatment levels for each factor are not ideal for characterising threshold responses; gradient/regression approach with several treatment levels are requested for identifying thresholds in climate change experiments (Kreyling et al. 2013).

The risk of non-compliance with regulatory thresholds (Figure 5c) has also been analysed with various approaches. For individual lakes, dynamic ecological lake models such as PROTECH have been used to predict the frequency of days with non-compliance (exceedance of regulatory threshold values for cyanobacteria) under different climatic scenarios (Elliott 2012). Dynamic models that also include stochasticity (e.g., parameter uncertainty) can be used for predicting probability distributions of biological responses (cf. Figure 5c), and thereby predicting the probability (as the proportion of simulation) of exceeding a regulatory threshold within a given time period (Law et al. 2009).

Large-scale analyses of multiple lakes have also been applied for assessing the risk of non-compliance with regulatory thresholds. Non-linear regression models (GAM, GLM and quantile regression) were applied to ca. 800 European lakes, to estimate the likelihood of exceeding WHO-based regulatory thresholds for amount of cyanobacteria at different levels of nutrient pressure (Carvalho et al. 2013a). A regression model was also developed for a smaller set of lakes (ca. 500) that included climatic variables, and a parameterised version of this model was used to assess the exceedance of the same regulatory thresholds under future climate scenarios (see section 4.1).

2.6. Climate change, nutrient pressures and threshold responses in lakes

2.6.1. Nutrient pressure and threshold responses for different BQEs

Assessment of ecological status for lakes should ideally incorporate assessments for all four BQEs (phytoplankton, macrophytes, macroinvertebrates and fish), and be determined by the BQE with the lowest status (EC 2005). Non-linear responses to nutrient pressures are therefore of importance for all BQEs. However, phytoplankton and macrophytes are generally the BQEs most sensitive to nutrient pressures, while phytoplankton and fish are the most sensitive to climate change (Hering et al. 2013). Hence, these three BQEs will receive most attention in this review. The different components (diversity, abundance etc.) for each BQE are listed in section 2.4. More details about the different metrics used for each BQE by different countries can be found in the WISER method database, under section 3.01 "List of biological metrics" (Birk et al., 2010).

Non-linear relationships between nutrient pressures and ecological responses have been thoroughly analysed in former EU research projects such as REBECCA (Relationships between ecological and chemical status in surface waters) (Moe et al. 2007). An overview of ecological threshold responses to increased P in European lakes and their applicability for the WFD is given by Lyche Solheim et al. (2008). For phytoplankton, the most abrupt threshold was found along the chl-a pressure gradient in low-alkalinity lakes: the proportion of cyanobacteria increased abruptly for chl. a in the range 5-10 µg L^{-1} (Ptacnik et al. 2008), which corresponds to 12-20 µg L^{-1} P (Phillips et al. 2008). The proportion of pennate diatoms increased markedly between 2-10 µg L^{-1} chl. a, and levelled off at higher pressure levels. The threshold response of pennate diatoms in the lower end of the pressure gradient makes this metric useful as an early-warning indicator of eutrophication. The threshold responses for both cyanobacteria and diatoms were more distinct in clear-water lakes than in humic lakes (Ptacnik et al. 2008).

Several macrophyte-based metrics have been developed to indicate eutrophication, but the clearest threshold-type response is reported for the presence of isoetids (which are sensitive to eutrophication) in low-moderate alkalinity lakes. In Nordic lakes, the 75%-quantile of this metric displayed an abrupt decline for TP above ca. 20 µg L^{-1}, and the abundance became very low above 30-40 µg L^{-1} (Penning et al. 2008). Hence, the TP concentration that induces a threshold response for macrophytes is more than twice as high as the concentration inducing a threshold response for phytoplankton. Light is probably a crucial factor determining the threshold responses for both phytoplankton and macrophytes (Lyche Solheim et al. 2008).

Effects of eutrophication on macroinvertebrates are generally weaker than for the botanical elements (Lyche Solheim et al. 2008, O'Toole et al. 2008, Hering et al. 2013, Lyche-Solheim et al. 2013). For example, an analysis of Swedish lakes suggests that trophic effects on benthic invertebrates are nested within substrate habitat effects, and are masked by local habitat heterogeneity (McGoff & Sandin 2012). Therefore, although macroinvertebrates may be useful indicators for other anthropogenic pressures (e.g. hydromorphology, Miler et al. 2013), threshold responses of macroinvertebrates to nutrient pressures will not be discussed further here.

A large-scale analysis of fish diversity in more than 1200 European lakes from the WISER project revealed that fish density was primarily predicted by in-lake TP concentration, due to higher productivity of food (Brucet et al. 2013a). According to regression trees, a TP concentration around 20-25 µg L^{-1} represents a threshold for a significant increase in fish numbers and biomass. Enhanced TP concentration also contributed significantly to an increase in fish species richness and diversity, after geographical, climatic and morphometric factors were accounted for. Hence, eutrophication in this range (mean 40, st.dev. 129) does not seem to represent an environmental pressure for fish metrics. However, individual body size of fish decreased with higher TP concentration, especially in high-altitude lakes which are naturally more oligotrophic; such changes can have important consequences for the food web and the response of other BQEs to eutrophication (see next section).

Although TP is generally the most important limiting nutrient, changes in TN concentrations can have important ecosystem effects when TP is not limiting (Jeppesen et al. 2011a). For submerged macrophytes in Danish lakes, a critical TN threshold around 1-2 mg N L^{-1} has been suggested as a maximum to maintain a stable high species richness, when TP concentrations are moderately high (Jeppesen et al. 2011a). The role of N for dominance of cyanobacteria seems to be more variable in different ecosystems, and threshold values in TN concentration have not been suggested for phytoplankton.

2.6.2. Multiple stressors

The Eurolimpacs, WISER and REFRESH projects, among other studies, illustrate the complexity of ecosystem response to synchronous changes in different drivers, and the difficulty of disentangling the effects of multiple, interacting pressures. This is a particular problem for enriched lakes where climate change itself promotes symptoms of eutrophication both directly through extending the growing season and indirectly through its effect on nutrient cycling and on food-web structure (cf. Moss et al. 2011). High nutrient concentrations and increased algal growth can be caused by either or both pressures. From a management perspective, climate warming thereby will tend to counter measures taken to restore lakes from the effects of eutrophication. Battarbee et al. (2012) point out that an added complication in detecting climate driven change is the different ways in which climate change is expressed, for example through changes in temperature or precipitation, through changes in seasonality or through changes in the magnitude and frequency of extreme events. Furthermore one has to account for inherent natural variability in the climate system on different timescales such as the North Atlantic Oscillation (NAO) (e.g. Gerten & Adrian 2000, Dokulil et al. 2006). Nonetheless, policy makers and managers need to know whether climate change is exacerbating existing pressures or creating additional problems. This is a key factor in determining how management strategies can be adapted to accommodate climate change, in particular the reference condition concept. Multiple stressors acting on freshwater systems are also likely to mean that good ecological status is even more difficult to achieve.

In their review of lake management options in a changing climate, Malve et al. (2012) conclude that “although there is a need to embrace the concept of the dynamic reference condition, this should not be seen as a 'get out clause' or a means of seeking exemption from WFD compliance”. They believe that climate change should be considered an anthropogenic stress within the context of the WFD even if it is not possible to mitigate some of the direct effects. In this way, where climate change results in increasing pressure from existing stresses, more action can be taken to reduce the impact of the latter. For example, in the case of nutrient enrichment where increasing temperatures are likely to exacerbate the symptoms of eutrophication through their impact on algal productivity, water column oxygen concentrations, nutrient re-cycling and increased planktivory, the response should be to further reduce catchment nutrient loading rather than revise the reference value. They state that where the direct effects of temperature dominate it will be important to minimise the impacts of other stresses to increase system resilience. They believe that only when climate change causes ecological thresholds to be crossed, recovery trajectories to deflect away from the reference condition or novel ecosystems to be created following species migration should achievable targets be reviewed and the reference value be revised accordingly. Likewise, Bennion et al. (2011) argue that for enriched waters subject to climate change measures needed to meet the good status target need to be intensified but they also recognise that the WFD classification system may ultimately need revision (Figure 1).

2.6.3. Effects of nutrient pressures under increased temperature

Increased water temperature is expected for all of Europe, but the environmental effects in lakes may be very different in different regions and in different lake types (see Table 5 in Kernan et al. 2010). Direct ecological effects of increased water temperature may be most conspicuous in shallow lakes. The effect of increased temperature on the dominance of cyanobacteria in phosphorus-rich lakes is well documented (Paerl & Huisman 2009, Elliott 2012, Merel et al. 2013) (see also section 2.4.1). Cyanobacteria generally grow better at higher temperatures than do other phytoplankton species such as diatoms and green algae. This gives cyanobacteria a competitive advantage at elevated temperatures (Paerl & Huisman 2008). Cyanobacterial blooms may even locally increase water temperatures through the intense absorption of light, creating a positive feedback mechanisms that provides additional competitive dominance of cyanobacteria over other phytoplankton (Paerl & Huisman 2008).

Within the WISER project a range of models were employed to explore the effects of climate change on phytoplankton (Malve et al. 2012). The eutrophication of European lakes was studied using a linear mixed effects chl-a model which was fitted to 461 European lakes. The results indicate that in warmer climatic conditions, a bigger reduction of nutrients is needed to achieve good ecological condition in a lake. In a case study of Lake Pyhäjärvi (Finland) warmer temperatures were predicted to increase algal blooms via intensifying internal load and phytoplankton production. The models showed that the adverse effect could be best compensated by reduction of external nutrient load and fisheries management. A multiple regression analysis of late summer data from 800 Danish lakes by Jeppesen et al. (2013a) indicates that warming will lead to increased chl-a and phytoplankton biomass, higher dominance of dinophytes and cyanobacteria, most notably of nitrogen-fixing forms, but lower abundance of diatoms and chrysophytes.

The combined effects of increased water temperature (up to +4 °C) and nutrients on the risk of cyanobacteria blooms in the eutrophic lake Esthwaite Water (UK), were assessed with the phytoplankton lake community model PROTECH (Elliott 2010). The model scenarios also included reduced (down to 50%) flushing rate, because decreased river flow in summer is predicted for this region of the UK. The model was used to predict the probability of exceeding a WHO-based regulatory threshold for cyanobacteria abundance: 10 and 50 µg L^{-1} cyanobacteria chlorophyll (low and moderate risk, respectively; corresponding to approximately 1 and 5 mg L^{-1} biomass). While diatoms (*Asterionella*) showed little response to the changing drivers, cyanobacteria (*Anabaena* and *Apahnizomenon*) showed enhanced abundance and community dominance under the future climate scenarios, as well as increased number of days exceeding the WHO-based threshold, although the pattern could be quite variable. Recently, Elliott (2012) reviewed the modelling literature for studies that examined the impact of climate change upon cyanobacteria. In general, and in agreement with the papers cited above, all studies predicted an increase in relative cyanobacteria abundance with increasing water temperature, decreased flushing rate (see also section 2.6.5) and increased nutrient loads. However, the results indicated that warmer temperatures will affect the timing and cyanobacteria dominance, but not the annual phytoplankton biomass.

Another consequence of higher temperature is increased vertical stratification and thermal stability, which reduces the vertical mixing, especially in deep lakes. Global warming causes lakes to stratify earlier in spring and/or destratify later in autumn (Straile et al. 2003, Law et al. 2009, Hobæk et al. 2012) which lengthens optimal growth periods for cyanobacteria. Many cyanobacteria can form intracellular gas vesicles that make the cells buoyant, and thereby exploit these stratified conditions better than other phytoplankton (Paerl & Huisman 2009).

Physical and chemical thresholds for cyanobacteria performance were analysed for Lake Müggelsee, a polymictic eutrophic lake in Germany (Wagner & Adrian 2009a) (see also case study in section 4.4). To identify key physical and nutrient thresholds favouring cyanobacterial performance during periods of summer thermal stratification, classification tree analysis was applied to a range of climate-related and chemical variables as well as zooplankton abundance. Although total P concentration was the principal force driving the proportion of cyanobacteria, climate-induced changes in the thermal regime, rather than direct temperature effects, positively influenced cyanobacteria dominance. In this lake, within a critical TP concentration range (70–215 µg L^{-1}), stratification periods exceeding 3 weeks and exhibiting a Schmidt stability of >44 g cm cm^{-2} additionally favoured cyanobacteria proliferation. Furthermore, a predictive model incorporating these thresholds was able to successfully predict cyanobacterial blooms in two recent years with heat waves (2003 and 2006). Given the observed broad range of TP thresholds within which climate warming enhances the probability of cyanobacteria dominance, the authors conclude that the incidence of cyanobacteria blooms will increase in many lakes under future climate scenarios.

Fish communities are particularly susceptible to increased water temperature in combination with phosphorus pressure. As described in section 2.4.2, certain species such as salmonids are particularly sensitive to elevated temperature and subsequent reduced O_2 concentrations (Jeppesen et al. 2012c). However, the interactive effects of increased temperature and nutrient pressures operate on fish communities through complex ecological mechanisms with cascading top-down effects (Jeppesen et al. 2010a). Higher temperature induces changes in the fish community structure from larger salmonids and perch towards smaller species such as cyprinids, which in itself can be an indicator of lower ecological status (the ratio of salmonids and perch to cyprinids). Moreover, this change in the fish community composition increases the predation pressure on zooplankton, which in turn releases the grazing pressure on phytoplankton. Hence, the effect of warmer water on fish community structure further stimulates the growth of phytoplankton in nutrient-rich lakes.

Although P is generally considered the most important limiting nutrient, the role of N should also be considered, especially in connection with climate change. It is not clear whether N concentrations in lakes will increase as a consequence climate change (Jeppesen et al. 2011a). However, higher water temperature can make ecosystems more sensitive to increased N input, for similar reasons as described for P above (change in fish community structure and trophic cascade). Moreover, change from a clear eutrophic state with macrophyte dominance to a turbid phytoplankton-dominated state with high abundance of cyprinid fish reduces the capacity of lakes to function as an N filter (Jeppesen et al. 2011a).

Even though warmer water generally promotes phytoplankton growth, contrasting findings are also reported from shallow lakes. At non-limiting nutrient conditions, warmer water may also promote growth of filamentous green algae, which suppress phytoplankton growth and may promote clearer water (Trochine et al. 2011). The study of Huber et al. (2008), involving application of a simple dynamic model to Müggelsee, a shallow lake in Germany, emphasises that trophic state must be considered when determining the mechanisms underlying the effect of warming on phytoplankton bloom formation. Their data show that the diatom bloom was more intense and earlier under conditions of reduced ice cover and increasing water temperatures independent of phosphorus concentrations. However, when P was high the spring bloom collapse was caused by the bottom-up effect of silicate limitation,whereas when P was low it was caused by the top-down effect of *Daphnia* grazing.

The general implications of the above studies, together with the findings reported in section 2.4.1, are that in a future warmer climate, nutrient concentrations may have to be reduced substantially from present values in many lakes if cyanobacterial dominance is to be controlled.

2.6.4. Effects of nutrient pressures under increased precipitation

Increased precipitation is forecasted for most of Northern Europe, especially winter precipitation (EEA 2010). With increased water flow in streams and rivers, higher run-off of P and higher loading to lakes is expected (Jeppesen et al. 2009). Higher run-off and loading of N may also be expected, although predicted increase in lake N concentrations are more uncertain and depend on i.a. the climate scenario model (Kaste et al. 2006, Jeppesen et al. 2011a). Thus, increased precipitation in the future is likely to increase the nutrient pressure in many European lakes (Jeppesen et al. 2010a), and may even result in lower ecological status for lakes where biological indicators are close to a threshold (cf. Figure 7a). However, the effect of increased river discharge on the in-lake P concentration and consequently the chl-a biomass may depend on the nutrient source, as demonstrated by simulations with the lake model PROTECH (Elliott et al. 2009). If P was from a point source (and largely independent of the total river discharge), then increased discharge (lower retention time) resulted in lower summer chl-a biomass, due to loss of algae by higher flushing rate. In contrast, if P was from diffuse sources and thus proportional to the river discharge, higher discharge implied higher summer chl-a biomass.

In the shallow Lake Võrtsjärv (Estonia), extremely high precipitation has apparently induced a lasting regime shift in the phytoplankton community (Nõges et al. 2010a) (see also case study in section 4.5). The extreme rainfall in summer and autumn of 1978, after long dry periods in the 1960-70s, increased the water level of the following year by more than 1 m. The increased water level impaired light conditions, which gave certain cyanobacteria (*Limnothrix*) a competitive advantage. These species were able to build very dense populations, which increased turbidity and further deteriorated the light conditions for other species. This positive feedback mechanism contributed to the regime shift and stabilised the new status, with dominance of species that were both shade-tolerant and shade-inducing. This positive feedback also made the lake more resistant to restoration effort, and the authors state that reduction much below the current levels of around 50 µg L^{-1} is needed in Lake Võrtsjärv to induce a decline in cyanobacteria abundance (Nõges et al. 2010a).

More precipitation will have other consequences for the chemistry of lakes, such as "brownification" - increased organic content (TOC - total organic carbon and DOC - dissolved organic carbon). For example, TOC concentrations in boreal lakes in Norway are predicted to increase by >50% in the long term (Larsen et al. 2011), based on data analysis and space-for-time modelling of ca. 1000 lakes covering a wide climatic range. The climatic driver was increased precipitation in combination with increased temperature (although the effect of precipitation depended on the temperature). Likewise, Hansson et al. (2012) showed that DOC has notably increased during the past 25 years in three Swedish lakes; oligotrophic Lake Fiolen, humic Lake Stengårdshultasjön, and eutrophic Lake Ringsjön. Moreover, a study from ca. 1000 boreal lakes in Sweden indicates that DOC concentrations will increase non-linearly (accelerating) with increased temperature (Weyhenmeyer & Karlsson 2009). The co-occurrence of increased temperature and water colour in North temperate lakes has interactive effects on aquatic communities (Ekvall & Hansson 2012) and important implications for the quality of waters. For example, as described in section 2.4.1, browner water seems to favour the nuisance alga *Gonyostomum semen* (Trigal et al. 2013).

Important ecosystem processes may be affected by higher in-lake dissolved organic concentrations and higher humic content. Increased organic carbon load can result in a higher proportion of bacterial production compared to autotrophic algal production, likely leading to a limited availability of fatty acids essential for zooplankton and fish (Jeppesen et al. 2012c). Succession towards higher bacterial production, together with light limitation, may result in lower overall production available to the higher trophic levels in certain lakes (Jeppesen et al. 2012c). Again, this indirect effect of climate change on fish top predators implies reduced control on phytoplankton, and enhanced effects of eutrophication.

The predicted increase in TOC also has consequences for ecosystem services such as drinking water quality. Applying a 5 mg TOC L^{-1} threshold for suitability for drinking water production, 18% of the surveyed Norwegian lakes are currently above this threshold, while this fraction will almost double to 32% under the predicted changes (Larsen et al. 2011) (cf. Figure 5c).

The additional pressure of TOC implies that it may be more difficult to achieve the management target of good status for many lakes, since humic lakes naturally have higher chl-a concentrations than clear lakes. However, the increase in TOC may eventually shift the lake type from clear to humic (see section 2.3.3). The good/moderate boundary will then become higher (less strict) and more appropriate for combined nutrient and climatic pressures of these lakes.

2.6.5. Effects of nutrient pressures under reduced precipitation

Reduced precipitation and more drought is forecasted for most of Southern Europe (EEA 2010), and in consequence the water level of shallow lakes may be reduced. Increased temperature will also lead to increased evaporation from lakes, which can reinforce the negative effects on water level (Beklioğlu et al. 2007, Beklioğlu et al. 2011). Moreover, higher temperatures and evaporation will result in a higher demand for freshwater, for instance to irrigation in the Mediterranean zone. While extensive knowledge exists on the relationship between nutrient loading and nutrient concentrations in lakes in the cold temperate region, fewer studies have been conducted in warm arid lakes. This is unfortunate as a larger proportion of the world's lakes will be situated in arid climates in the future due to climate change, and a larger proportion will suffer from a higher frequency of intensive drought (Özen et al. 2010).

Two shallow Mediterranean lakes in Turkey were analysed by a comprehensive >10 year mass-balance study, covering a period with substantial changes in climate conditions (Özen et al. 2010). Dry, warm years reduced the water level by reduced inflow and by evaporation. In dry years, TP and inorganic N increased despite reduced external loading, in contrast to experience from northern temperate lakes. In-lake TP became more dependent on internal processes (evaporation, internal loading) than on external loading. Moreover, also in contrast to cold temperate lakes, extensive growth of submerged macrophytes did not result in lower inorganic N concentrations. As in north temperate lakes, fish removal enhanced the N retention, but the effect was not long-lasting. Lower thresholds of nutrient loading for shifting turbid shallow lakes to a clear water state are therefore to be expected in arid zones in a future warmer climate (cf. Figure 7a), with important management implications.

Strong fluctuations in water level can be disadvantageous to many submerged plant species through either reduced light availability or drying out of shallow sites, which may exceed the physiological limits of many submerged plant species (Beklioğlu et al. 2011, Jeppesen et al. 2012a) (see also section 2.4.3). In another study from Turkey, an artificial neural network model was used to assess the probability of submerged plant occurrence in five shallow Anatolian lakes (Tan & Beklioglu 2006), and the shift in state from clear, macrophyte-dominated to turbid phytoplankton-dominated water state. The model predicted a relatively strong negative impact of the water level fluctuation (both z-score and amplitude), although the strongest predictor was the proportion of carp (to total fish biomass). The thresholds for inducing those shifts between ecological states were identified mainly in the hydrological variables. The thresholds in water level amplitude for the breakpoints of the system were estimated to be 3 m. Notably, a similar threshold of 3-4 m was found for effects of hydromorphological alterations (winter drawdown level) on the presence of senstitive macrophytes (*Isoetes lacustris*) in Nordic lakes, depending on the Secchi depth (Mjelde et al. 2013). For these lakes, accordingly, a threshold of 3.4-3.5 was proposed as the Good/Moderate boundary.

Another consequence of reduced precipitation and higher evaporation is increased salinity of lakes in arid areas (Jeppesen et al. 2007, Meerhoff et al. 2012). Sea level rise may also contribute to increased salinity in coastal lakes (Schallenberg et al. 2003). Salinity might play an important role for the ecological state of lakes by affecting the zooplankton community structure (Schallenberg et al. 2003, Brucet et al. 2010). Increases in salinity may change the species composition toward smaller, more salt-tolerant zooplankton species (Brucet et al. 2010). The decrease in the density of large-bodied zooplankton might reduce the grazing on phytoplankton, and might thus reduce the chances of maintaining the clear water state in these ecosystems (Brucet et al. 2010). In slightly brackish lakes (lagoons), the indirect effects of temperature changes on aquatic communities, such as changes in salinity and hydrology, could be more important than the direct effects of warming (Brucet et al. 2009). The shift in trophic structure occurring at increasing salinity will lead to a higher risk of a shift from a clear to a turbid state of brackish lagoons. Lower critical loadings of nutrients for a shift from a clear to a turbid state can therefore be expected in the Mediterranean zone in a future warmer climate (Brucet et al. 2010) (cf. Figure 7c).

In shallow brackish lagoons, increased salinity can even induce an ecological regime shift from clear to turbid water at high nutrient concentrations (Jeppesen et al. 2007). A factorial designed enclosure experiment revealed that at both low and high nutrient loading, a salinity threshold of 6-8 ‰ induced a shift in zooplankton dominance from *Daphnia* to smaller-bodied calanoid copepods and rotifers, which is the likely reason for the regime shift. The authors conclude that (i) improved water quality can be obtained by reducing the nutrient loading or enhancing the freshwater input to a level triggering a shift to *Daphnia* dominance (typically <2 ‰), (2) fish manipulation is probably not a useful tool for brackish lagoons, unless the salinity is below the threshold for a potential shift to a clear *Daphnia*-dominated state, and (3) more abrupt changes will expectedly occur in low-saline coastal lagoons at increasing salinity during summer in a future warmer climate.

Although the strongest effects of reduced precipitation are expected in Southern Europe, rediced river flow in summer (but increased flow in winter) is predicted also for regions in Northern Europe, such as North-West England (Jones et al. 2011). Application of the model PROTECH to Bassenthwaite Lake under such climate scenarios with reduced summer flow and with flow-independent (point-source) nutrient loading, predicted that that phytoplankton abundance in summer could increase by up to 70%, including an increased proportion of cyanobacteria. Conversely, when the nutrient loading is flow-independent (diffuse), the chl-a biomass may be expected to fall with reduced summer river flow (see also section 2.6.4), but also depending on the lake's retention time. The effects of reduced precipiation on lake nutrient concentrations and ecological state thus will depend on many factors, including nutrient source and lake morphology.

2.7. Summary and conclusions from the literature review

This review has shown that measuring reference conditions and pressure-state relationships is likely to become more difficult as climate change increasingly affects the structure and functioning of ecosystems. The scientific literature suggests that phytoplankton, fish, invertebrate and macrophyte communities will change in response to climate change. The review highlights the fact that in addition to direct effects on lake temperature and water levels, climate change will exacerbate other anthropogenic pressures such as eutrophication. Changes to the physical structure, food web structure, biogeochemical processes and land water interactions of lakes arising from climate change are likely to prevent re-establishment of communities found over the past centuries. In this context, water managers may be faced with water quality targets that are impossible to achieve (Malve et al. 2012). Indeed, metrics based on indicator groups and species are likely to become redundant and ecosystem structure and process-based metrics are likely to become more relevant (Hering et al. 2010a). It may be possible to include climate change effects by assessing the impact of climate change on existing WFD metrics and then adjusting the existing assessment systems accordingly. Hering et al. (2010a) propose that one approach would be to add ‘climate specific components’ to assessment systems (i.e. metrics which account for the temperature sensitivity of species). Moreover, changes in hydromorphology, physico-chemistry and biological communities may lead to a redefinition of WFD lake types and thus the adjustment may be even more challenging. There is a strong argument, therefore, for considering climate change within the policy framework and for including it as one of the ‘significant pressures’ in the next stages of WFD implementation (Quevauviller et al. 2012).

Effects of climate change on threshold responses are more complex to study. Large data sets are required to quantify the pressure-response curves (even without climate effects), which are often associated with high natural variability and other sources of uncertainty. Hence, many of the studies reviewed here have demonstrated combined and often synergistic effects of nutrient pressure and climate change, although they have not specified a non-linear response or quantified the climatic effect. Nevertheless, from several of the papers it can be concluded that abrupt ecological changes (such as cyanobacterial blooms or disappearance of sensitive macrophytes) are more likely to occur at lower nutrient pressures due to climate change. Moreover, other studies indicate that regulatory thresholds (notably the good/moderate boundary) will more often be exceeded in the future climate (see also new analyses in section 4.1). These results imply that it will be more difficult to comply with current management targets in the future, and that a revision of class boundaries may be justified. However, as long as the intercalibrated classification systems are legally binding, further reduction of nutrient pressures to account for climate change seems to be the only option.

There is still much uncertainty about how climate change will alter reference conditions, nutrient pressures and pressure-state relationships, and there is clearly a need to better understand the extent and causes of variability and change at both reference sites and impacted sites, especially those most vulnerable to climate change. In a review of how climate might affect or confound the use of reference values in ecological assessment, the Eurolimpacs project concluded that the reference condition is not static or oscillating around long-term means, but showing monotonic climate-driven trends (Johnson et al. 2010). Hence, approaches that explicitly include inter-annual variability in weather and/or long-term trends in climate should be given greater consideration. They argue that further research is needed to disentangle the effects of short-term climatic events, such as the influence of interannual NAO oscillations, from long-term climate-driven trends. The concept of a shifting reference condition needs, therefore, to be underpinned by periodic monitoring of reference sites, allowing adjustments of reference values to be proposed which account for long-term natural processes. Moreover, frequent monitoring of impacted sites increases the probability of detecting potential effects of climate change on ecological thresholds (e.g. in pressure-state relationships) as well as on exceedance of regulatory thresholds. The WFD requires reviews of river basin characterization every six years and thus could incorporate a re-evaluation of reference values and class boundaries depending on changes observed at both pristine/true reference sites and impacted sites.

3. New analyses of climate and reference conditions

3.1. Trajectories of ecosystem change in response to multiple stressors as revealed through diatom records with a focus on nutrients and climate

Contributor: UCL (Helen Bennion, Gavin Simpson, John Anderson)

3.1.1. Introduction

The aim of this study is to employ the sediment record to assess the degree of compositional change in the diatom community of European lakes over approximately the last 100-200 years in relation to nutrients and climate.

3.1.2. Materials and methods

Methods. Existing diatom data from 37 dated sediment cores from 36 European lowland lakes (cores were taken from two separate basins in Loch Awe) were collated (Table 1). Key criteria for site selection were i) well dated (good ^{210}Pb record), ii) minimum of 12 samples for the post-1900 period, iii) samples not dominated by benthic *Fragilaria* spp as these taxa tend to swamp any signal in the data, iv) situated in lowland catchments where nutrient loading is the key pressure, and v) located in North-west Europe.

The degree of diatom compositional change over approximately the last 100-200 years was calculated for each core using Principal curves analysis (PCu). This is an alternative to indirect ordination methods and is particularly suitable for data sets with a single dominant gradient, which may induce an arch or horseshoe artefact in these other ordination methods. PCu tends to explain more variation than Principal Components Analysis and Correspondance Analysis for core data (Hastie & Stuetzle 1989, De'ath 1999). GAMM smoothers were fitted to the data for each core to extract the main patterns. Subsequently, groups of sites exhibiting similar trends were identified and a fitted smooth was plotted for each group. The group smoothers were then plotted against i) records of European air temperature for 1850-2007 expressed as annual temperature anomalies relative to 1901-1950 (source www.climatedata.info), and ii) phosphorus (P) and nitrogen (N) fertiliser usage in Europe from 1928-2011 expressed in ‘000 tonnes (source EFMA) to assess how timing of the changes in the diatom records relates to shifts in these climate and nutrient variables.

Table 1. Site details of the 36 study lakes

Site name	Core code	Latitude	Longitude	Altitude (m)	Lake area (km^2)	Max depth (m)	Current mean TP ($\mu g\ L^{-1}$)	Country / region	Reference to data
Loch Arkaig	ARKA1	56.970	-5.154	43	15.97	100.0	4	Scotland	(Clarke et al. 2007)
Etang d'Aureilhan	AURE1	44.220	-1.210	10	2.6	4.5	60	France	(Neunlist & Laczko 1999)
Loch Awe	AWE1 /AWE2	56.308	-5.226	36	38	94.0	4	Scotland	(Bennion et al. 2004b)
Lac d'Aydat	AYDA1	45.660	2.980	825	0.6	15.0	32	France	(Neunlist & Laczko 1999)
Lake Bala	BALA1	52.888	-3.623	158	4.15	40.0	13	Wales	(Bennion et al. 2003)
Bassenthwaite Lake	BASS1	54.653	-3.216	69	5.28	21.0	25	England	(Bennion et al. 2000b)
Lake Bled	BLED3	46.360	14.100	475	1.5	32.0	20	Slovenia	(Neunlist & Laczko 1999)
Bosherston Lily Pond Central	BOSHC1	51.617	-4.923	2	0.34	2.0	20	Wales	(Davidson et al. 2002)
Butterstone Loch	BUTT3	56.587	-3.534	96	0.43	7.5	25	Scotland	(Bennion et al. 2004b)
Carlingwark Loch	CARL12	54.931	-3.932	45	0.4	5.5	149	Scotland	(Bennion et al. 2004b)
Castle Loch	CASL1	56.271	-3.227	43	0.75	5.5	120	Scotland	(Bennion et al. 2004b)
Loch Davan	DAVA2	57.094	-2.923	165	0.42	2.7	27	Scotland	(Bennion et al. 2004b)
Loch Doon	DOON1	55.259	-4.368	210	8.2	40.0	4	Scotland	(Bennion et al. 2004b)
Loch Earn	EARN1	56.387	-4.203	100	9.5	88.0	11	Scotland	(Bennion et al. 2004b)
Esthwaite Water	ESTH1	54.359	-2.986	65	1	15.5	28	England	(Bennion et al. 2000b)
Lac de Gerardmer	GER3	48.060	6.990	660	1.2	37.0	12	France	(Neunlist & Laczko 1999)
Gjersjøen	GJER1	59.780	10.780	40	2.4	64.0	15	Norway	(Neunlist & Laczko 1999)
Kalandsvatnet	KALA1	60.270	5.420	53	3.3	110.0	13	Norway	(Neunlist & Laczko 1999)
Loch Leven	LEVE11	56.198	-3.376	106	13.7	25.5	53	Scotland	(Bennion et al. 2004b)
Loch Langavat	LGVT1	57.798	-6.974	44	1.4	20.0	9	Scotland	(Bennion et al. 2004a)
Lindores Loch	LIND1	56.334	-3.187	68	0.405	3.5	93	Scotland	(Bennion et al. 2009)
Llangorse Lake	LLAN3	51.930	-3.263	156	1.4	9.0	118	Wales	(Bennion & Appleby 1999)
Loch Lomond North	LOMO3	56.115	-4.622	8	71	190.0	6	Scotland	(Bennion et al. 2004b)
Loch of the Lowes	LOWE2	56.577	-3.549	99	0.88	12.5	25	Scotland	(Bennion et al. 2004b)
Loweswater	LOWS1	54.590	-3.350	121	0.64	16.0	16	England	(Bennion et al. 2000a)
Loch Lubnaig	LUBN1	56.288	-4.288	130	2.3	42.0	8	Scotland	(Bennion et al. 2004b)
Marsworth Reservoir	MARS91	51.814	-0.667	115	0.1	4.0	476	England	(Bennion 1994)
Lake of Menteith	MENT2	56.174	-4.292	20	2.5	23.0	19	Scotland	(Bennion et al. 2004b)
Mill Loch	MILL1	55.135	-3.449	55	0.11	16.8	92	Scotland	(Bennion et al. 2004b)
Lake Mjøsa	MjøsaB	60.765	11.0317	123	362	453.0	4	Norway	(Hobæk et al. 2012)
Loch Monzievaird	MONZ1	56.388	-3.880	64	0.2	10.0	37	Scotland	(Bennion et al. 2008)
Planina pri Jezeru	PLAN3	46.311	13.832	1420	0.0	10.0	60	Slovenia	(Neunlist & Laczko 1999)
Betton Pool	SCM27B	52.666	-2.725	85	0.1	11.0	87	England	(Brooks et al. 2001)
Slapton Ley	SLT4	50.277	-3.652	3	0.7	3.0	55	England	(Bennion 1998)
Loch Ussie	USSI1	57.579	-4.502	125	0.8	12.0	19	Scotland	(Bennion et al. 2004b)
White Loch	WHIE1	56.570	-3.353	48	0.0	11.0	28	Scotland	(Bennion et al. 2008)

Study sites. The 37 cores that meet the criteria given above are from lakes within the temperate climatic zone, located in six countries across North-west Europe, spanning a broad latitudinal gradient from Mjøsa in Southern Norway to Etang d'Aureilhan in Southern France (Table 1). They represent a range of lake types including 18 shallow lakes (max depth <15 m) and 18 deep lakes (max depth >15 m) and vary greatly in size from very small waterbodies of <0.1 km^2 to some of Europe's largest lakes with a surface area of >300 km^2. They lie in lowland catchments with altitudes generally < 200m with the exception of Lake Bled, Lac de

Gerardmer, Lac d'Aydat and Planina pri Jezeru which lie in the foothills of mountainous regions. The lakes cover a wide nutrient gradient with current total P (TP) ranging from oligotrophic concentrations of 4 µg L^{-1} to hypertrophic levels of >100 µg L^{-1}.

The dataset includes mostly impacted sites as the data are from national environmental agency and European Union projects that were explicitly addressing effects of cultural eutrophication (e.g. Bennion et al. 2004b, Bennion & Simpson 2011) and as a result are not a random selection of lakes in North-west Europe. The catchments are largely productive with nutrient loading from either point sources such as sewage treatment works and/or diffuse sources from agriculture. Several lakes have also experienced catchment erosion as a result of forestry activity (planting and felling). It should also be noted that some of the cores used in the analyses were collected approximately 20 years ago and, therefore, do not cover the post-1990 period during which air temperatures have seen the largest increase.

3.1.3. Preliminary results and discussion

The distance along the principal curve for the 37 cores plotted against age (years AD) is shown in Figure 8. Each site has experienced its own timing, rate and degree of diatom compositional change yet there are some overarching and common patterns. These patterns can be more clearly seen when the GAMM smoothers are fitted to the data for each core (Figure 9) and four groups of lakes can be defined, as follows, and as illustrated in Figure 10:

i) Change occurs at ~1900 AD: 9 cores ARKA, AYDA, BASS, BUTT, DAVA, DOON, ESTH, LOWE, MENT,
ii) Change occurs at ~1950 or later: 12 cores AURE, AWE1, AWE2, BETT, BOSHC, CARL, EARN, GER, LGVT, LIND, LLAN, WHIE,
iii) Change throughout: 10 cores BALA, CASL, KALA, LEVE, LOMO, LOWS, MILL, MONZ, SLT, USSI,
iv) Some evidence of reversal/recovery: 4 cores BLED, GJER, MJOESA, P91MAR.

The diatoms in LUBN experienced no change over the last 100 years and there was no clear directional pattern in PLAN hence these cores were not placed in any of the four groups.

In summary, diatom changes were observed in all cores, except LUBN, over the last 50-100 years. At most sites the diatom assemblages were relatively stable prior to this time, suggesting that the pre-1900 samples can be used to define reference conditions for these lakes. A similar conclusion was reached in a meta-analysis of a larger dataset of lake sediment cores by Battarbee et al. (2011a), which showed that there were few cases of acidification and eutrophication in European lakes prior to ~1850. The diatom shifts observed in our dataset are indicative of eutrophication and the timing seems to match with the European fertiliser records (Figure 11) whereby the most marked changes occur at the time when European fertiliser consumption escalated. It is difficult to see an association between the diatom shifts and changes in European annual air temperature (Figure 12). Indeed, four sites have experienced a degree of recovery over the last few decades during the period that has seen the most marked rise in air temperatures of 1-2 °C. Hence, nutrient loading reductions have resulted in lake recovery in spite of warming temperatures.

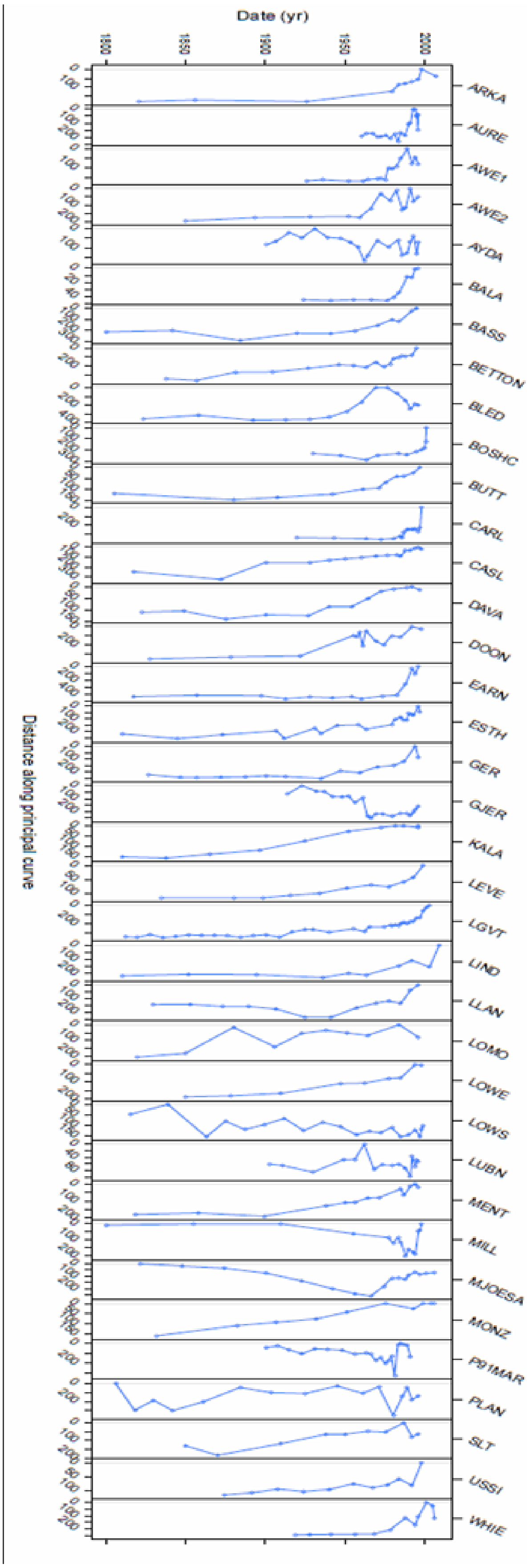


Figure 8. Distance along principal curve for 37 cores plotted against age (years AD).

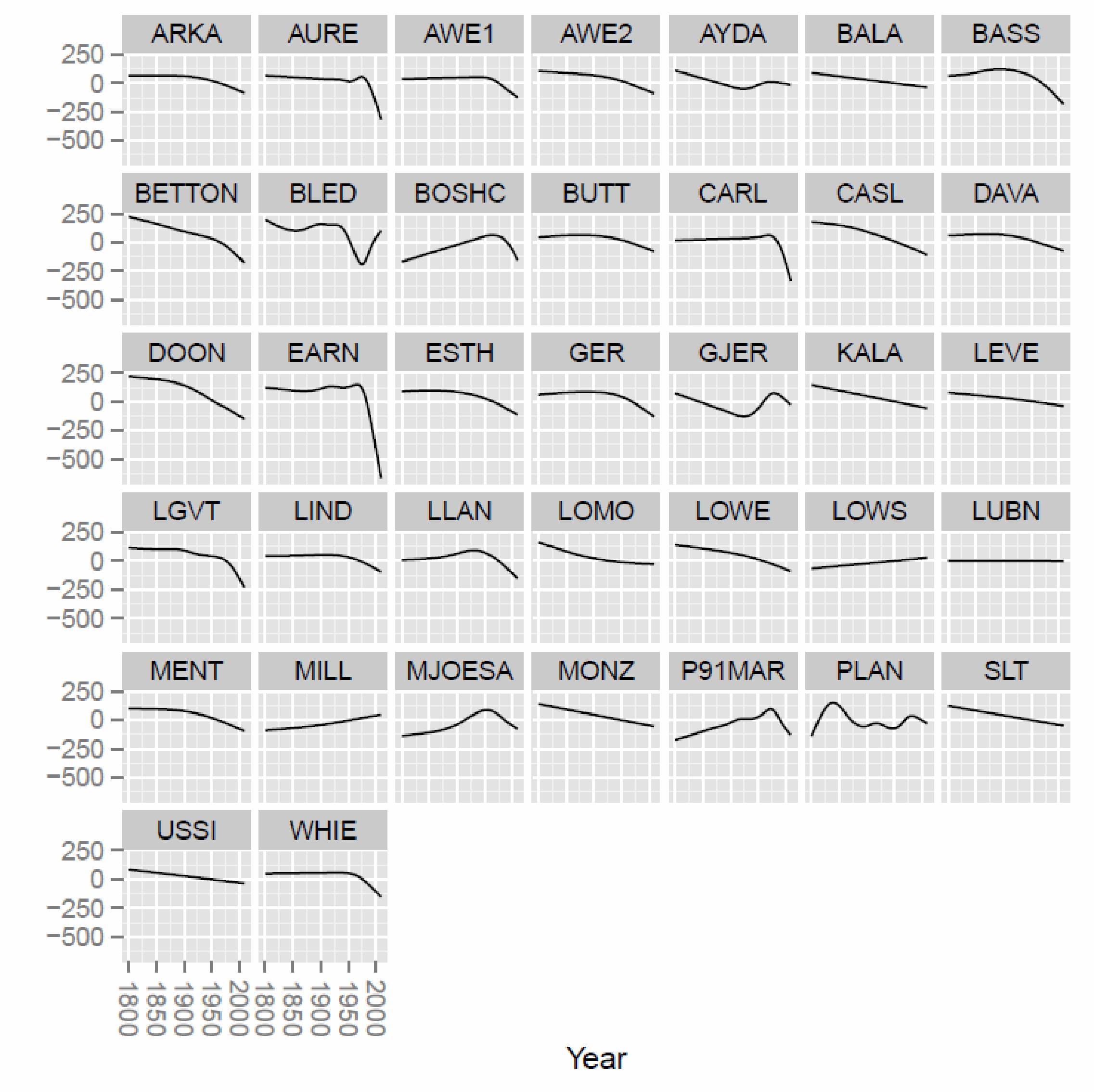


Figure 9. GAMM smoothers fitted to the data for each core.

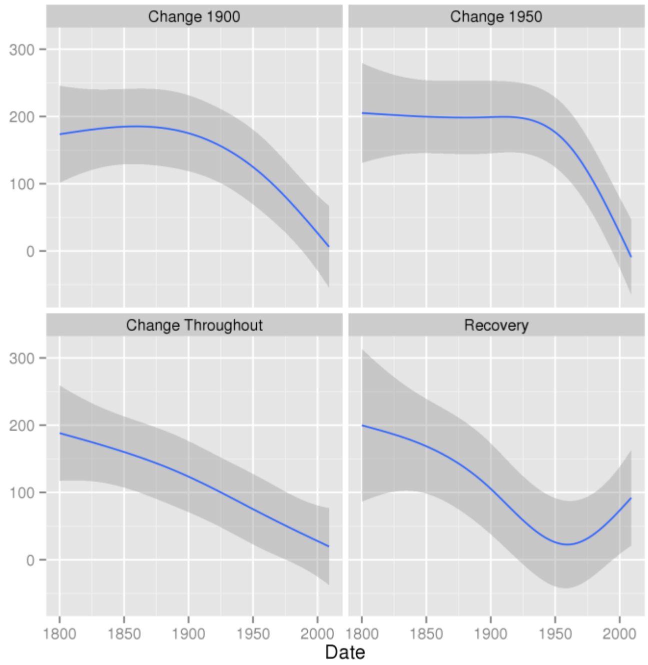


Figure 10. Fitted response smooths for four groups of lakes.

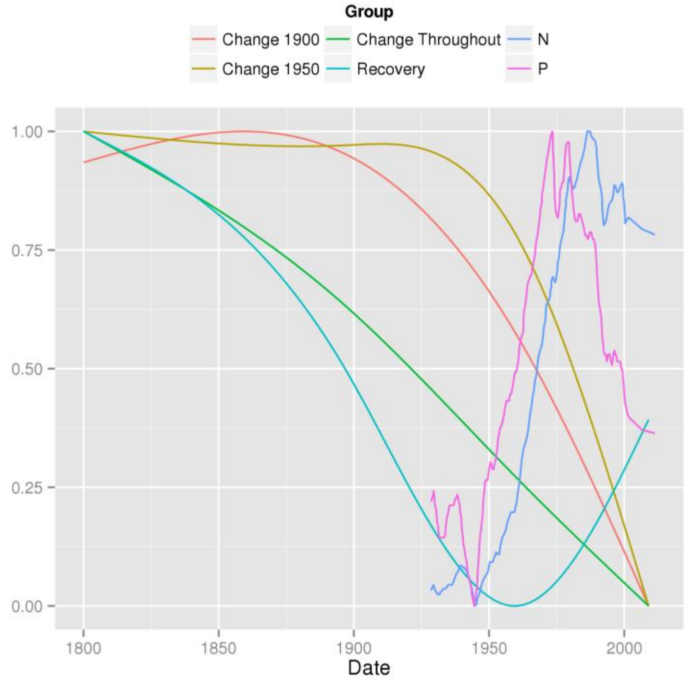


Figure 11. Fitted response smooths plus fertiliser N&P data plotted against age (years AD).

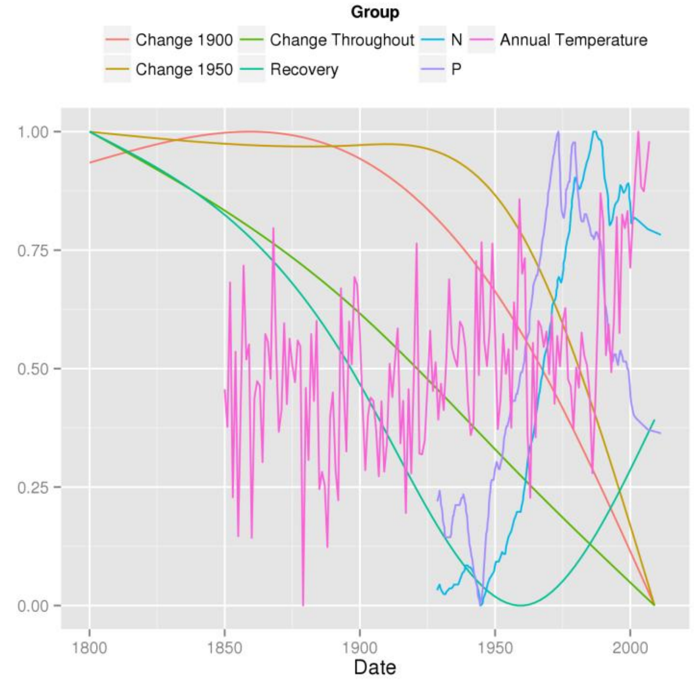


Figure 12. Fitted response smooths plus fertiliser N&P data and temperature data plotted against age (years AD).

The preliminary results suggest that nutrients are the dominant driver of diatom compositional change in our study lakes and hence management needs to focus on nutrient reduction. There is little evidence of diatom shifts in line with increased temperatures and hence insufficient evidence to suggest how reference conditions should be modified in light of climate change. Nonetheless these results must be viewed as provisional and further work is required to explore the relationship between diatoms and climate change in more detail.

It is expected that data from a further 10-20 lakes will be made available by John Anderson, Loughborough University. Once these data are collated, the data analyses will be repeated. Additionally, advice will be sought from ecological statisticians on whether the groups of lakes (in terms of diatom trends) can be defined in a more objective way than the eyeballing method employed here, such as a break point. There is also scope to obtain regional climate data for selected sites and plot regional fit to climate, for example all English lakes with the Central England Temperature series. A further possibility is to focus in more detail on sites with the highest resolution diatom data. Where there is a monitored decline in TP, the diatom data could be plotted against temperature to further explore whether lakes have recovered in spite of increased air temperature.

3.2. The role of climate for phytoplankton biomass in European reference lakes

Contributor: EC-JRC (Núria Cid, Ana Cristina Cardoso, Sandra Brucet)

3.2.1. Introduction

Biological assessment methods based on phytoplankton chlorophyll a (Chla) show the strongest response to eutrophication, as they are based on ecological rationale rather than statistical or expert judgment approaches and have the highest number of validated pressure–impact relationships (Brucet et al. 2013b). Furthermore, phytoplankton is the only organism group used by all European countries for ecological status assessment.

Although climate warming is expected to increase phytoplankton biomass (Lewis 1996, Flanagan et al. 2003, Michelutti et al. 2005, Kosten et al. 2011, Jeppesen et al. 2012b), effects of climate change may be difficult to distinguish due to other multiple interacting factors, including stressors of anthropogenic origin such as eutrophication and acidification (Adrian et al. 2009). This study is focused on reference lakes (i.e. lakes with minimal human disturbance or alteration) and we assume that mainly natural factors (e.g. lake morphometry, specific chemical properties and climate) may be interacting and affect chl-a.

Previous studies on European reference lakes have shown how Chla and total phosphorous (TP) concentrations strongly vary depending on humic type, lake depth and alkalinity (Cardoso et al. 2007, Carvalho et al. 2009, Poikāne et al. 2010), but the simultaneous effect of nutrients and climatic variables such as air temperature or precipitation has not been analysed. To do so, we analysed the relationship between Chla (µg L^{-1}) and lake typology, location and climate. Because phytoplankton is controlled by nutrient limitation in reference and good status lakes, we included also TP (µg L^{-1}) in the analysis, to take into account the effect of nutrient limitation under different climatic conditions. We followed a space-for-time substitution approach (SFTS), which includes cross-comparison studies across latitudinal and altitudinal gradients (Meerhoff et al. 2012). to predict the potential changes in phytoplankton biomass under a climate change scenario.

The specific aims of this work are: (1) to assess whether variability of Chla concentrations in reference lakes can be explained, apart from TP, by the relative influence of natural factors, including climatic variables, and (2) to discuss the potential shift in reference conditions baseline for Chla concentrations under the effects of climate change.

3.2.2. Materials and Methods

Lake data set. The data set consisted of EU WFD intercalibration reference lakes for the ice-free open water period from 1997 to 2007. The data are harmonized by lake types and selection criteria for reference conditions (see Poikāne 2009, Järvinen et al. 2013). The dataset includes phytoplankton biomass Chla (µg L^{-1}), Total phosphorous (µg L^{-1}), altitude (m), mean depth (m), lake area (km^2), alkalinity (meq L^{-1}), conductivity (µS cm^{-1}) and colour (mg Pt L^{-1}). Colour was transformed into a categorical variable (Non-humic, Colour <30; Humic, 30<Colour<90; Very humic, Colour> 90) following Poikane et al. (2009). Data on lake location and physico-chemical variables are in Table 2. The lakes used in this analysis (n=388) do not include reservoirs and therefore the Mediterranean region could not be considered, since Mediterranean lakes present in the above-mentioned intercalibration dataset were only reservoirs (Figure 13).

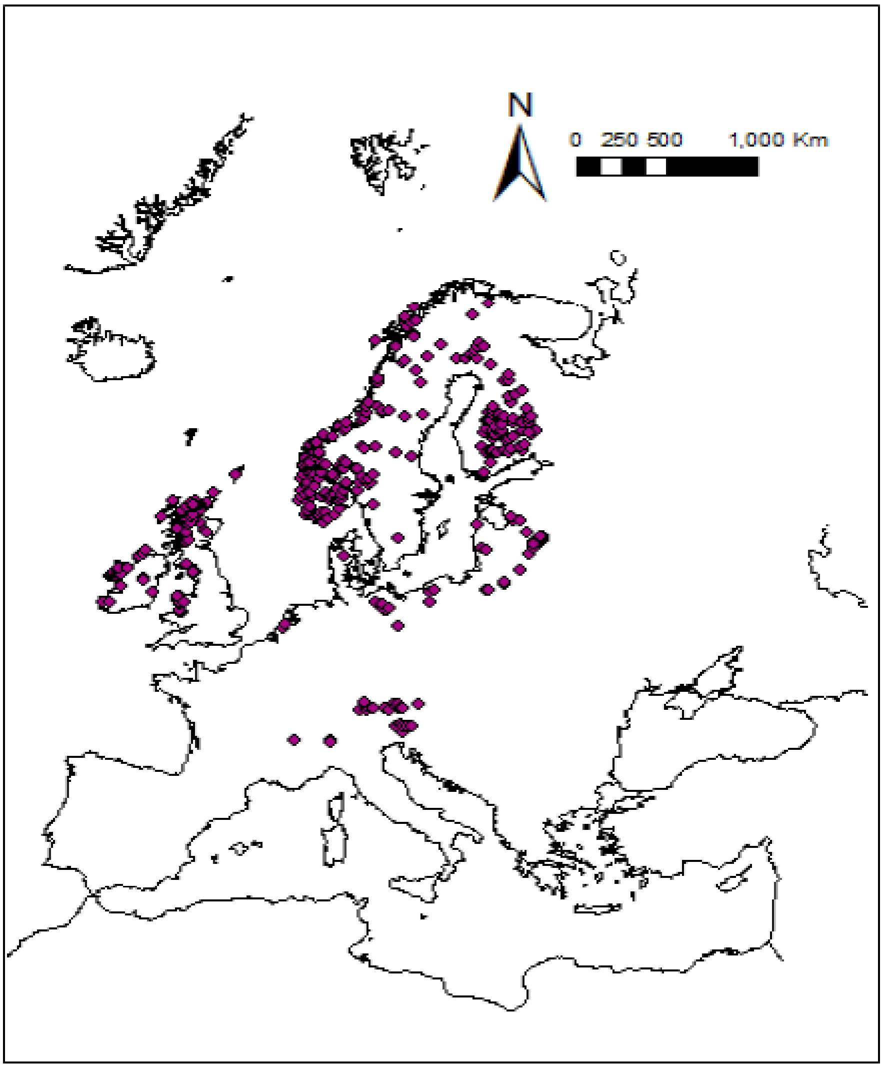


Figure 13. Geographical distribution of the 388 lakes.

Climatic data. Climatic data were obtained from Worldclim data set (http://www.worldclim.org/) (Hijmans *et al.* 2005). The data layers were generated through interpolation of average monthly climate data from weather stations on a 30 arc-second resolution grid, approximately "1 km^2" resolution (for more detailed information on methods, see http://www.worldclim.org/methods). The climatic variables used in our analysis included annual precipitation (Prec), annual mean temperature (T_{mean}), maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (Tmin), and temperature annual range (T_{range}). T_{range} was calculated from maximum temperature of the warmest month minus the minimum temperature of the coldest month, and used as a proxy for seasonality.

Table 2. Variables analysed in this study, with mean values, standard deviation, minima, maxima, range and number of lakes with data (n) for each variable.

	mean	**std. dev**	**min**	**max**	**range**	**n**
Response variable						
Chlorophyll a (µg L^{-1})	3.3	3.1	0.3	24.9	24.7	388
Predictors						
Climate						
Annual precipitation (mm)	1048.5	487.4	399.0	2459.0	2060.0	388
Annual mean air temperature (°C)	5.44	2.86	-3.00	11.80	14.80	388
Max Temperature of warmest month (°C)	18.97	2.45	12.30	27.10	14.80	388
Min Temperature of coldest month (°C)	-6.35	5.87	-19.90	3.40	23.30	388
Temperature annual range (°C)	25.33	7.07	13.20	38.50	25.30	388
Location						
Latitude (°)	58.873	5.131	45.783	69.956	24.172	388
Longitude (°)	10.790	11.698	-10.099	29.776	39.875	388
Lake typology						
Altitude (m)	180.5	201.5	0.0	966.5	966.5	380
Mean depth (m)	17.5	25.9	0.0	238.7	238.7	368
Lake area (km^2)	33.16	125.84	0.03	1377.04	1377.01	385
Alkalinity (meq L^{-1})	0.39	0.77	0.00	5.00	5.00	357
Conductivity (µS cm^{-1})	66.97	94.62	1.00	492.67	491.67	366
Colour (mg Pt L^{-1})*	35.87	34.39	3.20	175.71	172.51	177
Total phosphorous (µg L^{-1})	9.86	7.68	1.25	55.00	53.75	387

*Colour was transformed into categorical variables (Non-humic, Colour < 30; Humic, 30< Colour <90; Very humic, Colour >90) since those missing values correspond to non-humic lakes.

Statistical analysis. Preliminary analyses were conducted in order to investigate relationships and interactions among variables. First, we performed multipanel scatterplots between all variables (Figure 14). Latitude covaried highly with T_{mean}; Longitude covaried with T_{mean}, T_{min} and T_{range}; T_{min} covaried with T_{range} and T_{mean} and Prec; whereas Conductivity covaried with Alkalinity (Figure 14). Therefore, Latitude (°), Longitude (°), T_{min} and Conductivity were highly redundant predictors and were excluded from the analysis. Second, since Chla concentrations strongly vary depending on humic type in European reference lakes (Poikāne et al. 2010), we performed co-plots for Chla (response variable) and climatic variables for the different humic types (categorical) to assess potential different patterns (Figure 15). From this preliminary analysis, we can expect different Chla responses between non-humic, humic and very humic lakes. Therefore, further statistical analyses were performed separately for non-humic and humic lakes.

We ran generalized additive models (GAM) using Gamma error distribution with a logarithmic link function. Models were compared using Akaike Information Criterion (AIC) (Zuur et al. 2009). All the statistical analysis and graphs were carried out using the open-source software R (R Development Core Team 2011) with the package "mgcv" (Wood 2006).

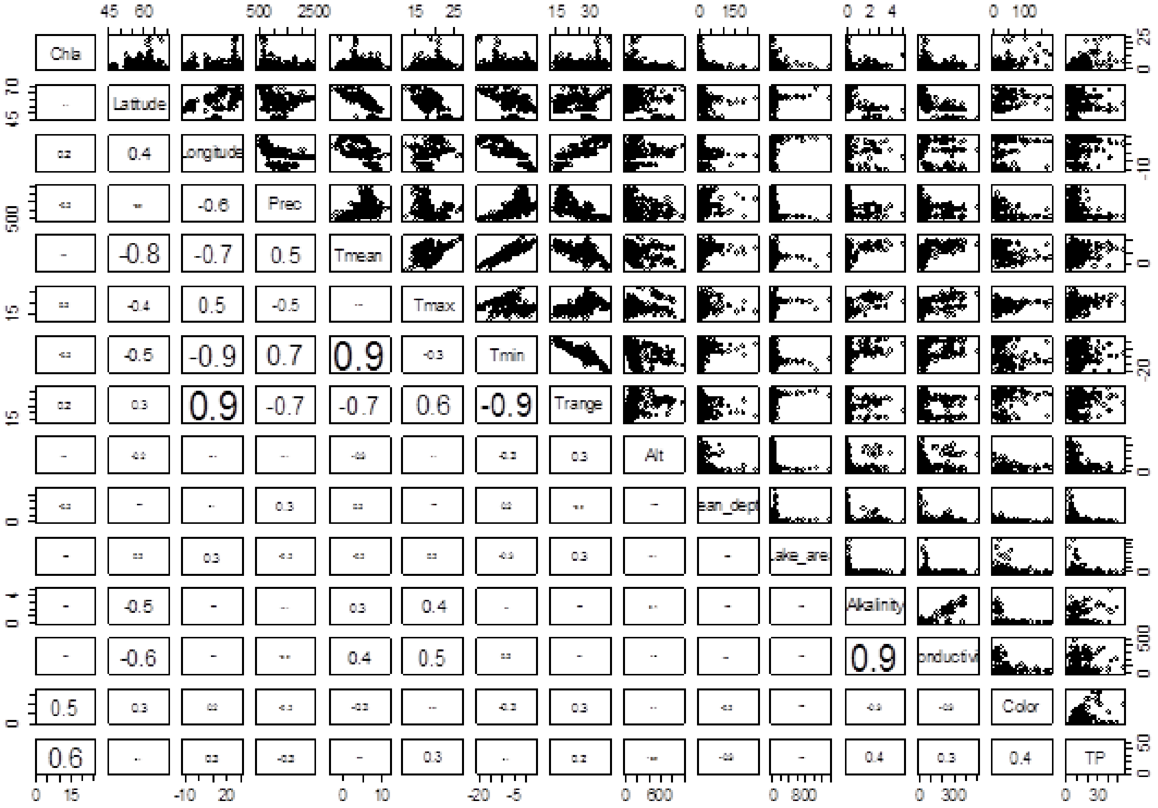


Figure 14. Multi-panel scatterplot of Chla predictors in European Reference Lakes. The upper/right panels show pairwise scatterplots between each variable, and the lower/left panels contain Pearson correlation coefficients. The font size of the correlation coefficient is proportional to its value.

3.2.3. Results

Generalized additive models showed that in both humic and non humic lakes Chla was significantly affected by TP (Table 3). For non-humic lakes, the analysis showed a highly significant effect of TP, although the model shows a slight decrease from 30 to 40 µg L^{-1} (Figure 16). There was also a substantial positive effect of T_{mean} on Chla, although it was not present from 6 °C upwards. For T_{range} the positive effect started from 30 °C. Mean Depth presented a negative effect on Chla, but this effect stabilized in lakes up to 100 m deep. The effect of alkalinity on Chla was highly variable, with a small positive effect in very low range values, a slightly negative effect from 0.5 to 2.5 meq L^{-1} and exerting again a clear positive effect from 2.5 to 5 meq L^{-1}. For humic lakes, the analysis showed a marked linear positive effect of TP on Chla (Figure 17). In these lakes, T_{mean} was not significant and was not included in the model since the AIC did not show any change when excluding this variable. On the other hand, annual precipitation and mean depth were not significant but increased significantly the robustness of the model and therefore were included. The strongest climatic effect on Chla in humic lakes was obtained from T_{range} (Table 3), whereas the effect of lake typology was attributed to alkalinity, which had a slight linear positive effect

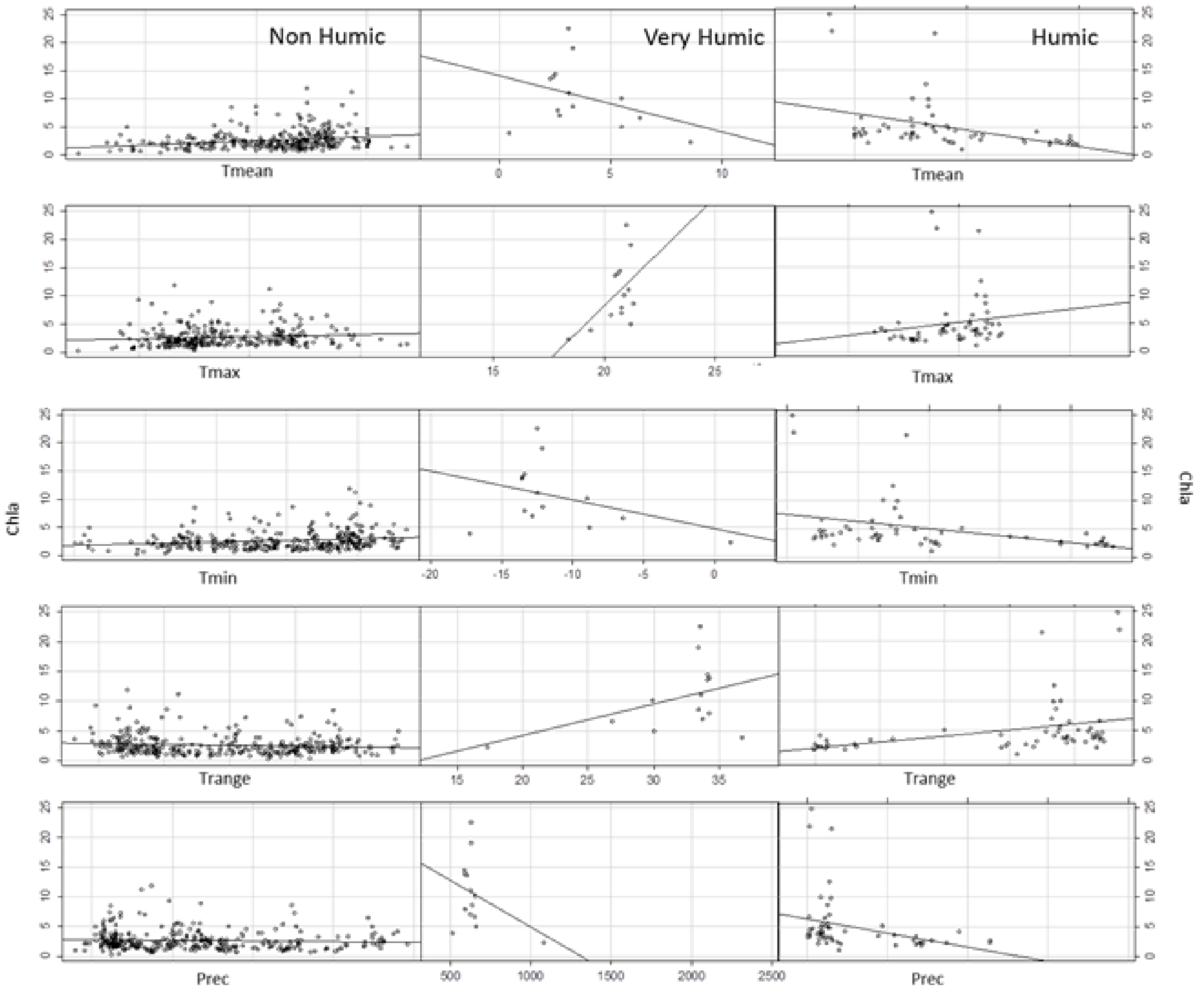


Figure 15. Scatterplot of Chla concentration versus climatic variables for the different humic types.

Table 3. Results of the generalized additive models (GAMs). The level of significance is indicated with ***(P=0.001), ** (P<0.01), * (P<0.05)

	Intercept	Prec	T_{mean}	T_{range}	Z_{avg_m}	Alk	TP	AIC	Dev. Expl. %	R sq	n
Non-humic lakes	0.90***	-	2.30***	2.35*	0.94*	2.84*	2.63***	736.0	57.30	0.46	73
Humic lakes	1.64***	1.37	-	1.96**	0.95	1.07*	1.84***	231.3	86.10	0.81	315

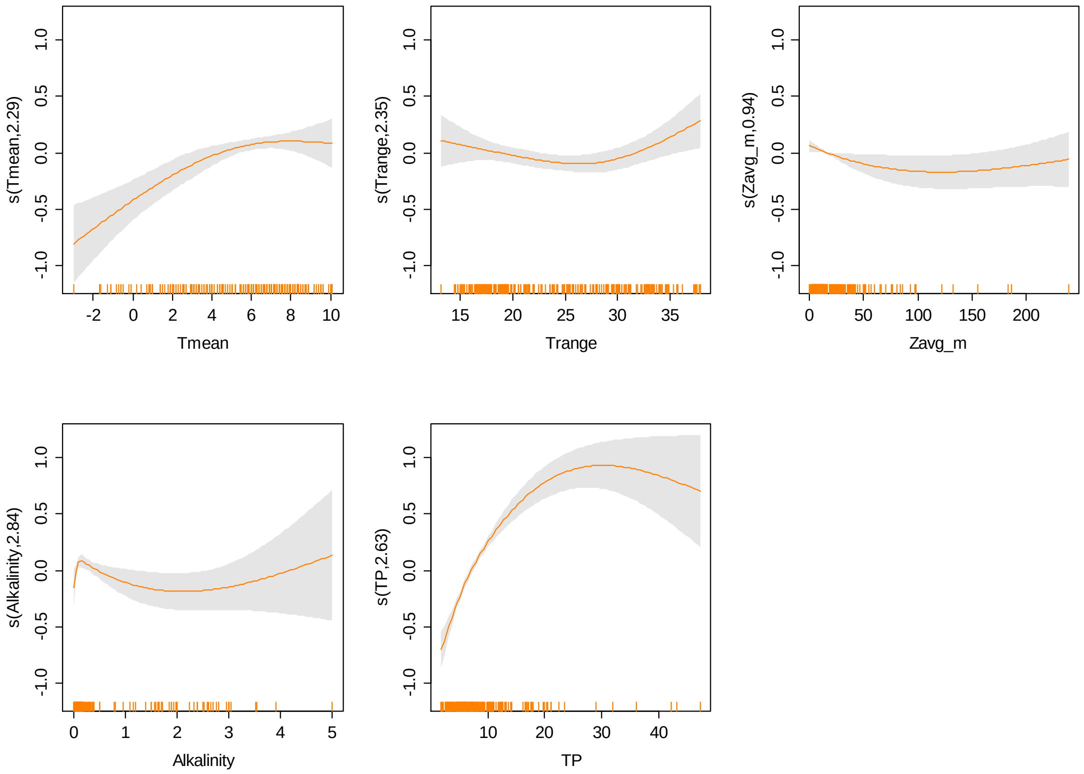


Figure 16. Estimated smoothers for predictors of Chla obtained from Generalized additive model for non-humic lakes. Each plot represents how Chla (Y) changes relative to its mean (the value of zero on the Y-axis) with changes in X : respectively Tmean, Trange, Mean Depth (Zavg_m), alkalinity and TP.

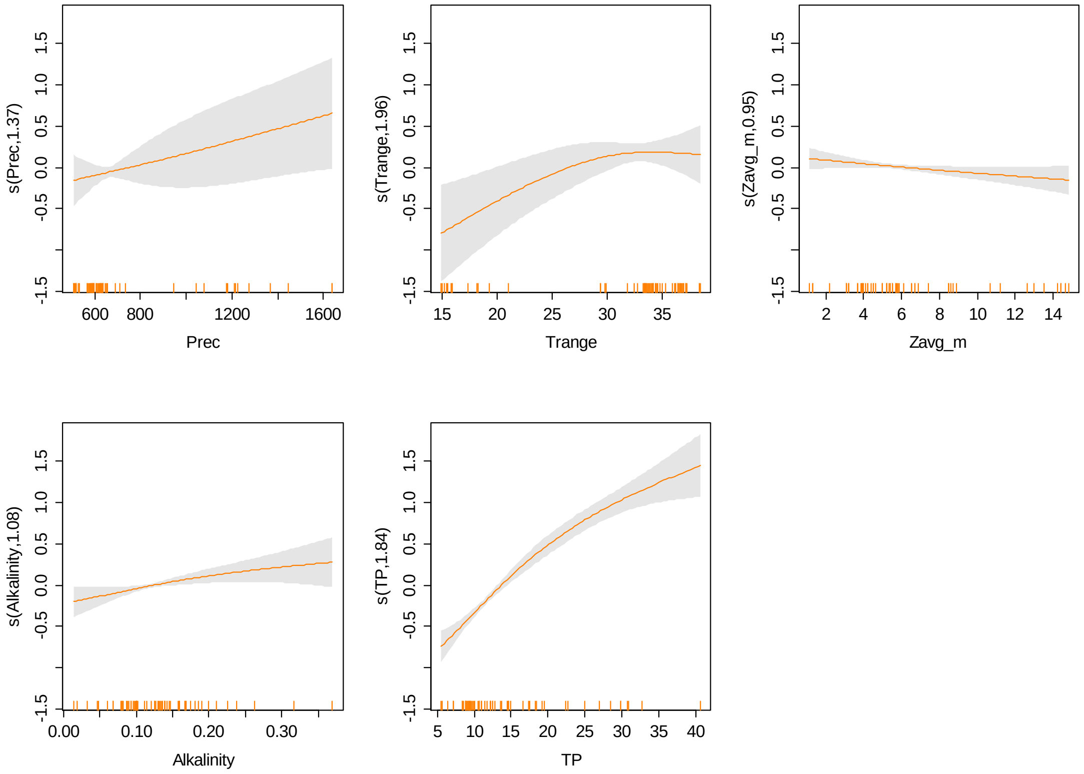


Figure 17. Estimated smoothers for predictors of Chla obtained from Generalized additive model for humic lakes. Each plot represents how Chla (Y) changes relative to its mean (the value of zero on the Y-axis) with changes in X : respectively Precipitation (Prec), Trange, Mean Depth (Zavg_m), alkalinity and TP.

3.2.4. Discussion and conclusions

The analysis of 388 European reference lakes showed that Chla was principally controlled by nutrient limitation (i.e. total phosphorous), with a secondary effect of climatic and lake typology-related variables. In our analysis, an increase in Chla occurred across all lakes with TP, but the effect of climatic variables differed for humic and non-humic lakes, considering also mean depth and alkalinity. The analysis for non humic lakes showed a positive effect of increased annual mean temperature on Chla. This is in agreement with results from other studies using latitudinal effects on phytoplankton biomass in non-reference lakes (Flanagan et al. 2003, Kosten et al. 2011). In humic lakes, the analysis showed an effect of temperature annual range on Chla, but not annual mean temperature. This suggests that the humic lakes included here are more sensitive to seasonality and extreme temperatures (e.g. annual maximum temperature) rather than mean annual temperature. Humic lakes have been considered unproductive ecosystems due to humic substances limiting TP availability, although this is contradicted by the high Chla values (associated with high TP concentrations and high maximum annual temperatures) shown in the present work, but also in other studies (Webster et al. 2008, Poikāne et al. 2010).

Cascade effects such as those of zooplankton grazers and fish community were not considered in the analysis and conclusions should be carefully drawn. For instance, apart from the synergistic effect of nutrients and temperature on Chla biomass, the higher dominance of small-sized planktivorous fish predicted under climate warming can reduce the grazing capacity of zooplankton on phytoplankton and thereby further increase Chla in lakes (Jeppesen et al. 2009, Jeppesen et al. 2011b, Jeppesen et al. 2013b).

Although these results highlight the stronger effect of nutrients compared to other environmental variables, thus making it difficult to disentangle the effects of climatic factors in reference lakes, they have potential implications for the Chla baselines and therefore for the assessment of ecological status of lakes. Considering that total phosphorous inputs will increase in temperate lakes due to higher winter rainfall (Jeppesen et al. 2009) and that an increase in temperature combined with higher nutrients increases Chla biomass (Jeppesen et al. 2011b), higher mean annual temperatures in non-humic lakes and increased seasonality (e.g. higher summer maximum temperatures) in humic lakes will likely contribute to increased Chla concentration in reference lakes under climate change. Thus, a shift in Chla reference conditions may potentially be expected in European lakes.

Further work is required to compare current Chla reference values with those expected under different climate change scenarios. For this reason, data on climatic scenarios will be obtained from Worldclim data set (http://www.worldclim.org/) and tested using the GAM models.

4. New analyses of climate and ecological thresholds

4.1. Climate change and exceedance of regulatory thresholds for phytoplankton

Contributor: NIVA (Jannicke Moe, Anne Lyche Solheim)

4.1.1. Introduction

This study has two main objectives: (1) to estimate relationship between the pressure (total P concentration) and biological responses (different phytoplankton metrics) in Northern European lakes, considering effects of geography, lake typology and climatic variables, and (2) to assess how changes in climate variables (temperature and precipitation) will affect the ecological status of these lakes. The emphasis is on thresholds in two senses: (1) non-linearities in relationships between the chemical, physical and climatic predictor variables and the responses of phytoplankton (cf. Figure 5b), and (2) the probability of exceeding regulatory thresholds (the good/moderate status class boundaries) under current and future climate (cf. Figure 5c).

Here we focus on the amount of cyanobacteria as a response variable, because the occurrence of cyanobacterial blooms is predicted to increase with higher temperature in the future (Paerl & Huisman 2009) (see also section 2.6.3). Data from 590 lakes in the Northern Geographical Intercalibration Group (N-GIG; United Kingdom, Norway, Sweden and Finland) were included in the analyses (Figure 18). Although the amount of cyanobacteria is a component of the national classification system for all of the countries, the exact metric and class boundaries varies among countries and lake types (Lyche-Solheim et al. 2011). In this study, therefore, we have followed the approach of Carvalho et al. (2013a) and adopted the WHO "low health alert" threshold value of 1 mg L^{-1} as a common regulatory threshold for all lakes.

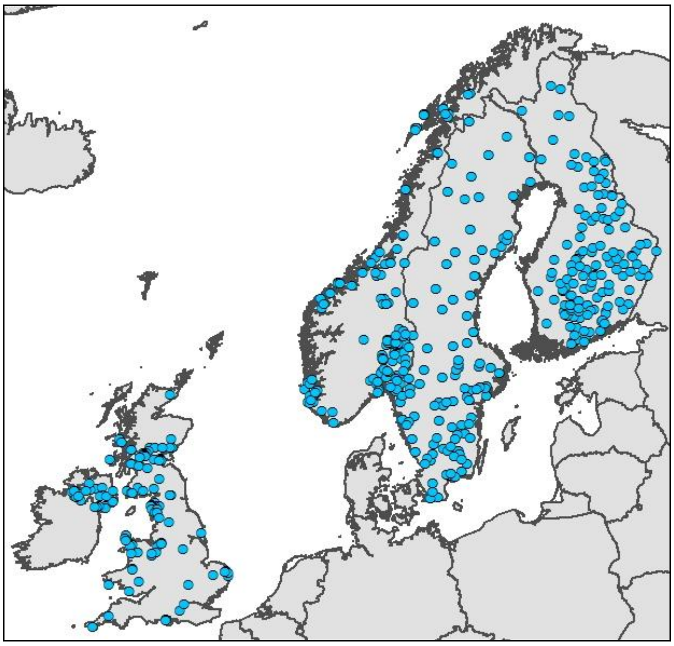


Figure 18. Map of lakes included in the analysis of threshold exceedance in European lakes.

The data analysis was carried out with several different exploratory methods. The purpose of using this set of approaches was to discover both non-linear effects of predictor variables on the response variable (concentration of cyanobacteria) and correlations between the predictor variables (which can make interpretation of results more difficult).

4.1.2. Materials and methods

Data. All data on nutrients, phytoplankton and lake properties are extracted from the WISER database (Moe et al. 2013b). A thorough description of the dataset can be found elsewhere (Lyche-Solheim et al. 2011, Phillips et al. 2013). For this analysis we selected only the 590 lakes that contained values for all typological variables (altitude, surface area, mean depth, alkalinity, humic level) in addition to longitude and latitude, total P, chlorophyll a (Chla) and cyanobacteria (Figure 18). (Lakes that contain only categorical information for one or more typology variables, e.g. "shallow" or "deep" for mean depth, were not included). Only data from months June - September were included. Climatic data (monthly average temperature and monthly precipitation) for the lakes were obtained from the Tyndall Centre for Climate Change Research (Mitchell et al. 2004) (in collaboration with Geoff Phillips, EA/UCL and Sebastian Birk, UDE). The precipitation variable (AvgPPT) was calculated as the mean of monthly precipitation for months June - September. The temperature variable (JaS) was calculated as "month-degrees": the sum of monthly average temperatures above zero for the months January - September).

Data analysis 1: Correlations. First, the correlation between all 66 pairs of variables was inspected in a pairs plot (Figure 19). All variables except longitude and latitude were log-transformed, to obtain a more normal distribution ((Figure 19); histograms on the diagonal panel). For some variable pairs, linear correlation was indicated by a high absolute value of the correlation coefficient (lower triangular panel; e.g. -0.86 for Log(Altitude) and Log(Temperature)). For other pairs, a non-linear relationship was indicated by the non-parametric regression curve (upper triangular panel; e.g., abruptly decreasing log(Chla) at high log(altitude), while the linear correlation coefficient was not particularly high (0.49).

Data analysis 2: Regression trees. Thresholds in the effects of environmental variables on cyanobacteria were analysed with regression trees, using the R package party (Hothorn et al. 2011). The explanatory variables were added stepwise, in the following order: (i) pressure (total P) and typology (area, depth, altitude, alkalinity, humic level); (ii) climate (temperature and precipitation); (iii) coordinates (longitude and latitude); (iv) country. Because of correlations it would be preferable to include only variables from groups (i) and (ii), but the additional role of coordinates and country was also investigated. Data were analysed in both natural and logarithmic scale.

Data analysis 3: Non-linear regressions. The shape of the relationships between predictor variables and cyanobacteria were first explored by non-parametric multiple GAM (generalised additive models), in the R package "mgcv" (Wood 2006) (see also section 3.2.2). To limit the number of correlating predictor variables, the variables were included stepwise as described above (pressure and typology; climate; coordinates; country). The different models and all possible submodels were compared by AIC, using the function dredge in the R package MuMIn (Barton 2013). Based on the selected GAM model, a parametric regression model version was formulated with specified functions for each predictor variable (i.e., a linear model). For predictor variables where the GAM regression indicated a non-linear response curve (estimated degrees of freedom > 1), a quadratic term was also tested. Interactions were not included, both because the high number of predictor variables would make the model selection intractable and because the correlations would make the interpretation difficult. The performances of the different parametric regression model versions were also compared by AIC.

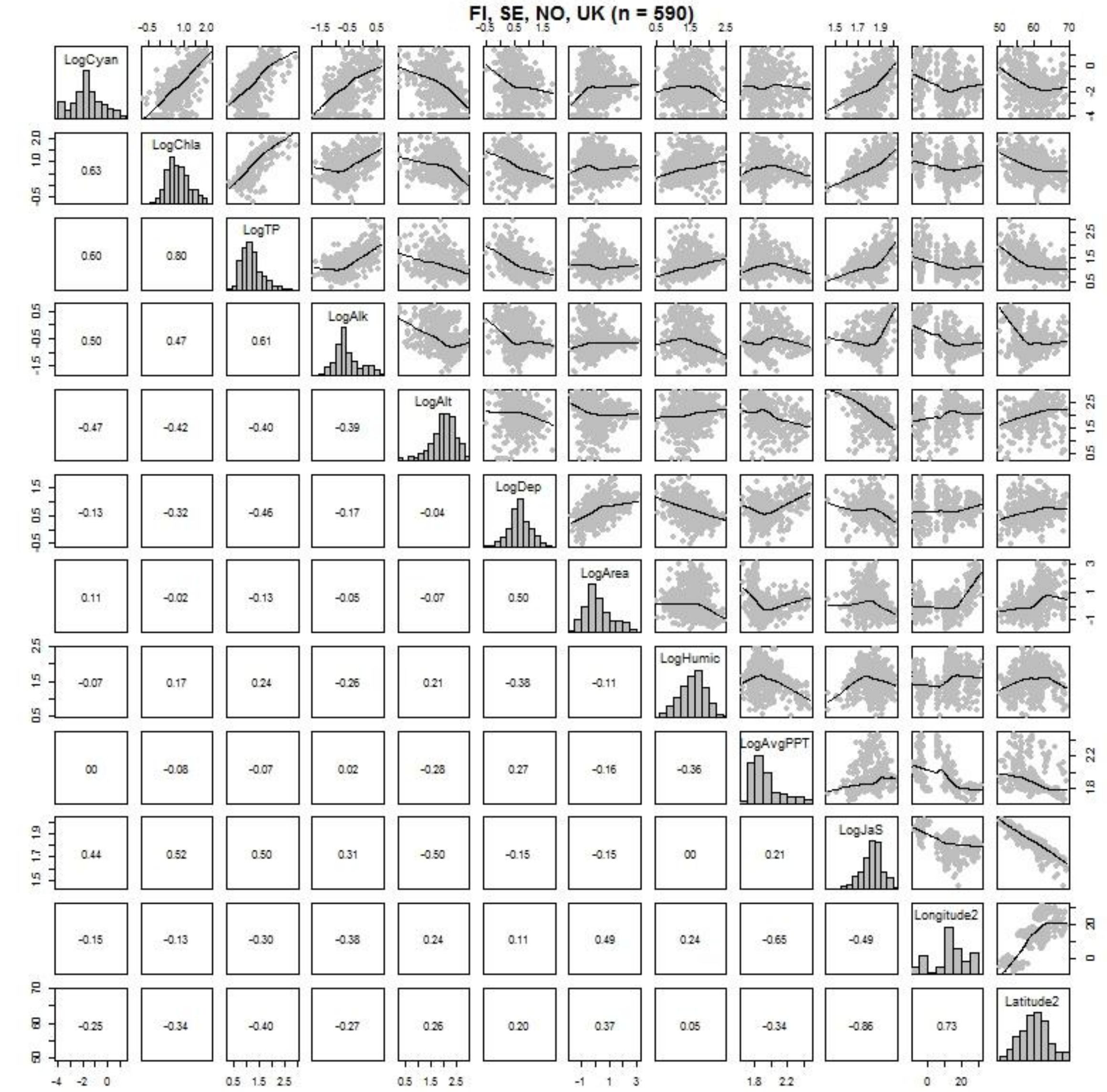


Figure 19. Correlation between all variables. Histogram for each variable is displayed on the diagonal panel. The upper triangle panel shows scatterplot of data and a non-parametric regression curve (LOESS). The lower triangle panel shows the correlation coefficient. JaS: Month-degrees from January to September.

Predictive model. The selected parametric regression model was converted into a predictive model using the estimated coefficients as model parameters. This model was then used to simulate effects of future warmer and wetter climate on the probability of cyanobacteria exceeding the threshold value 1 mg L^{-1}. For each lake, the temperature (month-degrees) and/or the precipitation were increased by 10% and 20%, respectively, compared to the recorded climate variables for that lake. This space-for-time approach simply assumes that, for example, a given lake with its particular physico-chemical properties would, in a future with 10% higher temperature, behave like a lake with similar properties in a different location where the temperature is currently 10% higher. This approach does not consider more complex effects of climate change, e.g. on nutrient pressures or on food-web processes.

4.1.3. Results

Correlation analysis. The highest linear correlations were found between the following variable pairs (Figure 19): Latitude and temperature (-0.86), Chla and TP (0.80), longitude and latitude (0.73; see also map in Figure 18), longitude and precipitation (-0.65), Chla and cyanobacteria (0.63), alkalinity and TP (0.61), TP and cyanobacteria (0.60), altitude and temperature (0.50), temperature and total P (0.50), alkalinity and cyanobacteria (0.50), longitude and area (0.49), and temperature and cyanobacteria (0.44). Non-linear correlations were indicated i.a. in the relationship between area and cyanobacteria (biomass increasing with area in smaller lakes, but not in larger lakes), as well as among several predictor variables.

Regression trees. The selected regression tree for cyanobacteria contained only pressure and typology variables (Figure 20). Inclusion of climatic variables did not result in additional thresholds. In natural scale, the three most important thresholds were found along the TP gradient (32.4, 26.6 and 15.7 µg L^{-1}). The two upper branches had on average 3.16 and 0.45 mg L^{-1} cyanobacteria, respectively. For lakes with TP in the range 15.7-26.6 µg L^{-1}, the next threshold was found in the humic level (34.4 mg L^{-1} TOC), which reduced the amount of cyanobacteria from 0.30 to 0.052 mg L^{-1}. For lakes with TP <15.7, the next thresholds were defined by Altitude (162 m). In the lower altitude range, a new TP threshold was identified at 8.25 µg L^{-1}, below which cyanobacteria decreased from 0.053 to 0.022 mg L^{-1}. The regression trees in logarithmic scale were slightly different, but also suggested that the most important thresholds were found in the variables: TP and altitude. Again temperature did not have a significant threshold effect, possibly because of the high correlation with altitude. In logarithmic scale, however, thresholds were estimated also for precipitation (negative effect) and for alkalinity (positive effect) in lowland lakes.

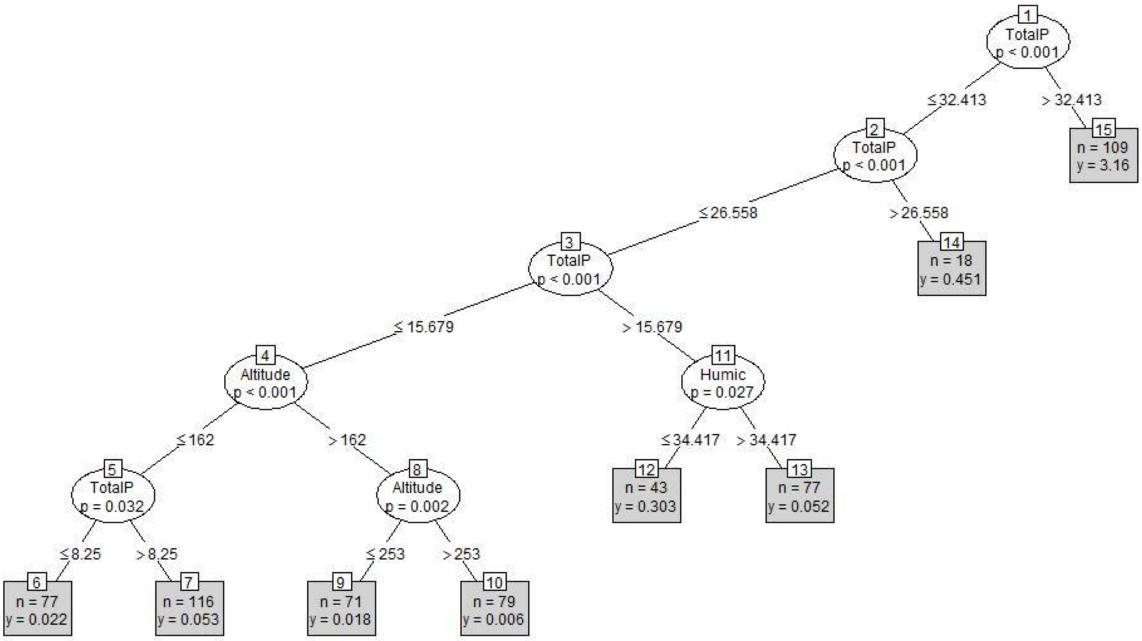


Figure 20. Regression tree for Cyanobacteria, indicating the most important thresholds in explanatory variables: Total P, Altitude and Humic level. Numbers on branches are estimated thresholds for explanatory variables. Boxes: n = no. of observations, y = mean cyanobacteria biomass (mg L^{-1}) for each branch.

Non-linear regressions. The multiple GAM regression (Figure 21) indicated unimodal-shaped effects of TP, alkalinity, area and temperature on cyanobacteria. Comparing with the individual correlations (Figure 19), a unimodal response curve was appropriate only for alkalinity and area (the others were probably due to correlations among predictor variables). The final selected model (Eq. 1) therefore contained quadratic terms only for these two variables.

$$\text{LogCyano} = -5.38 + 1.43*\text{LogTP} - 0.39*\text{LogAltitude} + 0.25*\text{LogArea} - 0.13*(\text{LogArea})^2 - 0.74*\text{LogAlk} - 1.02*(\text{LogAlk})^2 - 0.45*\text{LogHumic} + 3.03*\text{LogTemp} - 0.94*\text{LogPrec} \quad \text{(Eq. 1)}$$

The final regression model explained 53% of the variation in cyanobacteria biomass, and all coefficients included were highly significant ($p < 0.001$) (Table 4).

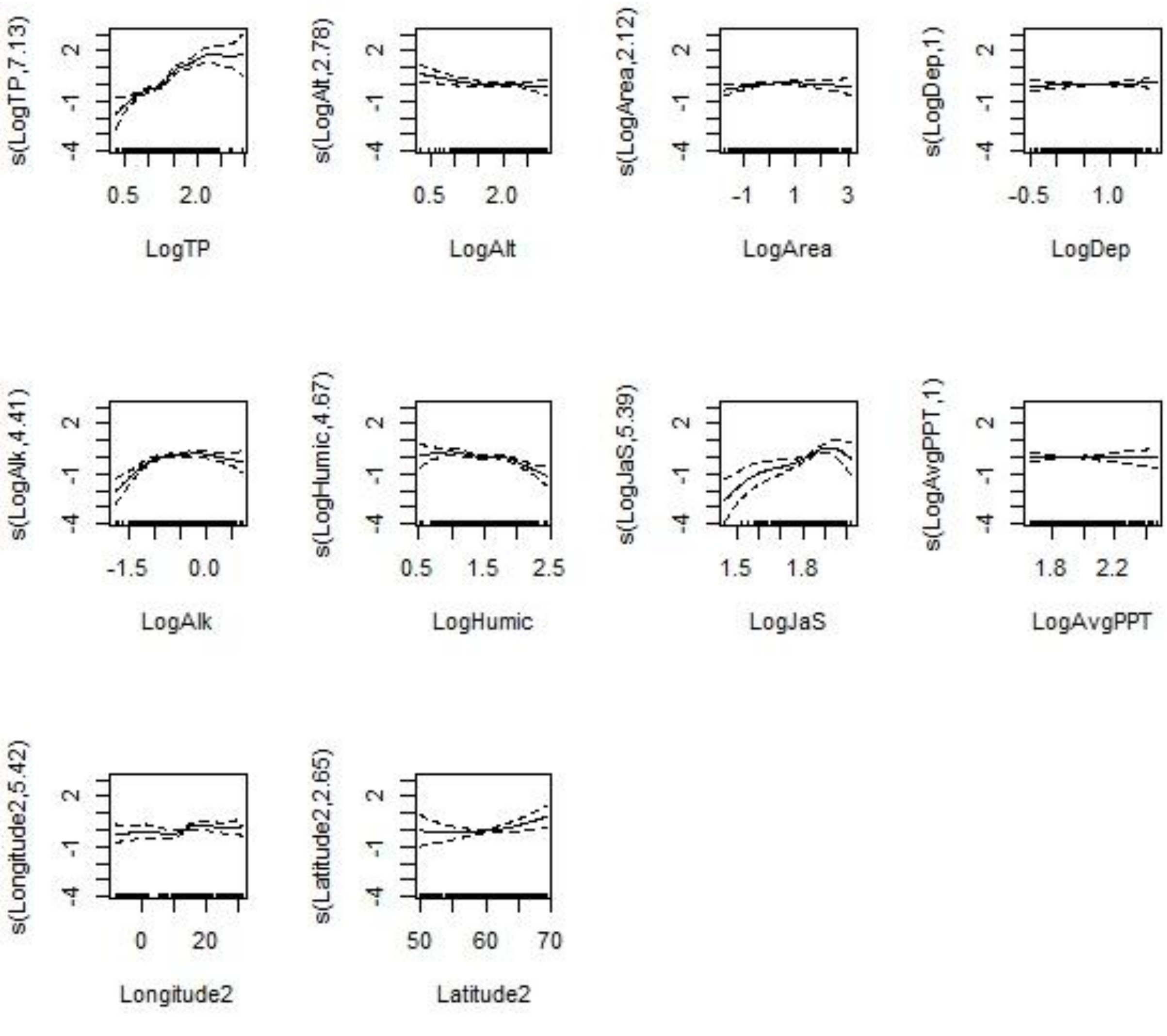


Figure 21. Multiple regression of Cyanobacteria against explanatory variables with GAM (generalised additive model). The number in the y label indicates the estimated degree of non-linearity (1 = linear, higher = more non-linear).

Table 4. Parameter estimates for the selected parametric regression model. Adjusted R2: 0.53.

Variable	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-5.37769	1.04448	-5.149	3.60E-07
LogTP	1.42927	0.14128	10.116	< 2E-16
LogAlt	-0.39482	0.09073	-4.352	1.60E-05
LogArea	0.25435	0.05422	4.691	3.40E-06
LogAlk	-0.7414	0.18869	-3.929	9.55E-05
LogHumic	-0.44675	0.13224	-3.378	7.78E-04
LogTemp	3.0342	0.51122	5.935	5.05E-09
LogPrec	-0.9445	0.23708	-3.984	7.64E-05
$(\mathrm{LogAlk})^2$	-1.02342	0.1528	-6.698	5.01E-11
$(\mathrm{LogArea})^2$	-0.1346	0.03141	-4.285	2.14E-05

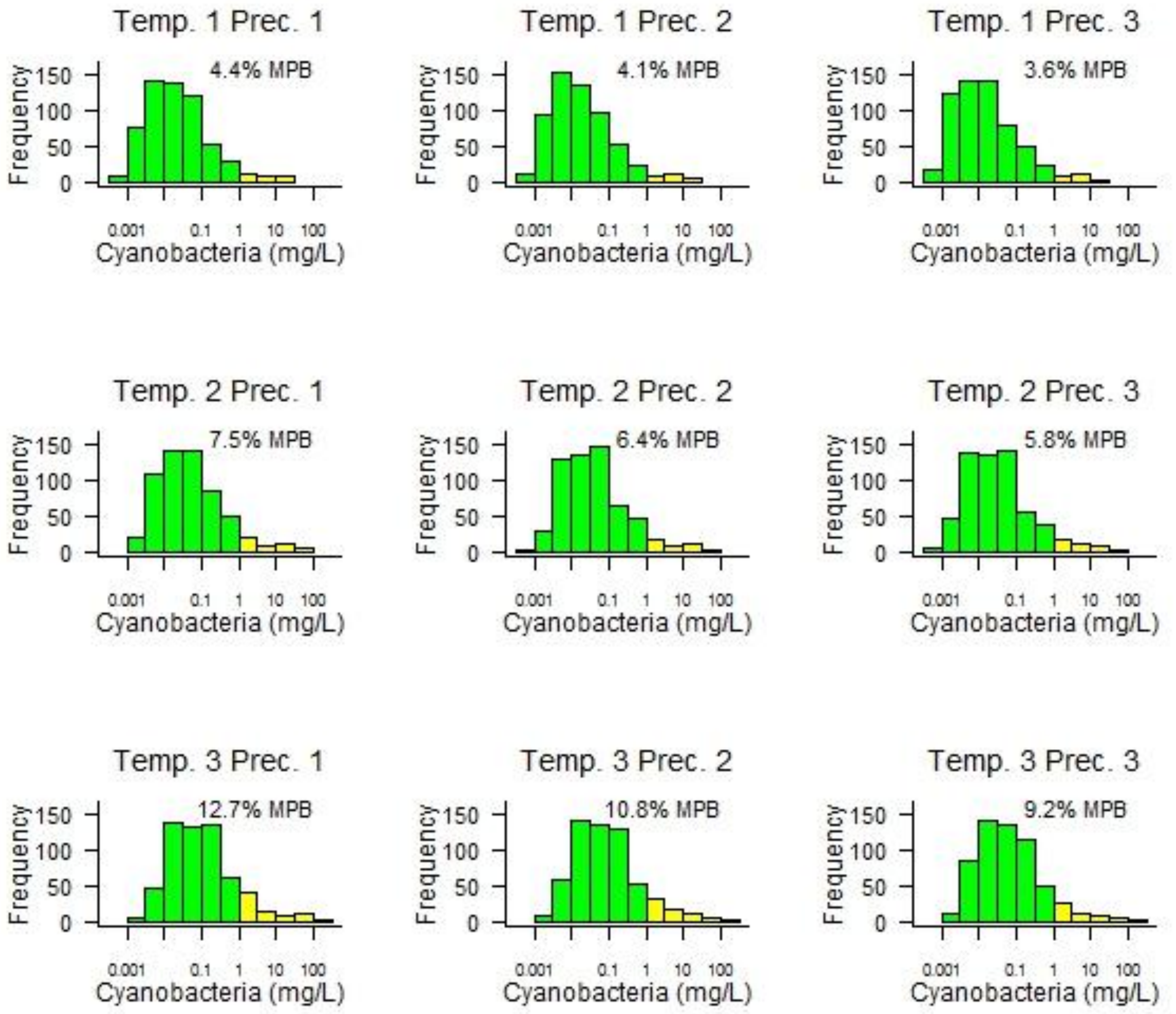
Predictive model. The predictive model (Eq. 1) suggests that under a future warmer climate (10-20% increase in month-degrees), the percentage of lakes with cyanobacteria exceeding the regulatory threshold is increased from the current 4.4% to 7.5-12.7% (Figure 22). However, increased precipitation will to some degree counteract the effects of higher temperature: with 10-20% increase in precipitation, the percentage of lakes exceeding the threshold is reduced from 12.7% to 9.2% (in the highest temperature scenario).

4.1.4. Discussion

This analysis of 590 lakes has shown that the impacts of climate change and nutrients on cyanobacteria are strongly affected by lake typology, which should be considered in large-scale analyses and predictions. In general, the estimated effects of typology variables (water colour and alkalinity) on cyanobacteria support results from corresponding GAM analyses of lakes in the UK (Carvalho et al. 2011). Moreover, the estimated effects of climate (temperature) on cyanobacteria are in accordance with a similar multiple regression analyses of Danish lakes (Jeppesen et al. 2009).

A simple predictive model was constructed based only on empirical relationships in the data (and consideration of correlations), but without including mechanistic processes. While accounting for typology and geography, the model predicted a positive effect of increased temperature and a slightly negative effect of increased precipitation on the risk of exceeding regulatory thresholds for cyanobacteria. These predictions are in accordance with results from more advanced dynamic lake models, which generally predict that increased temperature will increased the amount of cyanobacteria, while increased precipitation will have the opposite effect due to increased "flushing" of the lake (Elliott 2010, Elliott 2012). Thus, this simple predictive model seems reliable and may be used for a coarse assessment of large-scale effects of changed climate on ecological status of phytoplankton in Northern European lakes, e.g. for different lake types or in different regions. Moreover, more precipitation will lead to higher humic content of lakes (brownification; see section 2.6.4). Browner water is infavourable for cyanobacteria (as estimated in Table 4) and may also to some degree counteract the effects of warmer climate.

This model can be improved in several ways, and the next planned steps include: (i) Improving the model fit and better accounting for correlations by more advanced regression methods (e.g. mixed models, structural equation models, Bayesian hierarchical regression); (iii) expand the response variable to include normalised EQR values for each lake (i.e., all lake types where a WFD-compatible classification system is available), and (iii) including more realistic climatic changes for prediction of future scenarios.


Temp. 1 Prec. 1

Temp. 1 Prec. 2

Temp. 1 Prec. 3

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Temp. 3 Prec. 3

Figure 22. Predicted biomass of cyanobacteria in the 590 lakes, based on selected the regression model (Eq. 1). Yellow = cyanobacteria in Moderate or worse status (percentage given in plot); green = cyanobacteria in Good or better status. Note: x-axis is log-transformed.

4.2. Case study Lake Mjøsa: Effects of nutrient reduction and climate change on phytoplankton and zooplankton communities

Contributor: NIVA (Jannicke Moe, Jonas Persson)

4.2.1. Introduction

The phytoplankton and zooplankton communities of Lake Mjøsa have been monitored regularly during the last 40 years. In the 1950s-70s there were severe eutrophication problems and cyanobacterial blooms (Holtan 1990). The campaign "Save Lake Mjøsa" (1977-1981) resulted in substantially reduced P loading and re-oligotrophication, and the lake has obtained good-to-high ecological status during the last couple of decades (Løvik et al. 2013). Climatic changes have been observed since the 1970s: epilimnion temperature has also increased by ca. 2°C, the duration of stratification has increased, and ice-free years have become more frequent (Hobæk et al. 2012). Ecological changes have also been detected during this period: both phytoplankton and zooplankton biomass have been reduced, while the diatom assemblage has been altered (Hobæk et al. 2012). Moreover, certain changes in the zooplankton species composition have been recorded (Løvik & Kjellberg 2003). However, disentangling the potential ecological effects of increased temperature and from the strong effects of reduced nutrient pressure has been a challenge (Hobæk et al. 2012). In this study, we analyse more closely both long-term trends and abrupt changes in (1) climatic, chemical and biological time series, (2) plankton community composition and (3) the seasonal dynamics (phenology) of phytoplankton and zooplankton, and try to relate the observed ecological signals to changes in both nutrient pressure and climatic conditions.

4.2.2. Materials and methods

Lake Mjøsa. Lake Mjøsa is Norway's largest lake (Figure 23) with surface area 362 km^2 and mean depth 155 m. The main tributary drains mountainous regions, and during snow melt, this river feeds Lake Mjøsa with cool water into early summer. Lowland areas around the central part of the lake constitute agricultural districts, and the total population in the catchment is about 200 000. Since the campaign, summer phytoplankton biomass has declined to 2-4 µg L^{-1} chl-a and cyanobacteria no longer cause problems. However, large pennate diatoms continue to develop densities that are considered a nuisance during late summer (Hobæk et al. 2012).

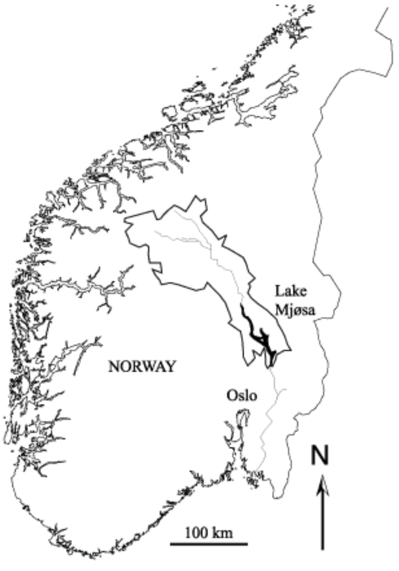

Figure 23. Location of Lake Mjøsa and its catchment in South-East Norway.

Data series. The data included in this study are chemistry (total P, total N, NO_3, SiO_2), temperature, phytoplankton (biomass per species) and zooplankton (biomass per species). All physico-chemical variables are measured weekly, while plankton are sampled bi-weekly, in May-October. All variables were aggregated to biweekly intervals for analysis. Temperature was measured at several depths, while the other variables were integrated for the epilimnion (0-10 m). Two other climatic variables were calculated from the temperature data: the onset and end of stratification (criterion: min. 12 °C at depth 8 m), and the Schmidt stability (Winslow et al. 2013). Phytoplankton were analysed by total biomass (chl-a) and by biomass of individual species, genera and/or classes. Zooplankton were analysed by total biomass and by biomass of individual species.

Ecological status. Ecological status was calculated based on phytoplankton data, following the Norwegian ecological classification system. Ecological quality ratios (EQRs, see section 2.1) were calculated for the metrics chl-a, total biomass, PTI (phytoplankton trophic index, Phillips et al. 2013) and yearly maximum of cyanobacteria (cyanomax). The EQRs were normalised (nEQR) and combined as follows. (i) nEQRs for chl-a and total biomass were averaged. (ii) The value in (i) was combined with the nEQR for PTI by average. (iii) If the nEQR for cyanobacteria was lower than the value in (ii), the final nEQR was calculated as the average of the value in (i) and the nEQR for PTI by average; otherwise the value in (ii) was used as the final nEQR.

Statistical methods. All analyses were performed in R (R Development Core Team 2011). (1) *Univariate time series*. Simple monotonic trends were analysed by the non-parametric Mann-Kendall trend analysis (McLeod 2011). Long-term trends in all time series were explored by decomposition into seasonal, smoothed nonlinear trend (loess) and remaining components by the function stl. Furthermore, abrupt changes and linear trends in combination in both mean and seasonal dynamics were analysed by the packages "changepoint" (Killick & Eckley 2013) and "bfast" (breaks for additive season and trend) (Verbesselt et al. 2010). Thresholds in the relationship between nutrients, climate and biological variables were analysed by regression trees in the package "party" (Hothorn et al. 2011)

(2) *Community composition*. Changes in community composition of phytoplankton and zooplankton respectively were analysed by correspondence analysis (CA) in the package "vegan" (Oksanen et al. 2013). The relationships between environmental variables and community composition were analysed by canonical correspondence analysis (CCA). Rare taxa (<1.5% abundance in all years) were excluded from the analyses.

(3) *Seasonal dynamics*. The phenology of phytoplankton and relevant environmental variables was characterised by the timing of both the maximum biomass and the central tendency (centre of gravity). An index for the timing of the central tendency was calculated following Edwards & Richardson (2004), using the "biweek" co-ordinate of the centre of gravity of the area below graphs of biweekly means (Eq. 2):

$$T = \sum_{i=11}^{22} i \times x_m / \sum_{i=11}^{22} x_m \,, \qquad \text{(Eq. 2)}$$

where x_m is the mean abundance in the "biweek" i (11 = ultimo May, 22 = ultimo October). Long-term changes in the timing of central and maximum biomass were analysed by Mann-Kendall trend analysis. Effects of environmental variables on mean, max and timing of biomass were analysed by GAM and by linear regression. Some of the environmental variables are strongly correlated, especially yearly mean temperature and total P (negative correlation). All analyses of effects of nutrients and climatic variables must therefore be interpreted with caution.

4.2.3. Results and discussion

Trends and abrupt changes in time series. The combined analyses of abrupt changes and linear trends showed that both temperature and Schmidt stability increased throughout the 1980s-90s, and then stagnated from the early the 2000s (Figure 24a-b). Changepoint analysis indicated that all climate-related variables showed the most abrupt change during the 1980s.

The largest increase in temperature was estimated in 1988 (mean before and after: 8 vs. 10 °C), and the largest increase in stability in 1985 (7 vs. 9 kJ m^{-2}). Ice cover duration dropped most abruptly from 1986 (65 vs. 22 days; Figure 25a), and stratification duration increased most abruptly from 1983 (78 vs. 105 days; Figure 25b). The prolonged stratification was caused by both earlier onset (Figure 26c) and later termination (Figure 26d).

Both nutrients and phytoplankton biomass displayed large fluctuations in the 1970s-80s (Figure 24c-e). Total P then declined steadily through the 1990s and early 2000s until an increase from 2005 (Figure 24c). Total N remained constant throughout the 1990s, but also displayed an increase from 2005 (Figure 24d). For phytoplankton biomass a change in seasonal dynamics (lower amplitude) was estimated from 1983, with a subsequent decrease in biomass (Figure 24e). Zooplankton biomass declined mostly linearly throughout the whole period. Changepoint analysis indicated that the most abrupt decrease occured in 1991 for TP (mean before and after: 8 vs. 5 µg L^{-1}), in 1988 for phytoplankton biomass (3.5 vs. 2 µg L^{-1} chl-a) and in 1990 for zooplankton biomass (1300 vs. 1000 mg m^{-2}). Hence, the most significant changes in plankton biomass are well linked temporally to the most abrupt changes in nutrients (around 1990) as well as to the most abrupt changes in climatic variables (during mid-1980s).

Year-to-year trend in biomass was also analysed for each of the 10 phytoplankton classes and each of the 11 zooplankton species. For phytoplankton, 7 classes showed significantly decreasing biomass (negative trend; all $p<0.05$), as exemplified by the dominating class Bacillariophyceae (diatoms, Figure 27a), while 2 of the smaller classes increased (both $p<0.10$). For zooplankton, 5 species showed decreasing biomass (all $p<0.10$), as exemplified by the dominating species *Bosmina longispina* (a cladoceran, Figure 27b), while one species increased (*Holopedium gibberum*, $p<0.05$).

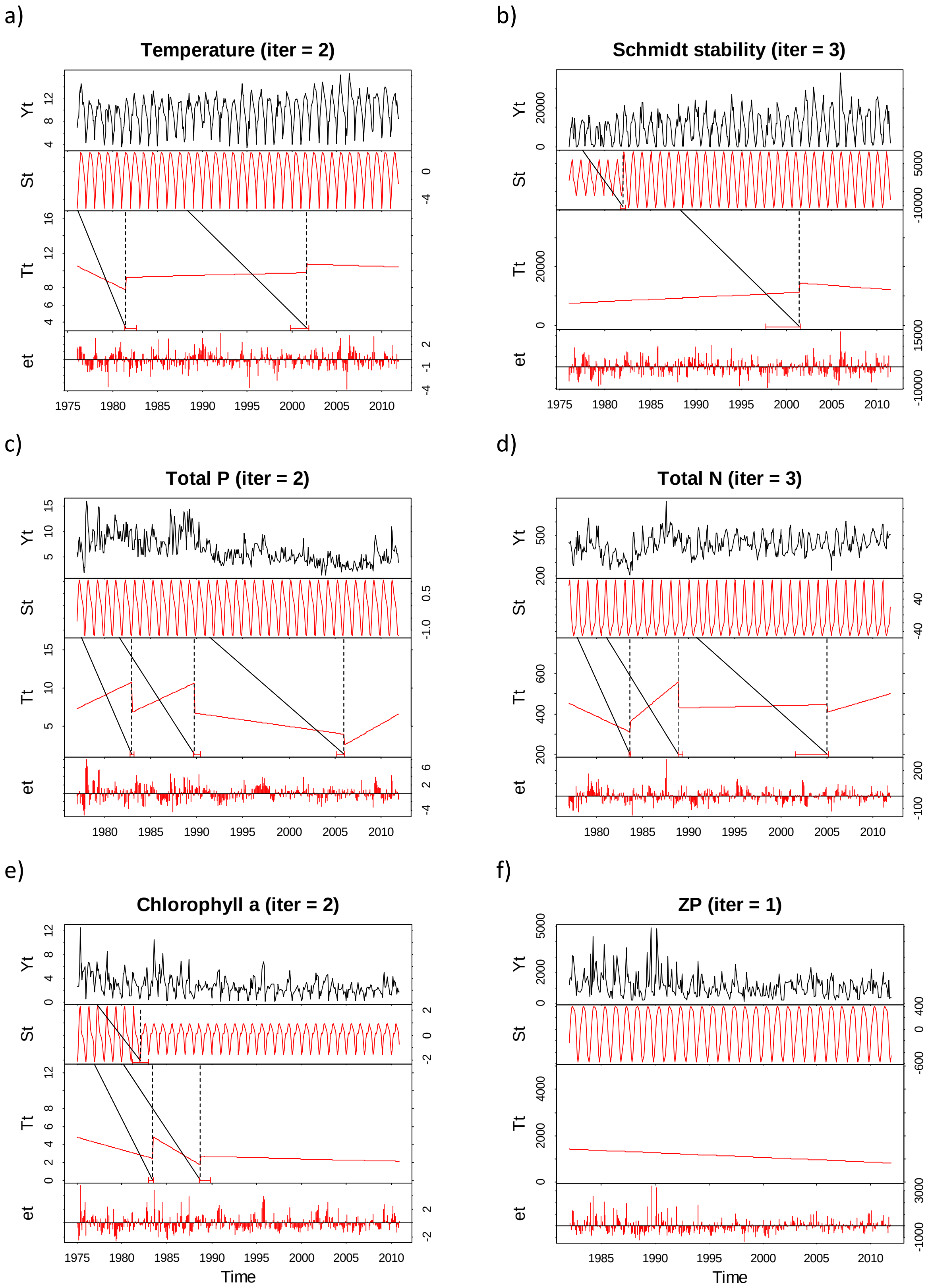

Figure 24. Time series analyses (bfast) for environmental and biological variables with biweekly or higher resolution: temperature (a), Schmidt stability (b), total P (c), total N (d), phytoplankton biomass (chl-a) (e) and zooplankton biomass (f). For each variable, the time series (Yt) is decomposed into a seasonal component (St), a linear trend component with abrupt changes (Tt), and the remainder (et). Vertical lines indicate the timing of abrupt changes, while horisontal lines below these indicate the confidence interval of the timing.

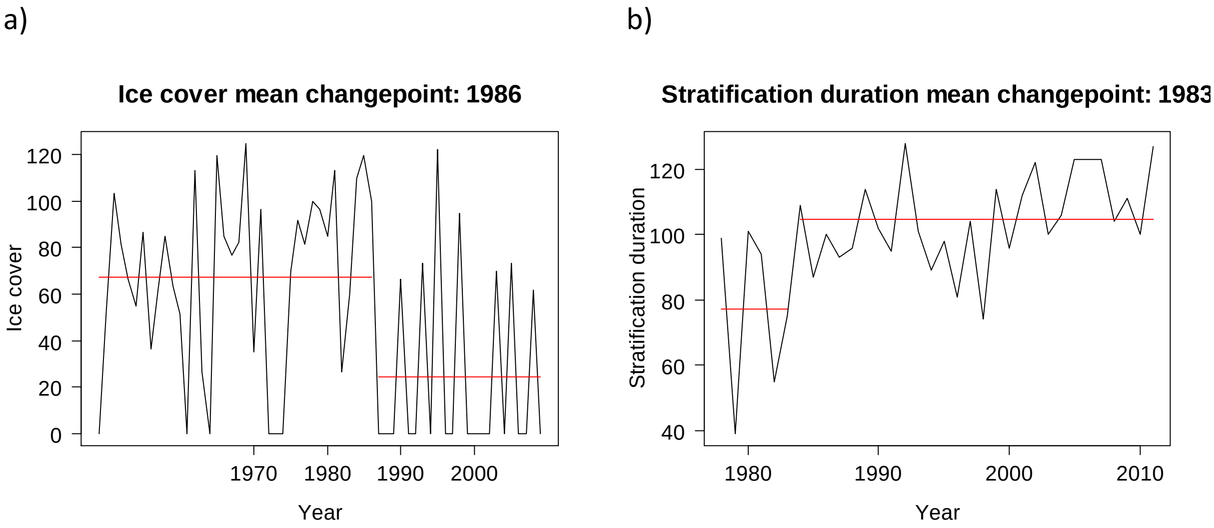

Figure 25. Changepoint analysis for climatic variables with yearly resolution: Duration of ice cover (a) and stratification (b). Horisontal lines indicate mean values before and after the changepoint.

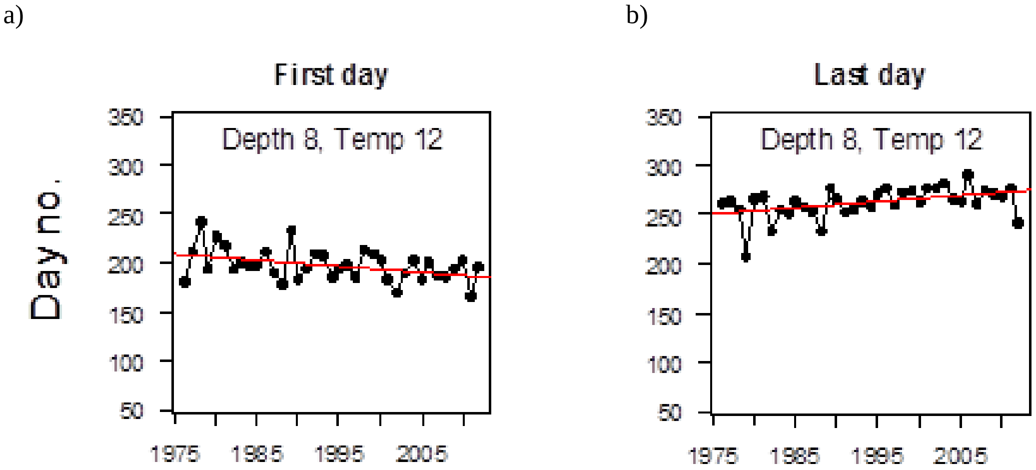

Figure 26. Trends in onset (a) and termination (b) of stratification, indicated by regression lines.

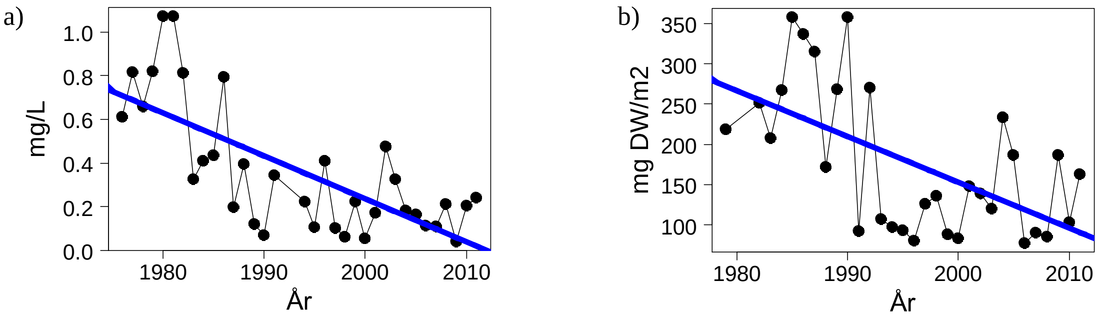

Figure 27. Trends in peak biomass of phytoplankton (Bacillariophyceae, a) and zooplankton (*Bosmina longispina*, b), indicated by regression lines.

Compliance with regulatory thresholds. The current regulatory threshold for Lake Mjøsa is the High/Good class boundary (nEQR 0.8), following the WFD principle of no deterioration of ecological status. A maximum TP value of 7.6 µg L^{-1} was estimated as the threshold for obtaining high ecological status in this lake (Figure 28), which occurred in 19 out of 32 years. No significant threshold values were estimated for effect of temperature or other climatic variables on the ecological status.

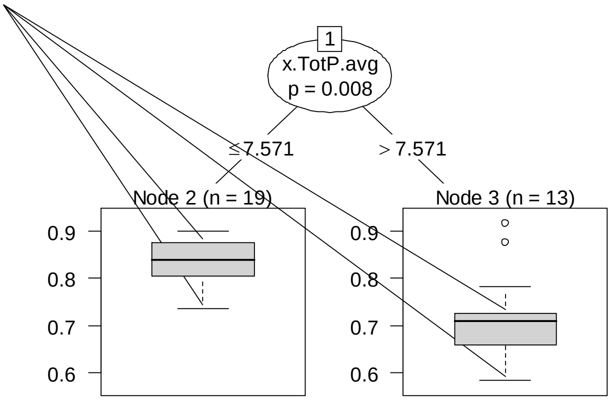

Figure 28. Regression tree for estimation of threshold effect of total P on nEQR (normalised ecological quality ration) for phytoplankton.

Changes in community composition. Analysis of phytoplankton species composition (Figure 29a) displayed a large variance during the 1970s, a clear shift during the early 1980s and more homogenous communities during the 1990s-2000s. The most significant explanatory variables for phytoplankton species composition were total N ($p < 0.0005$) and temperature ($p=0.002$), while the effect total P was not significant. The explanation might be that total P has more influence on the total biomass than on the species composition. Some change in zooplankton species composition is also indicated (Figure 29b; from the right-hand side to the left-hand side), although the trend is less clear than for phytoplankton. Temperature was the only significant explanatory variable for change in zooplankton species composition ($p=0.02$). Earlier studies have revealed significant changes in abundance of individual species of zooplankton during the last decades, which might be related to climate change (Løvik & Kjellberg 2003).

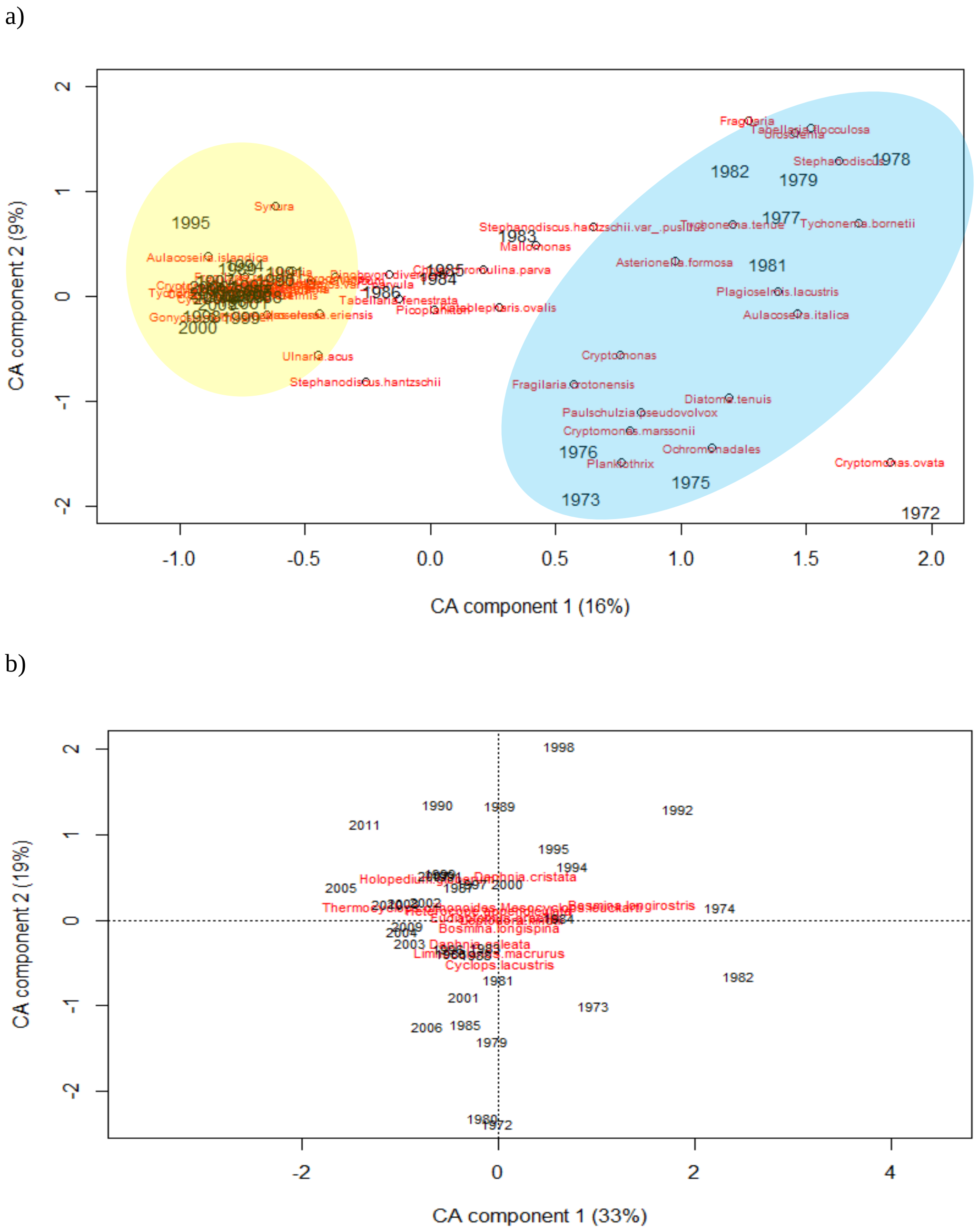

Figure 29. Changes in community composition of phytoplankton (a) and zooplankton (b) during 1972-2011, analysed by correspondence analysis (CA). The shaded figures in (a) indicates the two periods with markedly different species composition: 1970s (blue) and 1990s-2000s (yellow).

Changes and trends in seasonal dynamics (phenology). The seasonal dynamics of selected environmental and biological variables, and the change in dynamics over the decades, are illustrated in Figure 30. Total P levels were reduced during the decades, but the dynamics through the season were not much altered (Figure 30a). Correspondingly, peak temperatures increased during the decades, but the rate of warming in spring remains the same (Figure 30a). In contrast, both phytoplankton and zooplankton showed a change in seasonal dynamics from the 70s-80s to the 90s-00s, as well as a reduction in peak biomass. The peak in total phytoplankton biomass has shifted to later in the season (Figure 30c). There is some variation in seasonal dynamics among the different phytoplankton classes, but this general pattern is even more conspicuous for the most dominating class (Bacillariophyceae, Figure 30e). The peak in total zooplankton biomass, in contrast, was shifted to slightly earlier in the season (Figure 30d). Again, the most dominating species (*Bosmina longispina*) displayed this pattern even more clearly (Figure 30f).

Changes in the timing of the peak biomass from year to year were analysed for each phytoplankton class and each zooplankton species separately. Five out of the ten phytoplankton classes displayed a significant trend in earlier peak biomass (Bacillariophyceae, Chlorophyceae, Chrysophyceae, Dinophyceae, Synurophyceae; all $p < 0.10$). For zooplankton, in contrast, five species displayed a trend in later peak biomass (either maximum or central tendency; all $p<0.05$). The trends towards earlier biomass peaks for phytoplankton and later peaks for zooplankton, respectively, are illustrated for Bacillariophyceae (Figure 31a) and *Bosmina longispina* (Figure 31b).

The changes in yearly mean biomass (Figure 27) and in timing of peak biomass (Figure 31) for the selected examples of phytoplankton and zooplankton taxa were analysed against yearly mean values of nutrients and climatic variables. The reduction in phytoplankton biomass was best explained by reduction in total P ($p = 0.0007$). Likewise, the reduction in zooplankton biomass was best explained by the reduction in phytoplankton biomass ($p = 0.0001$). The later timing of phytoplankton peak biomass was also best explained by the reduction in total P ($p = 0.002$), while climatic variables had no significant effect. In contrast, the earlier timing of zooplankton peak biomass was correlated with higher temperature ($p = 0.02$), and even better explained by higher thermal stability ($p = 0.0003$).

The opposite changes in timing of peak biomass described for phytoplantkon and zooplankton, and the different causes (nutrients and temperature, respectively), are in accordance with other studies reviewed by De Senerpoint Domis et al. (2013). For phytoplankton, a cross-lake comparison of shifts in phenology over 58 years demonstrated that locally variable P levels had a more consistent effect on the timing than temperature (Feuchtmayr et al. 2012). For zooplankton, in contrast, lake comparisons suggest that the timing of biomass peaks is advanced by higher temperature (Straile 2002), although this effect might also be modified by trophic state.

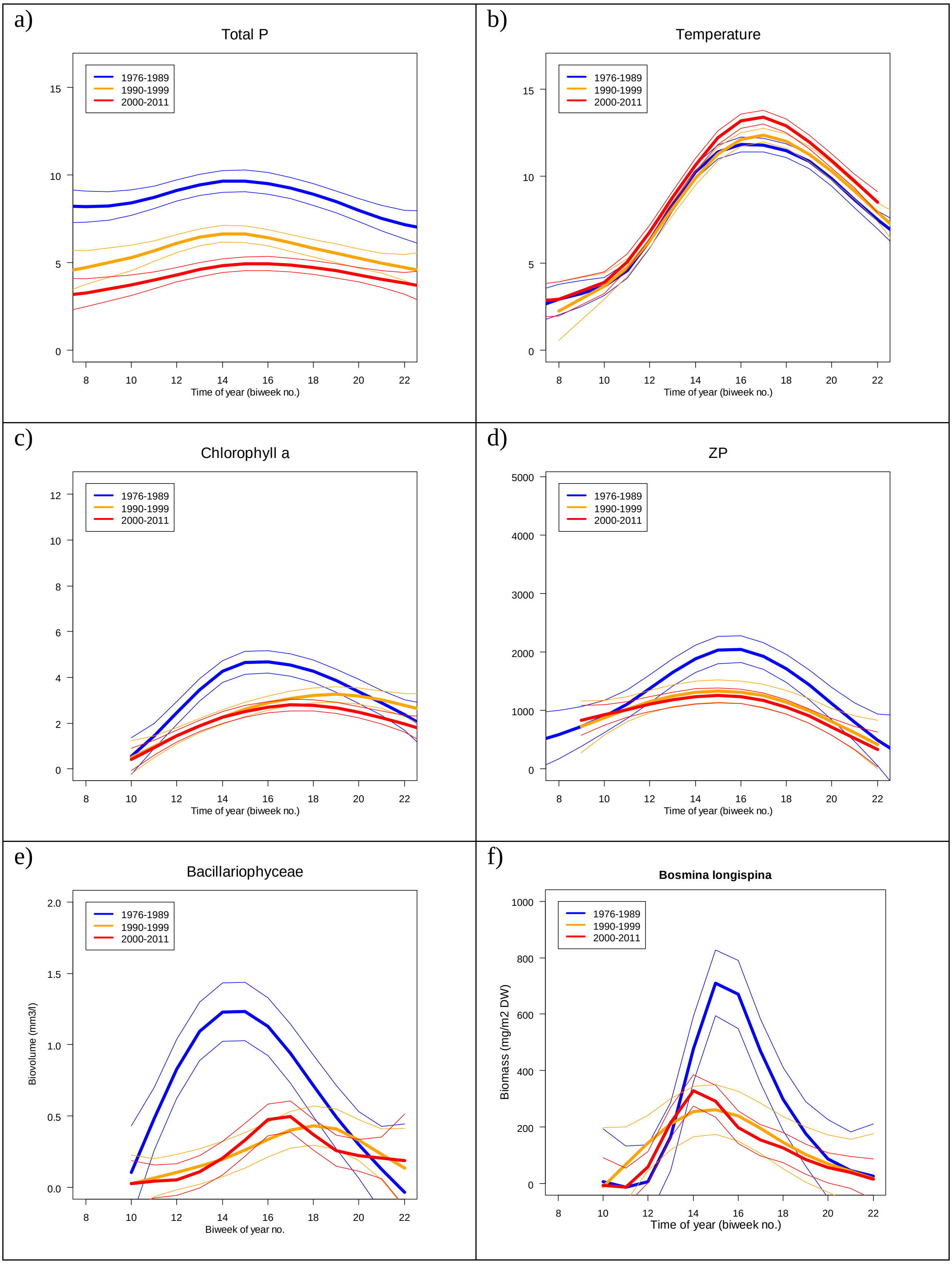

Figure 30. Seasonal dynamics of environmental and biological variables: total P (a), temperature (b), phytoplankton (chl-a) (c), zooplankton (d), Bacillariophyceae (e) and *Bosmina longispina* (f). Within each period (1976-1989, 1990-1999, 2000-2011), the seasonal dynamics of each variable are analysed by GAM.

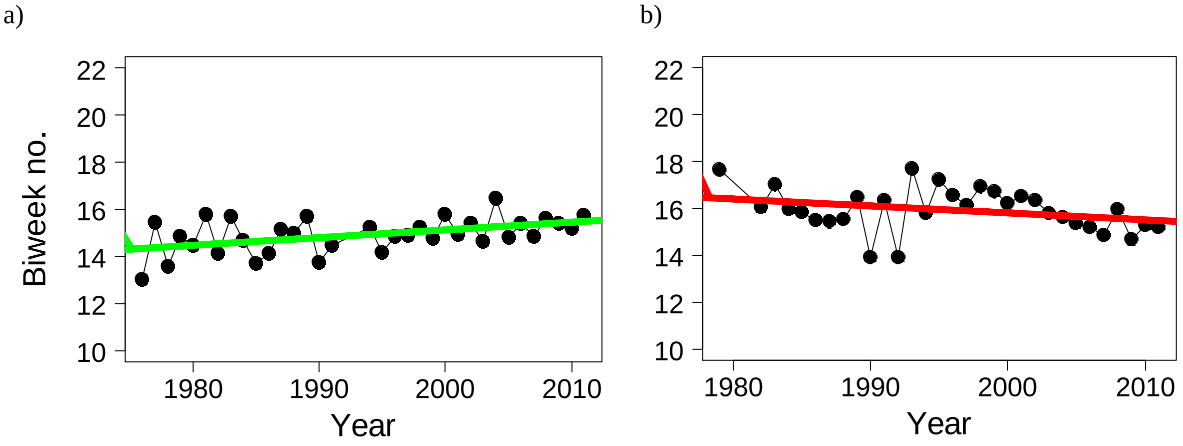

Figure 31. Trends in timing of peak biomass of (a) phytoplankton (Bacillariophyceae) and (b) zooplankton (*Bosmina longispina*), indicated by regression lines.

Conclusions. The strong reduction in total P in Lake Mjøsa since the 1980s is the dominating factor regulating the abundance of phytoplankton and zooplankton. Nevertheless, our analyses indicate that the increase in temperature during the last four decades has also affected the plankton communities. In particular, the earlier timing of zooplankton peak biomasses appears to be related to the increase in temperature or other climate-related changes (e.g. earlier stratification and thermal stability). More analysis of species-specific responses to the environmental changes and of species interactions is needed to better explain these phenomena. However, these results suggest that warmer climate contributes to diverging trends in phenology for phytoplankton vs. zooplankton. This implies that the zooplankton in a future warmer climate might be less efficient in controlling peak phytoplankton biomass by grazing. Moreover, a change in timing of zooplankton dynamics may have consequences for planktivorous fish, especially fish larvae for which the timing of hatching is coupled to the zooplankton dynamics. In the long run, therefore, climate-related changes in zooplankton phenology may have implications for the ecological status of lake Mjøsa through secondary effects on both phytoplankton and fish.

4.3. Case study Lake Vansjø: Effects of climate change on phytoplankton and exceedance of regulatory thresholds

Contributor: NIVA (Jannicke Moe)

4.3.1. Introduction

The combined effects of changes in climate and land-use management have been assessed by processed-based modelling for six European lakes (demonstration sites) in REFRESH (Wade 2012). A combination of regional climate models, catchment/river models and lake models have been applied to predict the effects on quality elements for lakes such as total P and chl-a concentrations. However, the WFD states that assessment of ecological status should primarily be based on biological quality elements, such as phytoplankton (algae) in lakes. Moreover, according to the ecological classification system for lakes in Northern European countries, phytoplankton should be assessed not only by total biomass (represented by chl-a), but by indices of species composition, including the amount of cyanobacteria (potentially harmful algae). Phytoplankton and in particular cyanobacteria are known to respond positively to eutrophication, as well as to climate change (increased temperature). Therefore, when assessing how land-use management in combination with climate change will affect the ecological status of lakes, it is important to consider the species composition of algae and not only the biomass. However, the dynamic process-based lake models applied for the REFRESH demonstration sites have not included prediction of the biomass of cyanobacteria.

In this study, we have extended the model predictions for one of the REFRESH demonstration sites, Lake Vansjø in South-Eastern Norway (Figure 32) (Couture et al. 2013, Couture et al. 2014), to also include amount of cyanobacteria. This is achieved by using an alternative probabilistic modelling framework, a Bayesian network (BN) model, where the outcome of the process-based catchment and lake models can be linked to effects on cyanobacteria based on empirical relationships in monitoring data. The modelling method has also been used in other case studies in REFRESH (Skeffington 2012), but it has not been used in connection with process-based modelling for any of the other demonstration sites.

The objective of this study is to assess how changes in land-use management in combination with climate change affect the ecological status of a lake, considering the amount of cyanobacteria in addition to the total phytoplankton biomass. Specifically, we assess the risk of exceeding the WFD-compliant regulatory threshold - the good/moderate class boundary - under the different scenarios.

4.3.2. Materials and methods

Lake Vansjø. The Vansjø-Hobøl catchment (area 690 km^2), also referred to as the Morsa catchment, is located in south-eastern Norway (59°24′N, 10°42′E). The Hobøl River drains a sub-catchment of ca. 440 km^2 into Lake Vansjø, which is the catchment's main lake. Lake Vansjø is humic, has a surface area of 36 km^2 and consists of several sub-basins, the two largest being the deeper, siliceous basin Storefjorden (eastern basin, L1 in Figure 32) and the shallower, calcareous basin Vanemfjorden (western basin, L2 in Figure 32). In addition, there are six smaller sub-basins which together represent less than 15% of the lake surface area. The Storefjorden basin water flows into the Vanemfjorden basin through a shallow channel. Here, we will show results only for the most impacted basin, Vanemfjorden (mean depth 3.8 m, maximum depth 19.0 m, area 12 km^2, residence time 0.21 year). The current physico-chemical and ecological status of Vanemfjorden is moderate (Haande et al. 2011).

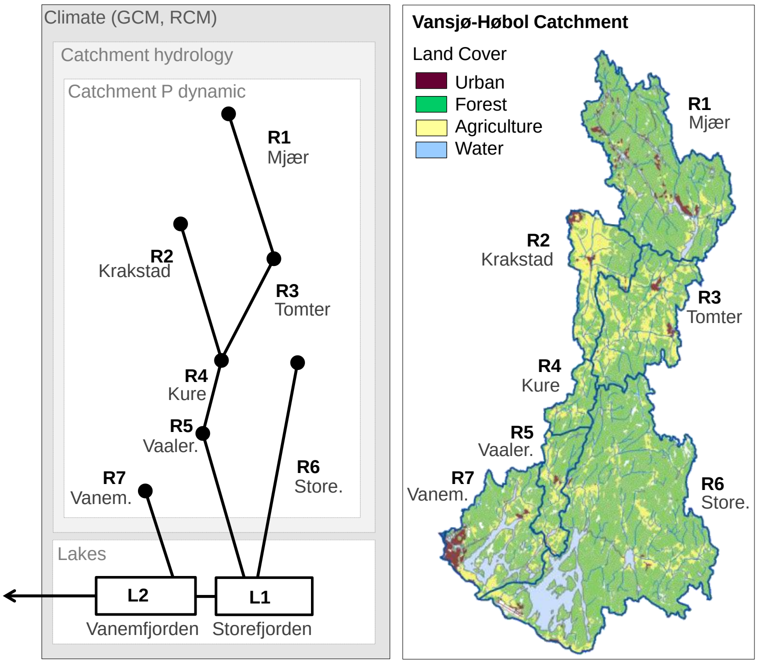

Figure 32. Land-use distribution of the Vansjø-Hobøl catchment (right panel) and corresponding schematic representation of the catchment-lake model network (left panel) indicating river reaches (R) modelled with INCA-P and lake basins (L) modelled with MyLake. The hydrological model PERSiST provides input for the catchment model, and the climate models provide forcing for all models.

Scenarios. The full set of climate and land-use scenarios are common for all eight REFRESH demonstration sites: 4 climate scenarios (years 2030-2052; see Shahgedanova 2011) combined with 3 land-use scenarios (Kouwen & Duel 2011, Waylen et al. 2011). More details for the application of these scenarios to the Lake Vansjø demonstration site are given by Couture et al. (2013). In this study we have used the outcome from one of these climate scenarios, **C1**: The global climate model HADCM3 combined with the regional climate model HADRM3. This scenario predicts changes in both yearly temperature (+1.6 °C) and yearly precipitation (+78.8 mm). Climate conditions during the reference period (1990-2012) are referred to as climate **C0**. The management scenarios are referred to as **M0** = reference (historical data), **M1** = "best case" (water-quality focus), **M2** = "worst case" (economic focus). The M1 scenario is defined by (1) a 10% reduction in agricultural land, which is converted to forest, (2) a 25% decrease in vegetable production, which is converted to grass production, (3) a 25% decrease in P-based fertilizer application, and 4) a 90% improvement in the P-removing performance of WWTPs. Conversely, the M2 scenario is defined by (1) a 10% reduction of forest cover, which is converted to agricultural lands, (2) a shift of 25% of the grass production to vegetable production, (3) an increase of P-based fertilizer application by 25%, and (4) a 25% increase in the P load of effluents from scattered dwellings and WWTPs throughout the catchment.

Outcome from process-based models. The modelling of the Vansjø-Hobøl demonstration sites applies the catchment model INCA-P (Wade 2012) to model the river hydrology and chemistry, and the lake model MyLake (Saloranta & Andersen 2007) to model the physical conditions and concentration of different P fractions in the lake. The concentration of organic particulate P is used as a proxy for chl-a (Saloranta & Andersen 2007). In this study, the following outcome of the lake model is used as input for the BN model: water temperature, Secchi depth, total P and chl-a (Figure 33).

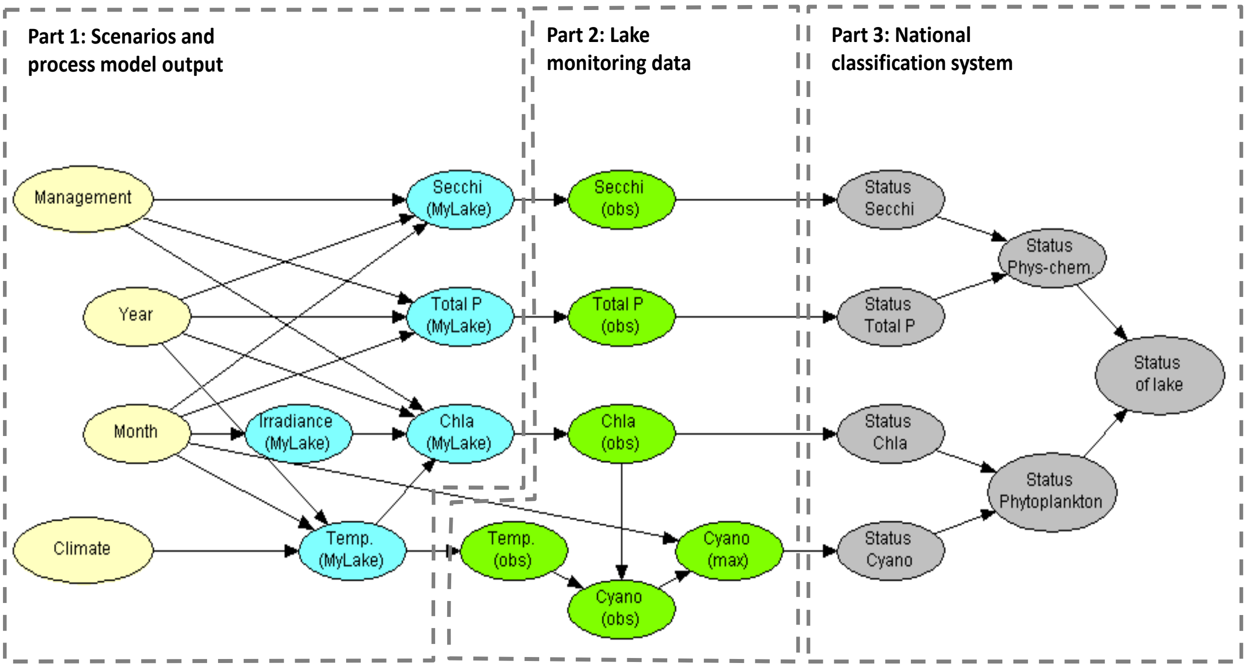

Figure 33. A Bayesian network (BN) model for ecological status of Lake Vansjø. The BN has three main parts: (1) Management and climate scenarios, and simulations from the process-based models INCA-P and MyLake (1992-2010). (2) Monitoring data from Lake Vansjø (1992-2010). (3) The WFD-compliant national classification system for lakes in Norway.

Monitoring data. Data series from Lake Vansjø (1993-2012) were downloaded from NIVA's monitoring database (http://www.aquamonitor.no). The following data were included in this study: water temperature, Secchi depth, total P, Chl-a and biomass of cyanobacteria (Figure 33). All variables were measured weekly during May - Oct, except for cyanobacteria, which were measured bi-weekly.

Lake classification system. The status assessment is based on the class boundaries and combination rules of the Norwegian lake classification system[1] for the lake type L-N8 (lowland, large, shallow, siliceous/moderate alkalinity, humic). The status for each individual quality indicator (seasonal averages of Secchi depth, total P, and chl-a, and seasonal maximum of cyanobacteria) is set according to the Good/Moderate and Moderate/Poor boundaries of the classification system. Combined physico-chemical status is obtained by weighting Secchi depth and Total P equally. Combined phytoplankton status is obtained by weighting chl-a and cyanobacteria equally when cyanobacteria have worse status than chl-a (but ignoring cyanobacteria when this indicator has equal or better status than chl-a). Finally, the overall ecological lake status is obtained by selecting the worse of phytoplankton status and physico-chemical status (or moderate status, if physico-chemical status is poor-bad while phytoplankton status is high-good).

Bayesian network (BN) modelling. In a BN model, each variable is defined as a discrete probability distribution (Figure 34). This structure enables different types of information to be linked by conditional probability tables (CPT) (Figure 34). The probability distributions in the CPTs also represent the uncertainty in the relationship between the variables (or in our knowledge about the relationships).

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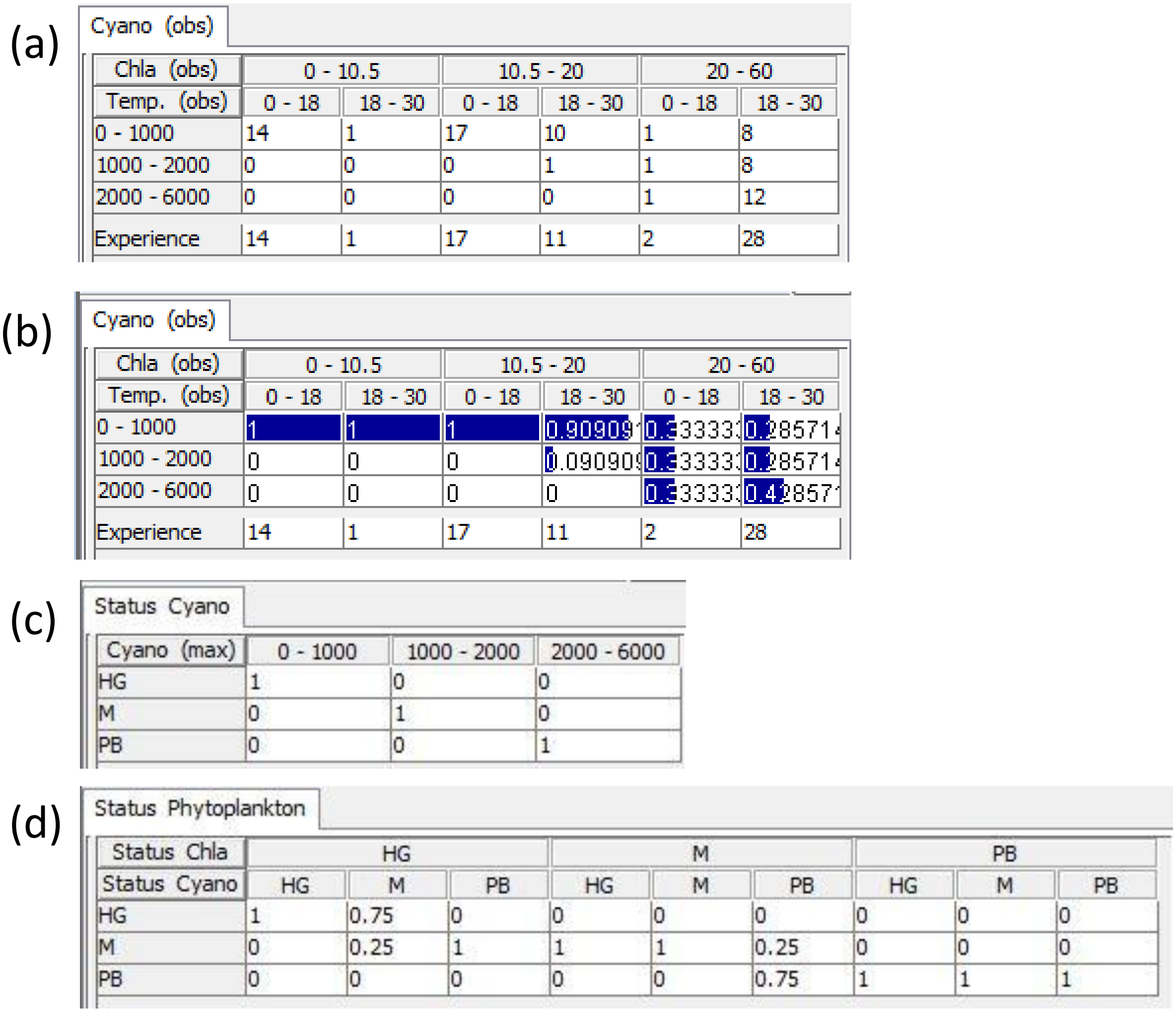
[1] http://www.vannportalen.no/Revidert_klassifiseringsveileder140123_VZIS-.pdf.file



(a)

Cyano (obs)

Chla (obs)	0 - 10.5		10.5 - 20		20 - 60	
Temp. (obs)	0 - 18	18 - 30	0 - 18	18 - 30	0 - 18	18 - 30
0 - 1000	14	1	17	10	1	8
1000 - 2000	0	0	0	1	1	8
2000 - 6000	0	0	0	0	1	12
Experience	14	1	17	11	2	28

(b)

Cyano (obs)

Chla (obs)	0 - 10.5		10.5 - 20		20 - 60	
Temp. (obs)	0 - 18	18 - 30	0 - 18	18 - 30	0 - 18	18 - 30
0 - 1000	1	1	1	0.90909	0.33333	0.28571
1000 - 2000	0	0	0	0.09090	0.33333	0.28571
2000 - 6000	0	0	0	0	0.33333	0.42857
Experience	14	1	17	11	2	28

(c)

Status Cyano

Cyano (max)	0 - 1000	1000 - 2000	2000 - 6000
HG	1	0	0
M	0	1	0
PB	0	0	1

(d)

Status Phytoplankton

Status Chla	HG			M			PB		
Status Cyano	HG	M	PB	HG	M	PB	HG	M	PB
HG	1	0.75	0	0	0	0	0	0	0
M	0	0.25	1	1	1	0.25	0	0	0
PB	0	0	0	0	0	0.75	1	1	1

Figure 34. Examples of conditional probability tables (CPT) for the BN model. (a) Frequency distribution of cyanobacteria biomass intervals (µg L^{-1}) dependent on Chla (µg L^{-1}) and Temperature (°C), based on observations from Lake Vansjø ("Experience"). (b) The same CPT displayed as probabilities. (c) Probabilities of cyanobacteria status dependent on cyanobacteria biomass, based on the national class boundaries. (d) Probabilities of phytoplankton status dependent on both Chla status and cyanobacteria status, based on combination rules of the national classification system.

The first part of this BN model (Figure 33) is based on output from process-based models predicting effects of the management and climate scenarios on nutrient loading in the catchment (INCA model) and on physico-chemistry in the lake (MyLake model). The second part links these model predictions to the observed time series for phytoplankton, including cyanobacterial biomass, from the same period. The third part links each of the physico-chemical and biological indicators to the classification system, predicting the probability of different status classes for each indicator as well as for the overall ecological status of the lake. The model has a monthly resolution, so that it can be run for a selected year and/or month.

Discretisation of the continuous variables (setting the boundaries between intervals) is done by different approaches, depending on the nature of the variable and its relationship with other variables. For variables for which WFD class boundaries are defined (i.e. observed Secchi, Total P, Chla and Cyano), class boundaries (Good/Moderate and Moderate/Poor) of lake type L-N8 are used as boundaries (displayed in Figure 35; boxes with green headers). For temperature, the boundary was estimated by regression tree analysis (see also section 4.1.2):

A threshold effect of temperature on cyanobacteria was found at 18 °C. For the corresponding variables predicted by MyLake (boxes with blue headers), the availability of more (simulated) data allowed a higher resolution. For these variables, a higher number of intervals of equal distance was defined in between the intervals based on WFD class boundaries (Secchi, Total P and Chla) and on regression tree analysis (temperature).

The discrete probability distributions in the CPTs (Figure 34) are also obtained by different approaches in the three parts of the BN model. In the first part (scenarios and process models output), a large amount of data is available (MyLake model runs for 60 different parameter combination). Here, the probability distribution of the output variable (e.g., water temperature) for each combination of the input variables (here: climate scenario, year and month) is determined by the corresponding frequency distribution in the model output (not shown). Likewise, the links from the predicted MyLake outcome to the observed monitoring data are based on the respective frequency distributions: comparing the number of predicted and observed data in the same intervals, for the same year and month (not shown).

In the second part (monitoring data), the observations on cyanobacteria are not sufficient for establishing reliable probability distributions (Figure 34a). In this case, the information from the observations is combined with expert judgement to make the probability distributions more realistic (Figure 34b). In the third part (classification system), the class boundaries and combination rules are translated into discrete probability distributions.

The model is run by altering the probability distribution of one or more nodes (e.g., selecting one management scenario) and recording the resulting change in probability distribution that are updated in linked nodes throughout the network (e.g., in the status of the lake) (Figure 35).

4.3.3. Results and discussion

The predicted effects of different scenarios on total P (Figure 36b) and on chl-a as simulated by MyLake (Figure 36d) are described by Couture et al. (Couture et al. 2014): more sustainable management improves the probability of obtaining good status for both of these indicators, while climate change slightly reduces the probability. For chl-a under current climate conditions, the probability of good status increased from 20% under current management (M0) to 41% with the best-case management (M1), but the probability decreased to 5% with the worst-case management (M2). Climate change only slightly reduced the probability of obtaining good status to 18%, 38% and 4%, respectively, for the three management scenarios.

The results of the BN model furthermore show a similar effect on the cyanobacteria indicator (Figure 36e) as described for the chla indicator. All scenario effects were weaker for the cyanobacteria indicator than for the chl-a indicator; this is partly because uncertainty in the relationship between chl-a and cyanobacteria is built into the link between the two variables (Figure 34b). The predicted probability of obtaining good status for phytoplankton based on both chl-a and cyanobacteria (Figure 36f) was slightly lower than for chl-a alone (Figure 36d). Under current climate conditions, the probability of good status for phytoplankton increased from 16% under current management (M0) to 33% with the best-case management, but decreased to only 4% with the worst-case management. Climate change slightly reduced the probability of obtaining good status to 14%, 30% and 3%, respectively. The difference in probability of good status for chl-a alone and for chl-a and cyanobacteria combined shows the importance of also including cyanobacteria in the modelling of future ecological status of lakes.

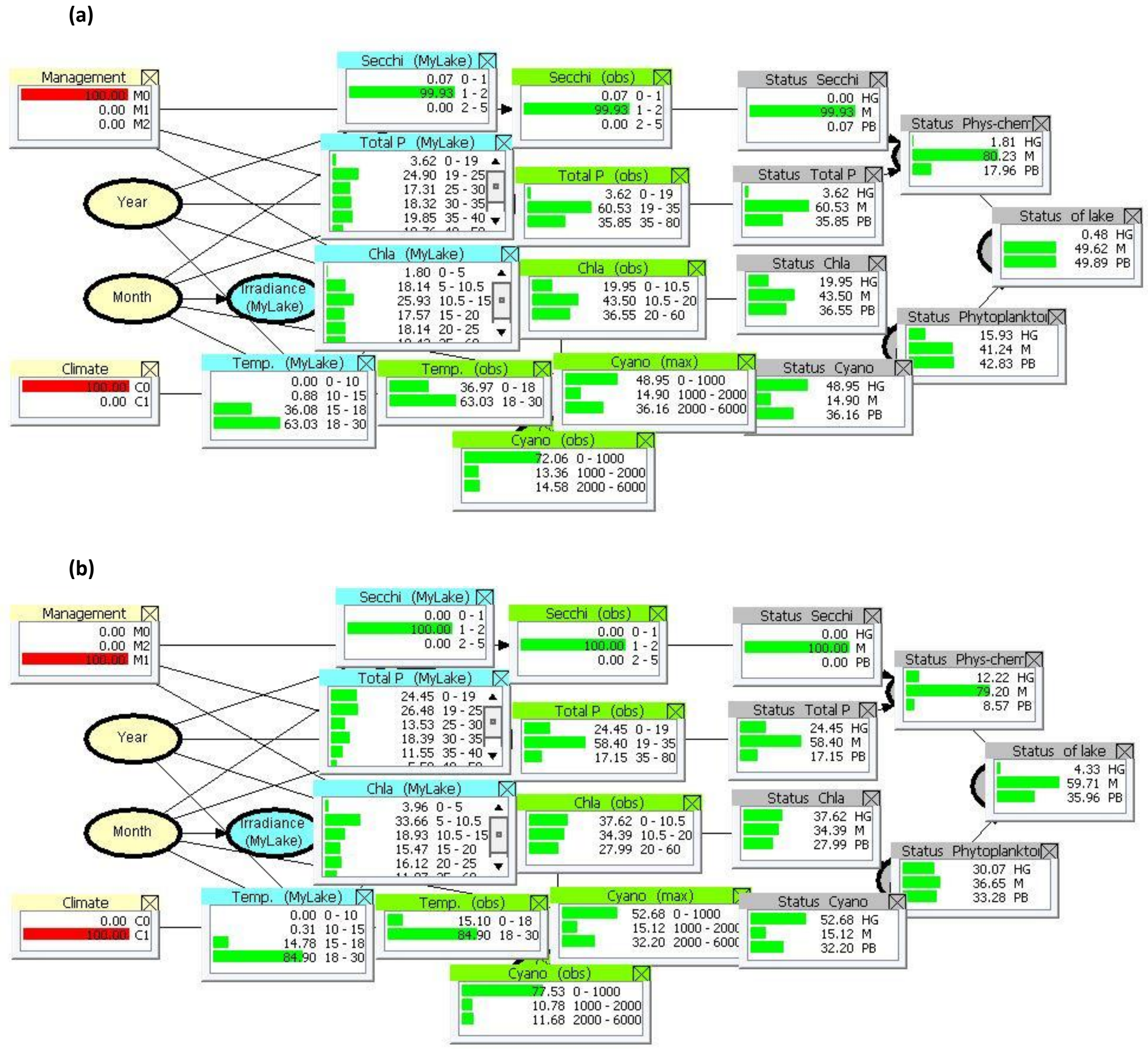


Figure 35. Example of scenarios and BN predictions. Status classes: HG = High/Good (required by the WFD), M = moderate, PB = Poor/Bad. (a) Scenario with current climate (C0) and reference management (M0). (b) Scenario with future climate (C1) and "best case" management (M1). Note the shift to higher probability of HG status.

Furthermore, when the physico-chemical element was also taken into account (Figure 36c), the probability of overall good lake status was considerably lower (Figure 36g); the lake status was actually worse (0.5% probability of good status) than either of the physico-chemical (Figure 36c) and the phytoplankton components (Figure 36f) (2% and 16%, respectively). This result can be explained by the combination rule: the physico-chemical component can only maintain or degrade the status of the biological components. This result is also in accordance with the current moderate status of Lake Vansjø (Vanemfjorden), and illustrates the importance of also implementing information from the relevant lake classification system in the modelling of overall lake status. Finally, this study has demonstrated that the BN approach can be very useful for modelling ecological status of lakes with focus on compliance with regulatory thresholds, by combining different types of information and knowledge in a probabilistic framework.

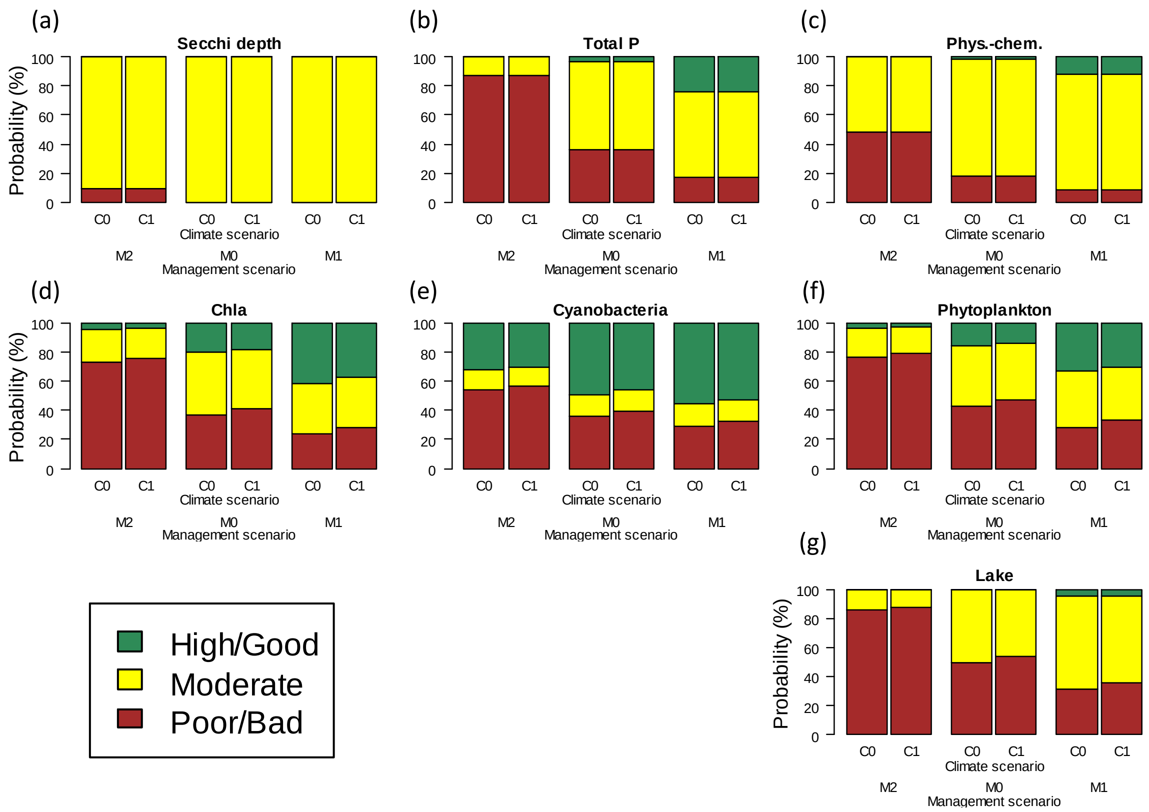


Figure 36. Predictions from the BN model: effects of climate and management scenarios on probability distribution of status classes for individual quality elements and for overall ecological status of Lake Vansjø. Climate scenarios are reference (C0) and HadRM3 (C1); management scenarios are "economy focus" (M2), reference (M0) and "water-quality focus" (M1). The figure shows that more sustainable management improves the probability of obtaining good status for both Chla and Cyanobacteria, while climate change slightly reduces this probability.

4.4. Case study Lake Müggelsee: Threshold-driven responses to climate change

Contributor: FVB/IGB (Rita Adrian, Ulrikke Scharfenberger)

4.4.1. Introduction

Ecosystems tend to be unstable. Populations fluctuate because of seasonality and fluctuations in weather and climate or internally generated dynamics such as predator-prey cycles and populations may change abruptly in the context of environmental changes (Scheffer et al. 2001, Wagner & Adrian 2009b). In earlier years modeling approaches have been developed e.g. to understand population dynamics, food web interactions (Carpenter et al. 1985), drastic changes in ecosystems such as regime shifts (Scheffer & Carpenter 2003), or changes in thermal regimes (Kirillin 2010). Theory predicts that regime shifts can be attributed to stochastic events such as extreme events or species invasion, surpassing of critical thresholds or purely by internally generated fluctuations (Carpenter 2003). The quantification of critical thresholds which may provoke abrupt changes of ecosystems is very much needed in order to understand and predict changes in the context of global change. There is, however, an apparent gap between theoretical frameworks concerning driving forces of food web interactions and regime shifts and their applicability to scenarios actually observed in nature; i.e. testing ecological theory with observational data (Scheffer & Carpenter 2003). In order to understand observed regime shifts it is desirable to link ecological theory with long-term observational data to identify potential drivers of observed shifts which have developed under natural conditions.

4.4.2. Lake Müggelsee

Müggelsee (52_260 N, 13_390 E) is a polymictic, shallow lake (mean depth 4.9 m, maximum depth 7.9 m) with a surface area of 7.3 km^2. An ongoing long-term sampling programme provides data on plankton, physical and chemical variables, with biweekly sampling in winter and weekly sampling in summer, beginning in 1979 (Driescher et al. 1993). Since the start of this sampling programme, the lake has experienced an increase in water temperature (around 0.5 °C per decade in summer) and quasi-simultaneously a decrease in nutrient loading (Köhler et al. 2005, Huber et al. 2008). Intermittent thermal stratification during summer is common in this shallow lake, with consequent effects on water temperature, oxygen, internal nutrient load and phytoplankton development (Wilhelm & Adrian 2008).

4.4.3. Example 1: Threshold driven regime shifts of two copepod species

The long-term dynamics (30 years) of two cyclopoid copepod species (*Cyclops vicinus* and *Cyclops kolensis*) were studied along a declining gradient in trophic state in a shallow, eutrophic lake. We showed that while under high nutrient conditions and thus high algal biomass the larger *C. vicinus* was the superior competitor (Figure 37), while it lost its advantage under medium productivity levels as it is a less effective exploiter of algal prey. We further predicted that the release of the smaller *C. kolensis* from competition for prey and predation pressure by *C. vicinus* enabled its sudden dominance of the winter copepod community. We further accessed the threshold density of the competitor, necessary for this shift to happen. Underlying mechanisms of that non-linear threshold driven response of both copepod species were tested by using two scenarios of regime shift theory in the context of intraguild predation theory. Only when the larger competitor, which exhibit higher requirements for algal prey, declined below a critical threshold in abundance - the coexisting smaller copepod species, exhibiting lower needs for algal prey, was able to thrive in the low algal food niche. The decline of *C. vicinus* followed the "Driver threshold" scenario described by Andersen et al. (2009) (corresponding to Figure 6b-d), while the increase in *C. kolensis* followed the "State threshold" scenario (corresponding to Figure 6f-h) (Figure 38). A detailed description of the study is given in Scharfenberger et al. (2013).

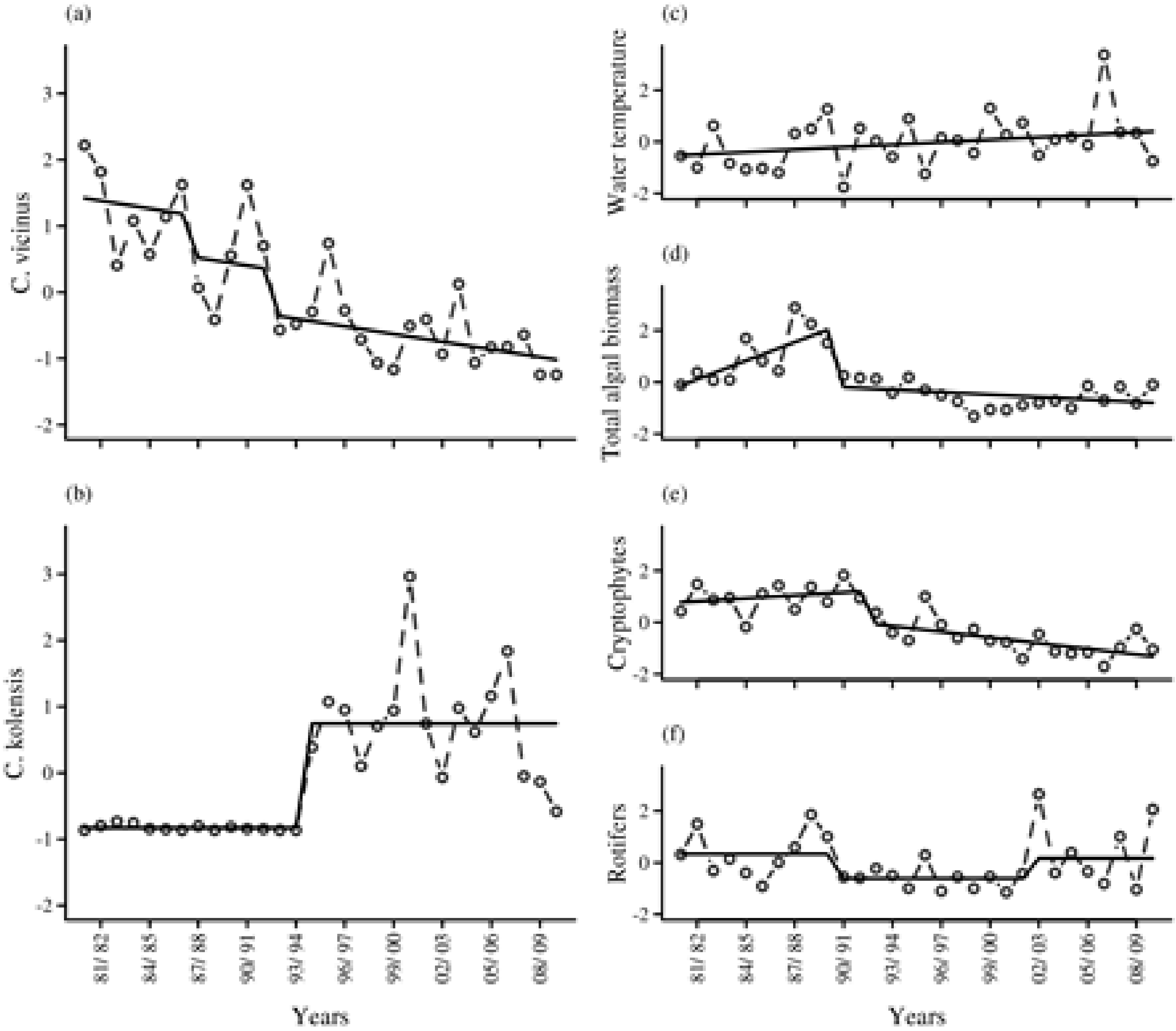


Figure 37. Trends in prey availability and water temperature. Abrupt and linear trend dynamics in yearly means. Solid lines depict robust regression models combining the largest abrupt changes in the mean from regression tree analysis for each variable, together with significant trends from monotonic trend analysis if these exist for the respective variable. *C. vicinus* (a), total algal biomass (d), and cryptophyte biomass (e) were dominated by both abrupt changes and gradual linear trends in the mean. *C. kolensis* (b) and rotifers (f) were purely breakpoint driven, while water temperature (c) was solely marked by a linear trend. Data were standardised with the maximum value of the respective variables. (From Scharfenberger et al. 2013).

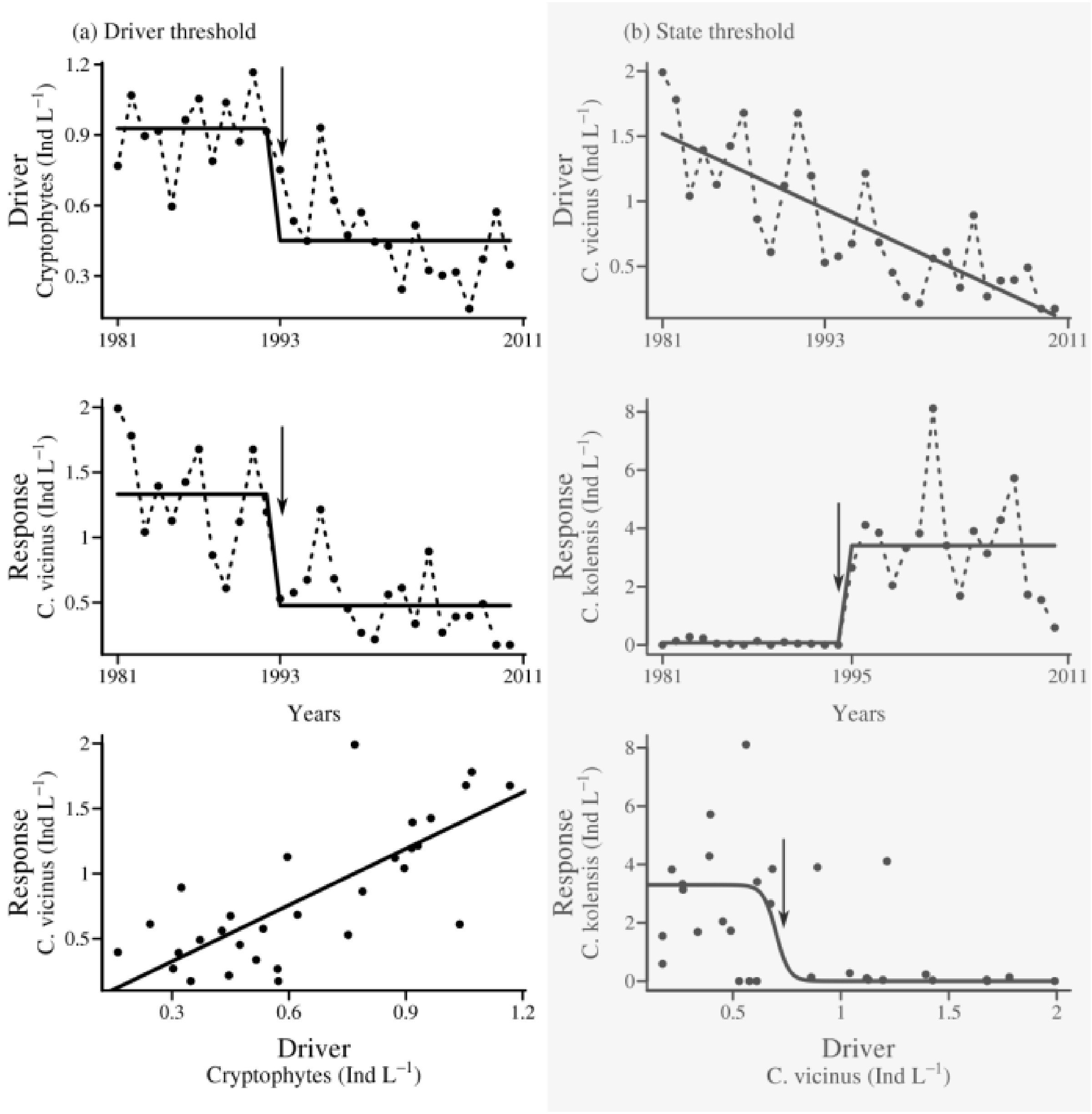


Figure 38. 'Driver threshold' and 'state threshold' regime shift scenarios. Analyses based on Fig. 1 in Andersen et al. (2009) (see also Figure 6). The driver threshold scenario refers to the existence of a threshold in the driver (cryptophytes in our case in Müggelsee), which is linearly mediated to a response (*C. vicinus* in our case). The regime shift in cryptophyte biomass in 1993 (a) was immediately followed by a regime shift in *C. vicinus* abundances, resulting in a linear driver (cryptophytes) response (*C. vicinus*) scatter plot. The solid lines in driver and response variables (panels a, and b) stress the breakpoint components in the dynamics of the two variables. The state threshold scenario (b) refers to the existence of a threshold in the response (*C. kolensis*), but not in the driver (*C. vicinus*). *C. kolensis* abundances underwent a regime shift after *C. vicinus* crossed a threshold, such that an abrupt change appears in the time series of *C. kolensis* and a threshold appears in the scatter plot between the two variables. The line in the upper panel solely depicts the linear trend component of *C. vicinus'* abundance, since only this part of the dynamics is relevant in this regime shift scenario. Arrows indicate the thresholds for the different regime shift scenarios. (From Scharfenberger et al. 2013).

4.4.4. Example 2: Thresholds derived from long-term records applied to two extreme heat wave years

Wagner and Adrian (2009a) showed in an earlier study that high TP concentration was the best predictor of elevated cyanobacteria dominance but that intensified and prolonged thermal stratification also promoted cyanobacteria dominance in Müggelsee. They extracted critical thresholds based on three decadal records. We tested whether the critical thresholds of environmental factors determined from these long-term records could explain the surprisingly contrasting development of cyanobacteria during the two heat wave years 2003 and 2006, where average water temperature were equally 1.5 standard deviations above the long-term average (Figure 39). Unexpected cyanobacteria biomass was at an all year record low in 2003, while 2006 was marked by a strong dominance in cyanobacteria as expected (Figure 40) (Huber et al. 2012). Critical thresholds of abiotic drivers extracted from long-term records (1993-2007) using classification tree analysis proved suitable to explain these contrasting observations. We found that cyanobacteria blooms were especially favoured in 2006 because thermal stratification was critically intense (critical threshold of >44 g cm cm^{-2}) and long-lasting (>3 weeks) (Figure 40).

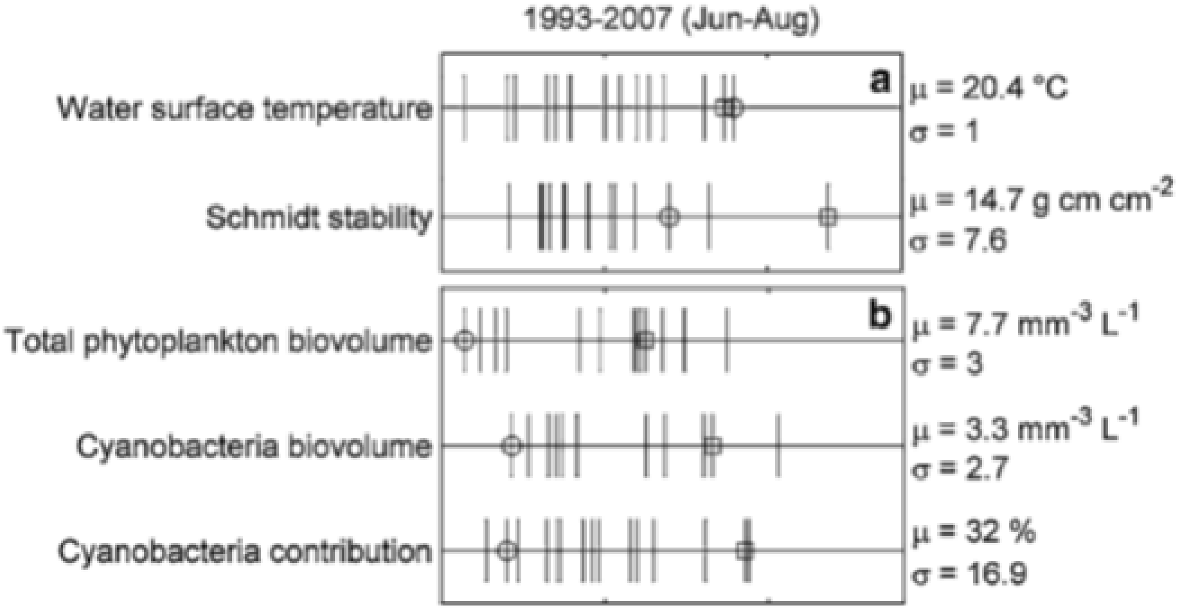


Figure 39. Summer averages of selected variables of (a) lake physics, (b) aggregated phytoplankton in Müggelsee, Germany, for 1993-2007 (vertical bars), with special focus on heat wave years 2003 (open circles) and 2006 (open squares). (From Huber et al. 2012).

By applying the quantified thresholds for total phosphorous (TP), the length of stratification (Sd), and Schmidt stability (Si) to the two extreme heat wave years we were able to successfully predict the contrasting response of cyanobacteria dominance in the two extreme years. There were only a few unsuccessful predictions marked by an asterisk in Figure 40. This study is an example of the situation illustrated in Figure 7c: effects of a climate-related variable (increased stratification) reinforce the biological response (cyanobacterial bloom) to nutrient pressure, and result in lower ecological status than the nutrient pressure alone.

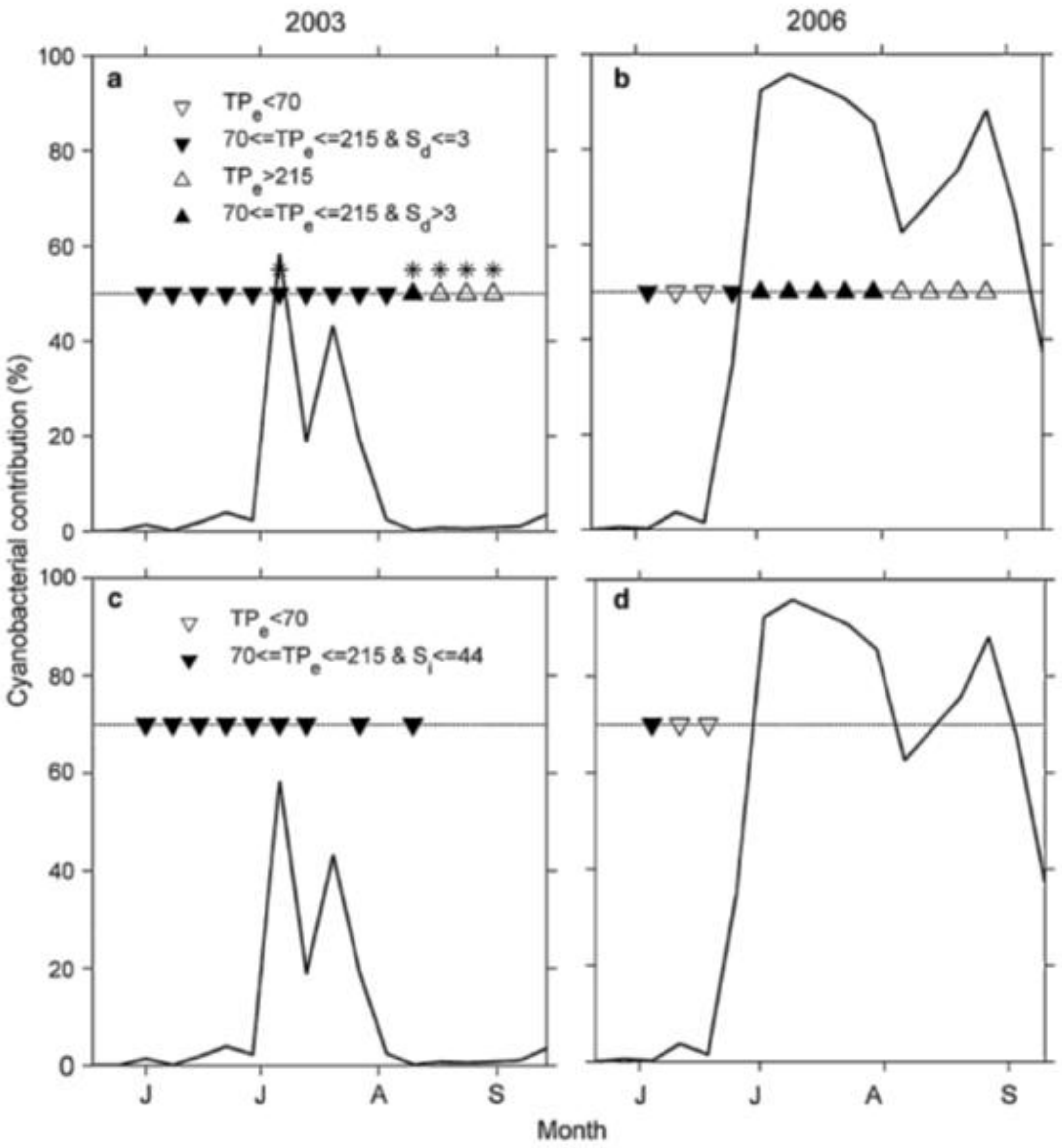


Figure 40. Observed cyanobacterial contribution to total phytoplankton mass (solid line) and rule-based predictions (triangles) for the summer 2003 and 2006. Classification rules predict cyanobacterial contribution to be above (upward-facing triangles) or below (downward-facing triangles) the chosen percentages of 50% (a,b) and 70% (c,d). (From Huber et al. 2012).

4.5. Case study Lake Vörtsjärv: Nutrient loads, water levels and regime shift of the phytoplankton community

Contributor: EMU (Peeter Nõges)

4.5.1. Introduction

A study of the 44-year data series on Võrtsjärv phytoplankton (Nõges et al. 2010a) suggests a non-linear response of phytoplankton to changing nutrient loadings and the occurrence of a regime shift between 1977 and 1979 triggered by an abrupt water level increase, which supported the establishment of the new highly shade-tolerant phytoplankton community dominated by the cyanobacteria species *Limnothrix redekei* and *L. planktonica*.

Lake Võrtsjärv is situated in central Estonia and is the second largest lake in the country with a surface area of 270 km^2 and a catchment area of 3,374 km^2. The lake is eutrophic, characterised by mean concentrations of about 1.4 mg L^{-1} total N and 50 µg L^{-1} total P. This very shallow (maximum depth 6 m, mean depth 2.8 m) non-stratified lake has six main inflows and one outflow that carries the water into Lake Peipsi. Owing to its shallowness and large wind-exposed area, the water-body is turbid (Secchi depth ranges from 0.5 to 1.0 m during the ice-free period). Large natural fluctuation of the water level within a range of 3 m is the main hydrological peculiarity of the lake affecting growth conditions for phytoplankton. At high water levels, average light conditions in the fully mixed water column deteriorate as the proportion of dark layers increases. This effect is amplified by the commonly increased humic matter content of water at higher water levels. At low water levels sediment resuspension releases more phosphorus but intensifies denitrification resulting in a drop of the N:P ratio. Besides year-to-year differences, the water level shows a multi-annual periodicity (Figure 41) well described by the NAO winter index.

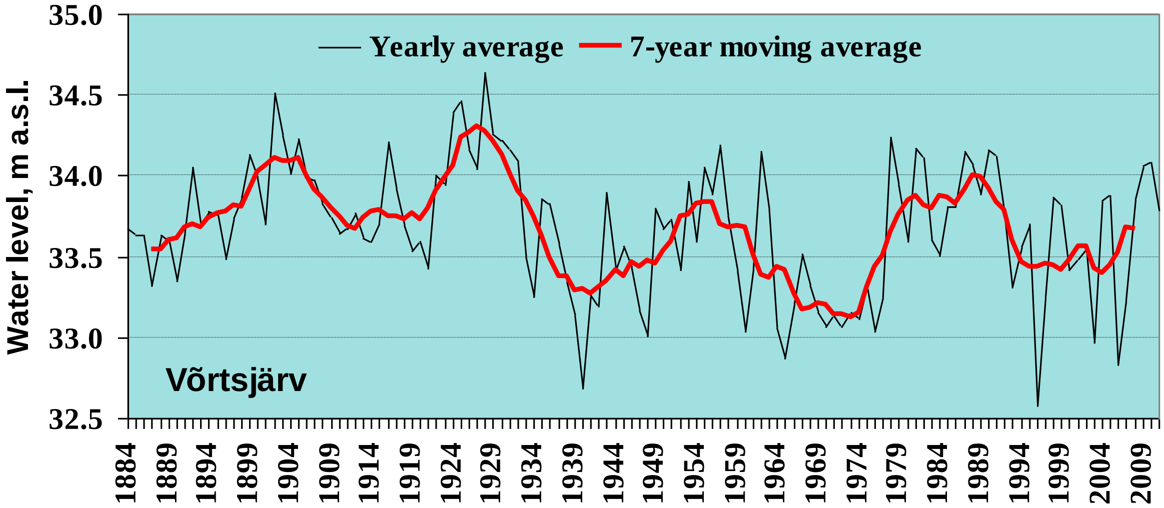


Figure 41. Long-term changes in the water level of Lake Võrtsjärv.

4.5.2. Results

The eutrophication history of Lake Võrtsjärv judged upon changes in carbonate content of sediments along a sediment core shows an increase since the 1950s with a peak during the 1980s (Heinsalu et al. 2008). The 1960s mark the onset of pronounced eutrophication. Measured nutrient loadings since 1975 showed a massive peak in nitrogen loading throughout the 1980s (Figure 42a) whereas P loadings had a general decreasing trend with still some extremes in the 1980s (Figure 42b).

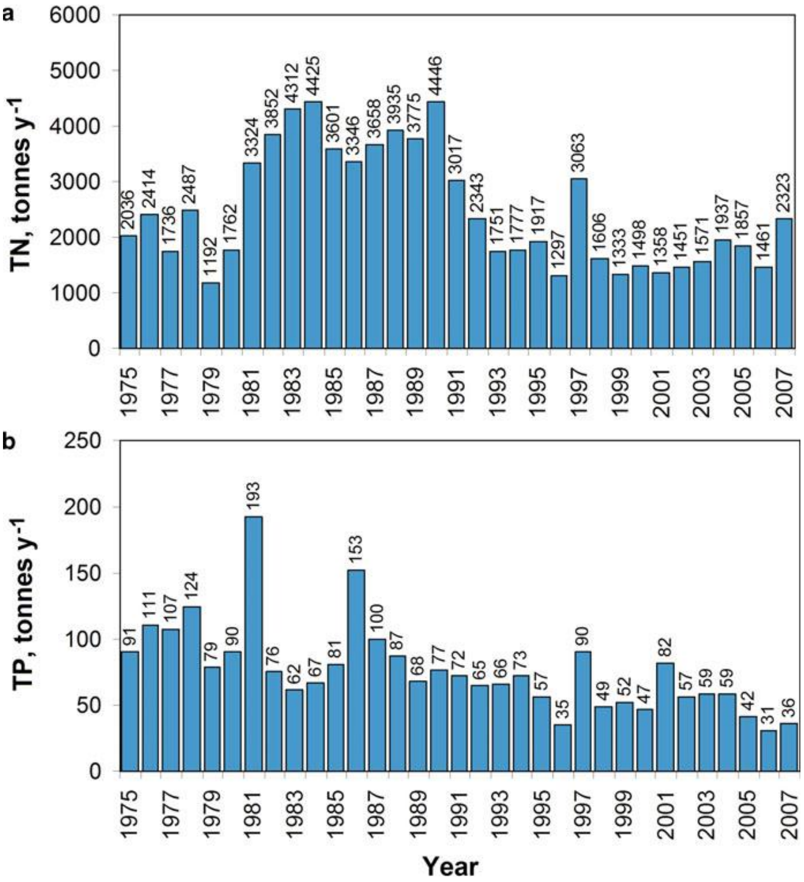


Figure 42. Long-term dynamics of nitrogen (a) and phosphorus loading (b) to Võrtsjärv.

With increasing eutrophication pressure, phytoplankton biomass increased and the 1970s can be characterised by highest biomass values for the whole study period since 1964 (Figure 43), but the phytoplankton composition remained largely the same as described during the first complex expedition in the years 1911-1923 (Mühlen & Schneider 1920). The dominant species was the cyanobacterium *Planktolyngbya limnetica*, accompanied by diatoms *Aulacoseira ambigua*, *Asterionella formosa* and others. Among green algae, several species of *Pediastrum* were most numerous. Water blooms caused by *Anabaena lemmermannii* in June recurred from year to year until the end of the 1970s.

Sudden change in plankton composition between 1977 and 1979 accompanied by a decrease in the total biomass, involved most of the functional groups and brought about a persistent change in phytoplankton dominant species which replaced *P. limnetica* with highly shade-tolerant species. Considering the abruptness, extent and persistency of the change, we can talk about a regime shift. Among several tested phytoplankton indices, the sharp change was best captured by the German PTSI index (Mischke et al. 2008) (Figure 44, Figure 45).

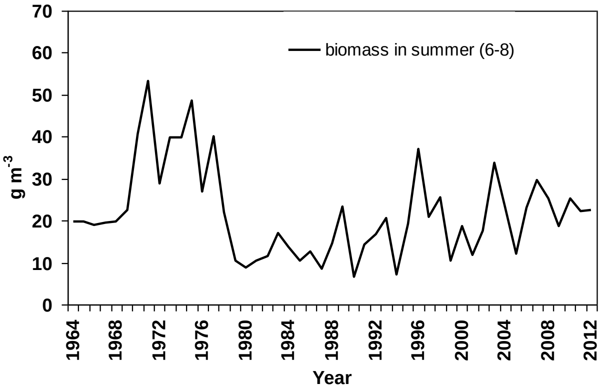


Figure 43. Long-term changes in summer (June-August) phytoplankton biomass in Võrtsjärv.

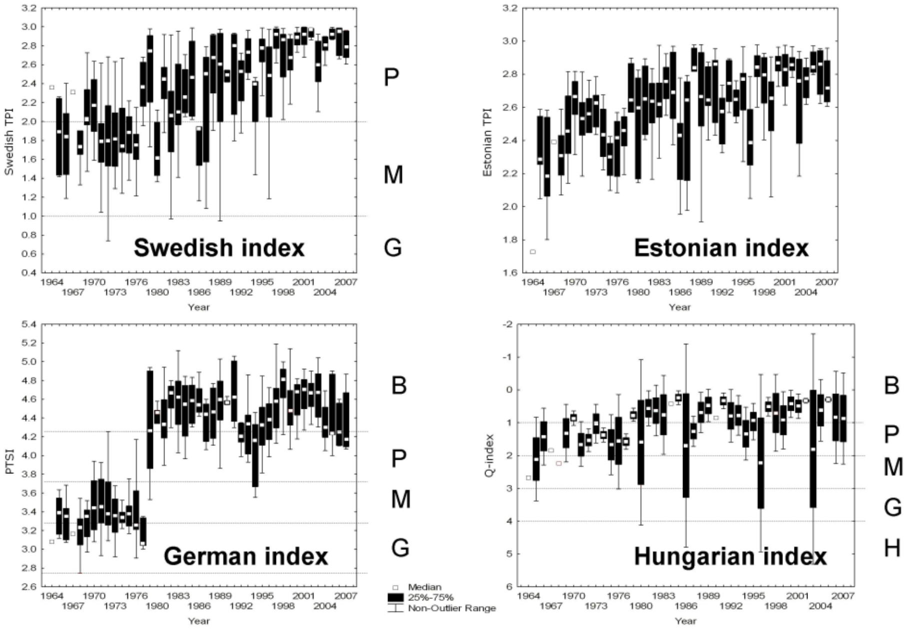


Figure 44. Long-term changes in ecological status of Võrtsjärv as indicated by some phytoplankton taxonomy based indices: the Swedish index (Willén 2007), the Estonian index, the German PTSI index (Mischke et al. 2008) and the Hungarian index (Padisák et al. 2006). The full German index is based on three metrics: biomass, algal classes and an indicator taxa-based index – PTSI, but here we used only the latter. The status classes H – 'high', G – 'good', M – 'moderate', P – 'poor', and B – 'bad' are based on WFD normative definitions

4.5.3. Discussion

Looking for an explanation for the regime shift around 1978, we first analysed the nutrient pressure. Although heavy loadings over the 1960s and 1970s had obviously destabilised the ecosystem and brought it to the boundary of breaking the resilience, changes in nutrients could not be the direct initiator of the change as a major increase in both TN and TP loadings occurred only in 1981, i.e. a couple of years after the change in phytoplankton (Fig. 5a). Plotting the PTSI index against water level changes revealed that the latter was obviously the triggering factor for the change. After a long dry period in the 1960s and most of the 1970s, the extremely rainy summer and autumn of 1978 increased the average water level for the following year by more than a metre. High water level and the increased water colour caused a sharp deterioration of light conditions in the lake and supported the succession of the dominating species. This situation might be illustrated by Fig. 7c: at high nutrient pressure, a climate-related change acts as a trigger that causes a drop in ecological status (although a pressure-response curve is not specified in this case). Moreover, the change was persistent and not reversed by single low water years such as 1996 or 2003. High shade tolerance of the *Limnothrix* species and their efficient use of nutrients for building up biomass (shade) create a self-supporting habitat in which other species are strongly suppressed. Despite a general and considerable decrease in nutrient loadings, the percentage of filamentous cyanobacteria does not show a decreasing trend. This situation might be represented by Fig. 7d: a climate-related change in environmental conditions impedes the recovery of the biological community, even when the nutrient pressure is reduced. Given the general "browning" trends in many lakes over the northern hemisphere (Jennings et al. 2010), an increase of humic matter content in Võrtsjärv as a mechanism stabilising the new status quo over a longer period cannot be excluded. Although we lack direct measurements of dissolved organic matter (DOM) content, the chemical oxygen demand COD_{Mn}, a common proxy for DOM, was significantly lower in the period 1968–1977 compared with that in 1998–2008 and had a highly significant increasing trend within both periods (Tuvikene et al. 2010).

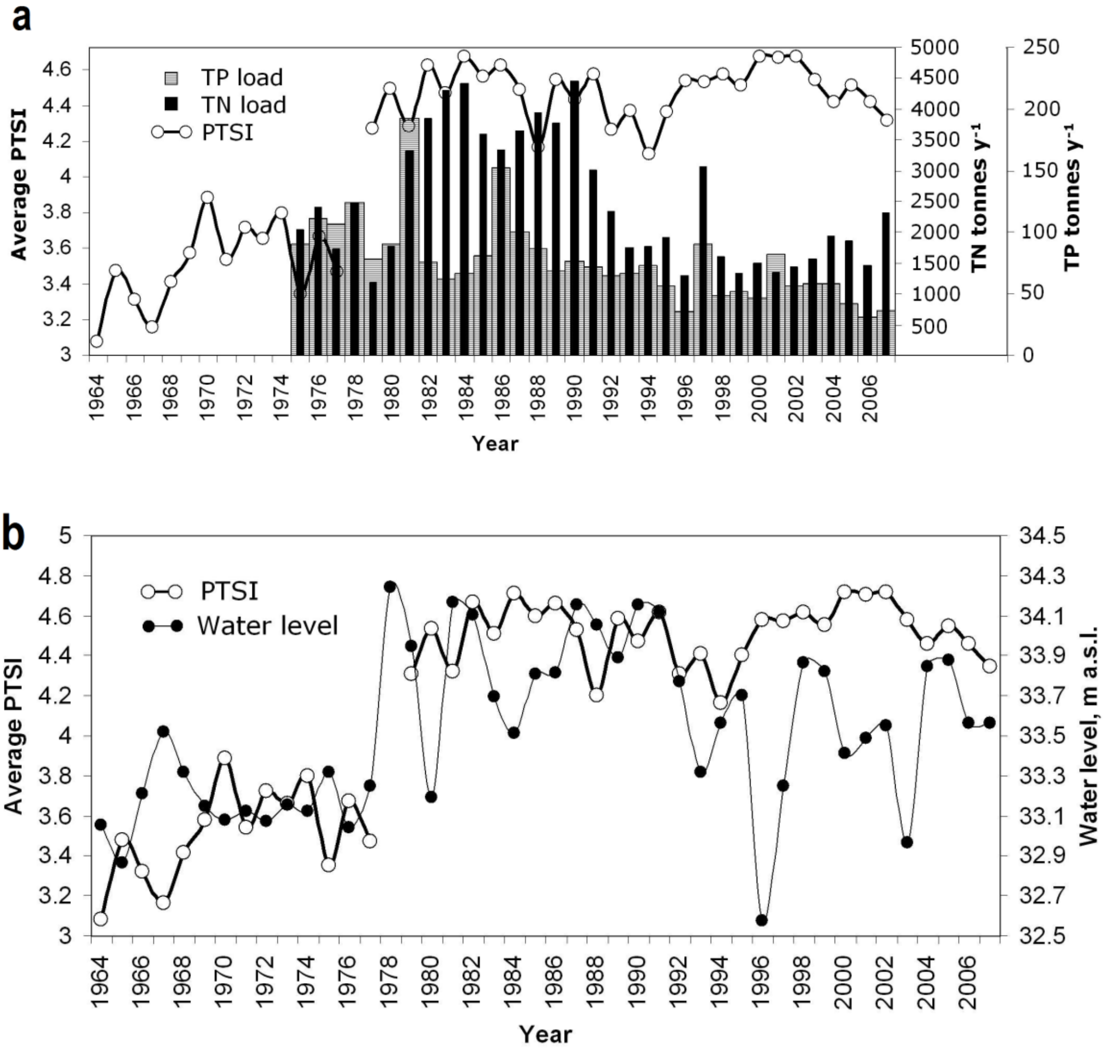


Figure 45. Long-term changes in the German PTSI index on the background of (a) nutrient loadings to the lake and (b) water level changes.

5. Synthesis and recommendations

The aim of this report has been to assess impacts of climate change on reference conditions and ecological thresholds in European lakes, to consider the implications for ecological classification systems (reference values, class boundaries and water body types), and to provide recommendations to river basin managers concerning monitoring programmes and programmes of measures. The EC guidance on river basin management in a changing climate (2009) states that "In general, reference conditions and default objectives should not be changed due to climate change projections over the timescales of initial WFD implementation (up to 2027) unless there is overwhelming evidence to do so" (section 5.4.4. Reference sites). Moreover, one should "avoid using climate change as a general justification for relaxing objectives" (EC 2009, section 5.5 Objectives setting), such as relaxing the Good/Moderate boundary.

Nevertheless, although national classification systems are already established and intercalibrated by most EU member states, the six-year River Basin Management planning cycle of the WFD offers an opportunity to review the methods for the adequate assessment of the ecological status of EU water bodies. Moreover, the programme of measures within the River Basin Management Plans should take account of climate change effects in other to achieve the WFD good status target and ensure ecosystem uses. In addition, impacts of climate change may affect lake ecosystem services and threaten the implementation of the EU Biodiversity Strategy 2020, specially target 2: Maintain and restore ecosystems and their services. Therefore, although not explicitly mentioned in the WFD, synergies between the WFD and the Biodiversity Strategy may contribute to both maintain and restore lake ecosystems and the services they provide.

The following key messages can be extracted from the literature review, new data analyses and case studies presented in this report as a basis for recommendations. In general, our results and recommendations support and expand on those given in the EC guidance (2009), by Moe et al. (2010a) and by Nõges & Nõges (2014).

5.1. Impacts of climate change on reference conditions and implications for classification systems (reference values)

- Changes in lake type may occur, e.g. (i) shifts from clear-water to humic lakes due to brownification of lakes in Northern Europe, (ii) to more turbid lakes due to increased erosion after heavy rains), or (iii) shifts from oligosaline to more saline lakes due to increased droughts in arid and semi-arid regions.

- Changes in the reference conditions for phytoplankton are expected for species composition, abundance and the onset and frequency of algal blooms due to the effects increased temperature in combination with nutrients and and degraded underwater light conditions, depending on lake type and ecoregion. This will potentially affect reference conditions of metrics such chl-a, the plankton trophic index (PTI), and cyanobacterial biovolume.

- Heavier rains in Northern regions may also cause reference concentrations of nutrients to increase. In consequence, more nutrient-demanding phytoplankton species such as cyanobacteria may increase their relative abundance also in reference lakes. Therefore, an increase in reference values of both nutrients and cyanobacteria (currently zero in many countries) may be warranted. The increased flushing of lakes in areas with increasing precipitation can, however, reduce the biomass of cyanobacteria and other phytoplankton. The net effects of climate change on phytoplankton are therefore difficult to predict.

- Warmer climate including earlier and prolonged summer stagnation will cause a decrease in cold-water species and increase in warm-water species, e.g. reducing large-bodied salmonid fish such as char and increase small cyprinid fish. These changes may also weaken the top-down control of zooplankton on phytoplankton. The same effects can appear due to phenological changes in peaks of zooplankton relative to phytoplankton.
- Changes in macroinvertebrate community composition due to predicted shifts in geographic distribution would have clear implications for reference conditions and the use of taxonomy-based metrics.
- More extreme climatic events will cause increasing water level fluctuations. These fluctuations and changes would have negative impacts on macroinvertebrates and macrophytes, and affect their community composition.
- Increased salinity in lakes in Southern Europe due to more prolonged droughts may affect species composition of all BQEs, and thereby also the reference conditions of metrics used to assess community composition.

5.2. Impacts of climate change on thresholds and implications for classification systems (class boundaries)

- The processes described above for reference conditions will also cause increased nutrient load and thus increased probability of exceeding the current management targets (such as the good/moderate boundaries) for one or more biological quality elements.
- Climate change will worsen underwater light conditions, and is therefore likely to cause the most sensitive macrophytes (e.g. isoetids and charaphytes) to disappear at lower nutrient levels than at present. This suggests that the current good/moderate class boundary for macrophyte metrics will be reached at lower nutrient levels in the future.
- Shifts of thresholds in phytoplankton metrics due to climate change are more difficult to predict so far. However, most of the results presented in this report suggest that climate change is likely to increase the proportion of cyanobacteria, as well as other shade-adapted harmful algae such as *Gonystomum semen* (the latter mainly in humic lakes). Hence, the concentration of cyanobacteria that currently comprise the good/moderate class boundary (e.g. 1 mg L^{-1} in some countries) will probably be reached at lower nutrient levels in the future. However, certain modelling studies suggest that increased flushing of lakes in areas with more precipitation may partly counteract these changes.
- Fish metrics based on abundance of salmonids or on ratios between salmonids (or perchids) and cyprinids may need adjustment of class boundaries to account for climate change, as salmonids are sensitive to increased water temperature and also to brownification that reduce the oxygen concentration in the water.
- The above-mentioned probable changes in the dose-response relationships of BQE metrics against nutrients could be dealt with in two different ways: a) keeping the current G/M boundaries for the BQEs, but make the nutrient standards more stringent, or b) relaxing the G/M boundaries for the BQEs, as these are due to climate change, and keep the current nutrient standards. The latter option might lead to undesirable disturbance for users (e.g. more turbid water, algal blooms, lack of salmonids). Hence, the first option should be chosen if the ecosystem services are considered (see section 5.3).

5.3. Impacts on ecosystem services

- Increased costs will be needed for drinking water supply due to browner and more turbid water with increased probability of more harmful algae in areas with warmer and wetter climate.
- Water scarcity and droughts and related deterioration of water quality pose a major threat to water supply for drinking and for irrigation of agriculture in Southern Europe and in other areas with increasing dry periods in summer.
- The quality of bathing water will also deteriorate due to climate change for the same reasons as given above. Overflow of sewage may also increase microbial pathogens and cause unsuitable water quality for bathing after heavy rains.
- The value of lakes for sportsfishing may also be reduced due to less production of cold-water adapted salmonids (e.g. char) and of other top-predator fish (e.g. pikeperch).
- The overall value of lakes for recreation may be reduced due to more turbid or browner water with more harmful algae and less attractive fish species.

5.4. Recommendations for river basin managers

- Monitoring biological quality assessment metrics in a set of reference lakes to assess the nature and degree of any change will be required for assessing the effect of climate change on reference conditions and setting reference values for the different BQEs, and for providng a basis for revision of lake types.
- Improved monitoring of lakes impacted by eutrophication is crucial to assess whether the nutrient reduction measures and other restoration efforts are sufficient to achieve good status. If possible, both increased frequency and increased number of lakes should be considered. If only one BQE can be prioritised due to limited resources, then phytoplankton should be selected as the BQE responding most strongly to eutrophication (Lyche-Solheim et al. 2013).
- The monitoring of both reference sites and impacted sites is essential to re-evaluate the
- classification systems for ecological status assessment (in particular the good/moderate class boundaries, including the nutrient standards).
- For single water bodies a type change should be considered before the programme of measures is revised. If a lake turns from a clear-water lake to a humic lake or a turbid lake as a consequence of climate change, it may be impossible to achieve good status, if class boundaries for clear-water lakes are still used to set the good status objective.
- Additional nutrient reduction measures may be needed to counteract the effects of climate change in lakes and achieve good ecological status and ensure continued provision of ecosystem services. Climate change impacts on lakes are probably still small enough to be compensated with small-moderate additional restoration efforts in the 2nd RBMPs.
- The climate change impacts are expected to increase in the coming years and may thus require major improvements in nutrient reduction measures for the 3rd RBMP if good status and sufficient provision of ecosystem services should be attainable in 2027.
- More specific recommendations for development of climate change adaptation, mitigation and restoration strategies for lakes are given by Nõges & Nõges (2014).

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