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WISER

Water bodies in Europe: Integrative Systems to assess Ecological status and Recovery

DELIVERABLE

Deliverable D5.2-5: Report on effects of global change on reference conditions and ecological status of lakes

Lead contractor: University College London (UCL)

Contributors: Helen Bennion, Ben Goldsmith, Martin Kernan, Xuhui Dong, Thomas Davidson, Jannicke Moe, Gavin Simpson, Erik Jeppesen, Laurence Carvalho, Carl Sayer, Juliane Wischnewski, Gina H. Clarke, David Morley, Bent V. Odgaard, Peter Rasmussen, Ruth Rawcliffe, Jorge Salgado, Susanne L. Amsinck, Stephen C. Maberly, Richard W. Battarbee, Tuomo Saloranta, Olli Malve, Niina Kotamäki & Anne Lyche Solheim

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Report on effects of global change on reference conditions and ecological status of lakes

List of contributors

Helen Bennion[1], Ben Goldsmith[1], Martin Kernan[1], Xuhui Dong[1&8], Thomas Davidson[1,2], Jannicke Moe[3], Gavin Simpson[1], Erik Jeppesen[2,6,7], Laurence Carvalho[4], Carl Sayer[1], Juliane Wischnewski[5], Gina H. Clarke[1], David Morley[1], Bent V. Odgaard[2], Peter Rasmussen[6], Ruth Rawcliffe[1], Jorge Salgado[1], Susanne L. Amsinck[2], Stephen C. Maberly[9], Richard W. Battarbee[1], Tuomo Saloranta[10], Olli Malve[11], Niina Kotamäki[11], Anne Lyche Solheim[3]

[1] Environmental Change Research Centre, UCL, UK

[2] Department of Bioscience, Aarhus University, Denmark

[3] Norwegian Institute for Water Research (NIVA), Norway

[2] Centre for Ecology & Hydrology (Edinburgh), UK.

[5] Alfred Wegener Institute for Polar and Marine Research, Germany

[6] Greenland Climate Research Centre (GCRC), Greenland

[7] Sino-Danish Centre for Education and Research (SDC), Beijing, China

[8] State Key Laboratory of Lake Science and Environment, Nanjing, China.

[9] Centre for Ecology & Hydrology (Lancaster), UK.

[10] Norwegian Water Resources and Energy Directorate (NVE), Norway

[11] Finnish Environment Institute (SYKE), Finland

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Content

Non-technical summary

WISER aims to support the implementation of the Water Framework Directive (WFD) by developing tools for the assessment of the ecological status of European surface waters. With many European lakes unlikely to achieve ‘good’ ecological status without restorative measures, the assessment systems used in the WFD are required to consider recovery in order to judge restoration success. Most previous projects dealing with assessment systems have focused on the effects of deterioration. WISER also deals with recovery.

The report summarizes the progress made within the WISER project in the following areas:

- Reviewing the current understanding of the impacts of climate change on lakes and how this can be utilised to develop and improve our understanding of lake restoration.
- Investigating the pathways of degradation in lakes where eutrophication has been the primary stressor and examining how these pathways react during lake recovery following remedial action.
- Two further studies are presented which use lake sediment records and long-term monitoring data sets to assess the relative importance of climate versus eutrophication.
- The role of cladocerans in tracking long-term changes in shallow lakes is explored; a study which highlights the sensitivity of this biological group and presents it as a strong candidate as the single best indicator for assessing trophic change in lakes.
- Finally Baysian network models are presented as an effective tool for unravelling the complex interaction between the impacts of lake restoration and climate change on the ecological status of lakes.

In addition to providing an assessment of the various tools available for tracking environmental change in lakes, this report highlights the complexities of ecosystem recovery under changing global conditions. A reduction of environmental stressors (e.g. eutrophication) will undoubtedly result in ecosystem improvement, but it is unlikely to simply be the reversal of deterioration and some examples show that recovery may lead to conditions very different from the original undisturbed stage. These studies contribute towards the scientific basis for underpinning the management of freshwaters in order that it is strengthened and targeted appropriately

The main achievement of societal relevance is the increased understand of how strategies for the sustainable management of freshwaters, for example, as required by the WFD, may need to be modified to take account of global, especially climate change.

Extended summary

Responsible: Ben Goldsmith Contributors: all authors

Chapter 1 gives an overview of the current understanding of the impacts of climate change on the ecological status of lakes. WISER has built on the experience and results from several European projects including STAR, REBECCA, THRESHOLDS and Euro-limpacs. Euro-limpacs was concerned with the effects of climate change on aquatic ecosystems and the outcomes are therefore very relevant to WISER. The review details work conducted on the direct impacts of climate change on lakes including the effects of temperature, ice cover and wind speed. The interactions with hydromorphology are also discussed in relation to catchments processes and increased sediment loads on deep lakes and impacts of higher sediment accumulation rates on shallow lakes.

Eutrophication of inland waters is now probably the most widespread problem in freshwater ecosystems. Spatial studies concluded that with increasing temperature, European lakes are likely to witness significant impacts on phytoplankton, zooplankton and macrophyte populations with implications for ecological status and biological assessments, particularly where there are barriers to migration. There will certainly be a deviation from notional reference conditions. A number of contemporary and palaeoecological studies are presented with the general agreement that that warming will exacerbate many, though not necessarily all, symptoms of eutrophication. It was also concluded that the complexity of the processes resulted in a high degree of uncertainty when it came to addressing specific problems and a precautionary approach was recommended.

Other stressors are examined including acidification, trace metal pollution and persistent organic pollutants and the many complex cause-effect chains that will be driven by climate change. These will be directly and/or indirectly influenced by temperature and precipitation and will be linked by numerous interacting environmental parameters. Euro-limpacs identified a potential set of indicators for lakes in cold, temperate and warm ecoregions. Most of these were indicators that could be accommodated within existing routine monitoring programmes and, in many cases, it was concluded that simple physico-chemical measurements are most appropriate.

The role of Euro-limpacs in defining reference conditions is discussed and the two main approaches detailed. Typology- and model-based approaches were in some cases very effective with for example latitude, altitude and catchment size being important predictors of invertebrate assemblages in boreal streams. There is evidence, however, that classifications based solely on landscape-scale predictors do not capture the fine-scale variability of aquatic communities. Site-specific predictors such as water chemistry also need to be included. Historical and palaeolimnological records have therefore also been used extensively, particularly for regions which today have few, if any, reference sites remaining. While these methods can in many cases produce very good estimates of reference conditions, there remains uncertainty and use of multiple approaches is recommended along with further research.

The complexities of lake restoration are considered in terms of bio-geographical mechanisms such as dispersal and connectivity and how these may be further impacted by climate change. The potential loss of aquatic ‘corridors’ as ponds dry in warmer climates is one such example. There is also acknowledgement that the reference condition is not static, but will likely show a monotonic climate-driven trend. Hence approaches that explicitly include interannual variability in weather and/or long-term trends in climate should be given greater consideration. 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 would be of interest.

In conclusion, the main outcomes of the Euro-limpacs project included:

i) increased understanding of the effects of climate change, both directly and through its interaction with other key stressors, on the ecological status and functioning of European freshwaters;

ii) identified and evaluated restoration efforts to recover the historical losses and degradation which have occurred due to human impacts;

iii) developed approaches and identified priorities for dealing with the effects of future global change scenarios relating to climate and hydrology, land-use and nutrients, acidity and toxic substances.

iv) developed a unified system of ecological indicators for monitoring freshwater ecosystem health, and new methods for defining reference conditions and restoration strategies.

Chapter 2 examines the degradation and recovery pathways as identified through the palaeolimnological record of both deep and shallow lakes. Efforts to restore enriched lake systems have increased over the last few decades, but there remains, considerable uncertainty about whether restoration targets can be achieved and over what timescales one might expect to see improvement. Here, palaeoecological techniques are employed to examine the degree of impact and recovery in thirteen European lakes that have been subject to eutrophication and subsequent reduction in nutrient loading. The response of several diatom metrics is explored including percentage plankton, diversity, community composition and diatom-inferred total phosphorus concentrations.

Changes in the diatom records reflect both the degradation and the recovery process. All sites, with the exception of two lakes where the patterns are less clear, exhibit progressive deviation from the reference sample (core bottom) during the period prior to nutrient reduction, indicating gradual compositional change with enrichment. The shifts in diatom composition following reduction in nutrient loading are more equivocal, with a clear reversal towards the reference flora seen only in four of the deep lakes and one of the shallow lakes. The compositional changes are gradual suggesting that ecological recovery may take several years to decades. In the remaining deep lakes, alternative nutrient sources would seem to explain the lack of apparent recovery. In three of the shallow lakes the diatom assemblages do not track back along the enrichment pathway following remediation but are replaced by a community associated with lower productivity. Factors such as internal loading and top down control may influence the recovery process in shallow lakes. Hence, ecosystem recovery is not simply a reversal of the degradation process. The recovery process has a long way to go in all sites as the present assemblages remain different from those seen in the pre-enrichment samples, as indicated by ordination analyses and high dissimilarity scores between core bottoms and tops.

By assessing ecological change over a centennial to decadal timescale, the study highlights the important role that palaeolimnology can play in establishing a benchmark against which managers can evaluate the degree to which their restoration efforts are successful.

Chapter 3 focuses on Loch Leven and explores the potential of a palaeolimnological approach, in combination with long time series, to assess the impacts of nutrients and climate on a range of timescales from several centuries to seasons. Changes in nutrients and climate have occurred over approximately the same timescales in many European lake catchments. This study attempts to interpret the sedimentary diatom record of Loch Leven (a large shallow lake), in relation to these pressures using information gained from analysis of long-term datasets of water quality, climate and planktonic diatoms. The core data indicate enrichment of Loch Leven starting in ~1800-1850, most likely from agricultural practices in the catchment, with a more marked phase since ~1940-1950 caused by increased phosphorus inputs from sewage treatment works, land drainage and a woollen mill.

While the recent diatom plankton remains are dominated by taxa associated with nutrient-rich conditions, an increase in *Aulacoseira subarctica* relative to *Stephanodiscus* taxa since the mid-1980s suggests that reductions in external catchment sources of nutrients (since 1985) may have resulted in partial recovery. This observation accords well with the long-term monitoring series of water chemistry and phytoplankton.

On a decadal-centennial scale, the eutrophication signal in the sediment record outweighs any evidence of climate as a control on the diatom community. However, at an inter-annual scale, while the diatom data exhibit high variability, there are several changes in species composition in the recent fossil record that may be attributed to climatic controls.

The study again highlights the value of a palaeolimnological approach, particularly when coupled with long-term datasets, for developing our understanding of environmental change at a range of temporal scales. The diatom record in the sediment can be used effectively to track recovery from eutrophication, but requires greater understanding of contemporary ecology to fully interpret climate impacts.

Chapter 4 exemplifies the use a long-term monitoring dataset of both phytoplankton and physicochemical characteristics of Esthwaite Water (England) that started in 1945. This provides a rare opportunity to understand the effects of climate and nutrients on a lake ecosystem. Monitoring records show that the lake experienced nutrient enrichment from the early 1970s, particularly after 1975, associated with inputs from a local sewage treatment plant, resulting in marked increases in concentration of soluble reactive phosphorus (SRP). Climatic variables, such as air temperature and rainfall, exhibit high variability with increasing trends observed after 1975.

Diatom analyses of an integrated ^{210}Pb-dated lake sediment core from Esthwaite Water, covering the period from 1945 to 2004, showed that fossil diatoms exhibited distinct compositional change in response to nutrient enrichment. Redundancy analysis based on diatom and environmental data sets over the past 60 years showed that the most important variables explaining diatom species composition were winter concentrations of soluble reactive phosphorus, followed by air temperature, independently explaining 22% and 8% of the diatom variance, respectively.

Additive models showed that winter SRP was the most important factor controlling the diatom assemblages for the whole monitoring period. AirT had little effect on the diatom assemblages when nutrient levels were low prior to 1975. With the increase in nutrient availability during the eutrophication phase after 1975 however, climate became more important in regulating the diatom community, although SRP remained the major controlling factor.

The relative effects of climate and nutrients on diatom communities vary depending on the timescale. RDA and additive model revealed that climate contributed little to diatom dynamics at an annual or decadal scale. The combination of monitoring and palaeolimnological records employed here offers the opportunity to explore how nutrients and climate have affected a lake ecosystem over a range of timescales. This dual approach can potentially be extended to much longer timescales (e.g. centuries), where long-term, reliable observational records exist.

Chapter 5 provides a very comprehensive insight in to the use of cladoceran remains in lake sediments for tracking long-term changes in shallow lakes. Shallow lakes in particular have been affected by human activities, profoundly altering their ecological structure and function with aquatic macrophytes often being used to determine the ecological condition of a site. Similarly, although not included as a BQE in the WFD, many studies have shown cladocerans to be useful tracking the changes resulting from a variety of drivers at a number of time-scales. In this study the plant macrofossils are compared with the sub-fossil cladoceran assemblages from 20 dated sediment cores. Co-Correspondence Analysis was used to determine the degree of commonality of change in community composition of the two biological groups through time.

The analysis revealed very high levels of agreement in the nature and timing of change at all the sites examined with very high correlation coefficients between the axis 1 scores for macrofossils and cladocerans. Furthermore, at all sites a high proportion of the variance (min 20%, max 54%) in the macrofossil data was explained by the change in the cladoceran assemblage. Sub-fossil macrofossil and cladoceran assemblages, from at least from 1700 AD onwards, were examined in more detail at three sites: Ormesby Great Broad, Felbrigg Lake and Lake Søbygaard. There was very good accord in the main shifts of the cladoceran and macrofossil assemblages at all three sites. This may reflect the long-term shift in the principal focus of primary production from the benthic to the pelagic habitat.

It is suggested that the combination of their central position in the food web and the presence of both pelagic and benthic taxa make cladocerans a strong candidate as the single best indicator of (palaeo) ecological condition related to changing trophic status and alteration in food-web structure in shallow lakes. This study provides compelling evidence for the inclusion of cladocera as a BQE in the WFD.

Drawing on many of the issues discussed above, **Chapter 6** outlines the use of Baysian modelling techniques to address the complex interaction of climate change and the ecological stats of lakes. Specifically, this modelling study focuses on the combined impacts of restoration and climate change on ecological status based on phytoplankton (chlorophyll *a)*. In addition, the effect of lake restoration in terms of reduced P loading is also modelled considering altogether 9 scenarios: 3 levels of restoration (no change; -20% P loading; -40% P loading) combined with 3 levels of climate change (no change; +2 °C air temperature; +4 °C air temperature). The impacts of these scenarios are explored through the lake status class according to a biological quality element (phytoplankton) as well as supporting physico-chemical elements (total P and total N). Since the ecological classification of lakes is dependent on the lake type, the work is limited to two common lake types of Northern Europe as an example (L-N2a - low altitude; L-N5 - high altitude).

A Bayesian network can be developed as a conceptual model, but can also be parameterised and used as a simulation model. In brief, each variable (e.g. Total P, Chl-a) is illustrated by a node, which represents a discrete probability distribution. This modelling approach has many benefits, especially in relation to environmental risk assessment and management: it can easily combine data or other information from different sources; it can explicitly model uncertainties (as probability distributions); and it can predict the probability of different outcomes of interest (such as different status classes).

Accepting the model limits and assumptions, the BN model predicts a climate change of +2 °C would almost counteract the benefit from 20% P loading reduction, while +4 °C would more than outweigh the benefits from 40% P loading reduction. The risk of not meeting good ecological status was less affected in this study. Although "good ecological status" is the main WFD management goal, preservation of high status is also a WFD requirement.

The Bayesian network modelling approach presented in this chapter is very general, and can easily be extended to include more lake types and other biological quality elements, as well as different scenarios. Based on the work presented here, the BN methodology has also been adopted by the ongoing EU project REFRESH, as a common approach for linking ecological responses to physico-chemical pressures for all water categories and all biological groups.

1. The impacts of climate change on the ecological status of lakes and on the use of reference conditions as a tool for lake restoration - a review of outputs from Euro-limpacs

Responsible: Martin Kernan

1.1 Introduction

1.1.1 WISER

The primary aim of WISER (Water bodies in Europe: Integrative Systems to assess Ecological status and Recovery) is to support the implementation of the Water Framework Directive (WFD) by developing tools for the integrated assessment of the ecological status of European surface waters.

A large proportion of European water bodies will fail to reach good status without restorative measures. The assessment systems used in the WFD are required to consider recovery as well as deterioration of freshwater ecosystems as they will be used to judge restoration success. Most previous projects dealing with assessment systems have focused on the effects of deterioration. WISER also deals with recovery.

It is now clear that ecosystem recovery is unlikely to simply be the reversal of deterioration and some examples show that recovery may lead to conditions very different from the original undisturbed stage. WISER examines ecological non-linear responses, regime shifts and changing baselines and is investigating cause-effect-recovery-chains for different water categories and for different Biological Quality Elements (BQEs) thus giving guidance on the expected outcome of restoration measures. The focus is on two key drivers affecting the status of BQE’s in European freshwaters:

i) recovery following reduction of pressures and remediation measures; and

ii) climate change which will pose additional threats directly (e.g. temperature changes) and indirectly through interactions with other drivers (e.g. land use change) and stressors (e.g. nutrient enrichment). Within this context WISER aims to assess how climate change may affect recovery trajectories by shifting baselines (or, more accurately, targets), altering stress intensity and causing biogeographical changes.

WISER has built on the experience and results from several European projects including STAR, REBECCA, THRESHOLDS and Euro-limpacs. Euro-limpacs (Integrated Project to Evaluate the Impacts of Global Change on European Freshwater Ecosystems) was concerned with the effects of climate change on aquatic ecoystems. The main aim was to increase understanding of the direct and indirect effects of global change and the implications of these management under the WFD and Habitats Directive. Euro-limpacs highlighted some key issues concerning the implementation of the WFD, in particular how the effects of future climate change should and could be accommodated within the current legislative framework. WISER considers how changing baselines of ecological status, partly defined in Euro-limpacs, will affect ecological status assessment and recovery processes. WISER also examines the impacts of climate change on ecological thresholds currently being used to define the class boundary between good and moderate status.

Although WISER is concerned with lakes, streams and transitional waters, this report considers only lakes. It reviews outputs from Euro-limpacs with particular focus on the effects of climate change on the ecological status of lakes and on the use and definition of reference conditions, to provide the foundation for an assessment of how climate change may affect recovery trajectories. It forms part of WISER Deliverable D5.2-5: 'Report on the effects of climate change on reference conditions and ecological status in lakes'.

1.1.2 Climate change and European lakes

It is likely that all lakes been impacted to some extent as a result of anthropogenic activities. In lowland regions the main impact results directly from activities within the catchment while In more remote areas the effects of atmospherically transported pollutants have been more pronounced. Over the past 150 years the threats to European lakes have included increased ultra-violet irradiation, acidification by sulphur and nitrogen compounds, mobilisation of organic substances from soils, accelerated catchment erosion and sedimentation rates, eutrophication by nitrogen and phosphorus compounds, discharge of toxic substances and the introduction of alien species and selective removal of others. In addition to these land use and pollution driven impacts European lakes now face additional pressures from climate change, directly and through interaction with these other stressors.

Climate affects freshwater ecosystems indirectly through socio-economic systems, such as land-management as well as directly by temperature and precipitation. Currently, in many cases, climate change is an additional stressor adding to the impacts of human activity. In future, however, the effects of climate change are expected to become more prominent, especially if the magnitude and rate of climate change is at the higher end of the projected range (cf. European Environmental Agency 2008; Solomon et al. 2007). A temperature increase of about 0.2°C per decade is projected for the next two decades for a range of emission scenarios.

For Europe the warming in northern regions is likely to be greatest in winter, while in the Mediterranean region it is expected to be greatest in summer. Based on Regional Climate Model simulations run under the EU PRUDENCE project (http://prudence.dmi.dk), interannual and daily temperature variability are likely to increase in summer in most areas, while in winter, temperature variability will tend to be reduced. The latter is the result of a feedback from projected reduced snow cover.

Annual precipitation is very likely to increase in most of northern Europe and to decrease in the 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.

Climate change can affect lakes physically through changes in temperature, precipitation and wind patterns. The impact of these varies across Europe. Evidence from long-term data-sets shows that many of the effects of changing climate are already occurring (Battarbee et al., 2008) and include;

i) increasing surface water temperature particularly at high altitudes and latitudes, and strengthening and lengthening of stratification in summer;

ii) increasing hypolimnetic temperatures of large deep lakes, causing a reduction in oxygen concentration in bottom waters, especially in summer;

iii) reductions in lake ice-cover increasing the length of the open-water growing season, the duration and intensity of the autumn overturn and deep-water oxygen concentration;

Such changes can be expected to have significant ecological consequences modifying the physical and biogeochemical character of aquatic environments (as described above) and through, for example, modification of species life-histories, changes to species abundance, composition and distribution, changes to food-web structure, and changes in the rates of species and community metabolism and in ecosystem processes (see Table 1.1).

The observed and expected impacts differ strongly between ecosystem types and regions. In cold regions of Europe (at northern latitudes and at high altitude) expected changes include higher primary productivity in response to an increase in the length of the growing season (because of shorter ice-cover) and to an increase in nutrient release from catchment soils and population declines or loss of cold stenothermic species such as arctic charr in response to increasing water temperature (Battarbee, et al., 2009). In temperate and warm humid ecoregions key changes are likely to include eutrophication following an increase in nutrient loading due erosion of agricultural soils, more frequent overflows of sewage treatment systems and increased release rates of phosphorus from sediments. Temperate regions will also see increased algal growth including more frequent and intense blooms of cyanobacteria and phenological change leading to possible mismatches of life-history patterns and complex impacts on plankton communities, food-web structure and lake ecosystem functioning (Battarbee, et al., 2009). For warm-arid ecoregions change in moisture balance is likely to be more important than changes in temperature.

1.1.3 Reference conditions and the Water Framework Directive

The Water Framework Directive requires surface waters to be restored to “good ecological status” by 2015. The Habitats Directive is designed to restore and protect biodiversity requiring member states to maintain or restore natural habitats (and listed species) at a favourable conservation status. Neither directive is currently explicitly formulated to allow for the potential effects of climate change, although both embrace the principle of protecting ecosystems from deterioration. These Directives will need to be amended to accommodate the likely effects of climate change on freshwater ecosystems. The WFD emphasises a whole-basin approach and requires both the determination and restoration of ecological quality rather than simply water quality. It is underpinned by the concept of baseline conditions or reference systems, defined as those unaltered or only negligibly altered by human activity. However, there are few, if any such systems left in Europe. Therefore developing schemes to determine ecological quality relative to baseline conditions is problematic. Nevertheless, tools for determining the status of phytoplankton, aquatic plants, macroinvertebrates and fish have been developed (UKTAG, 2007). However, climate change will inevitably undermine these schemes as species become eliminated or migrate into previous cooler habitats. As climate is now undergoing anthropogenically driven changes, the establishment of reference pristine standards has become conceptually impossible (Moss 2007, 2008). With ‘good ecological status’ defined as only slightly different from the high ecological status of the reference conditions, the way the reference state is defined will be of critical importance. A major challenge is to relate observed changes to climate as there have been many other changes to freshwater systems that have occurred during the period of climate change. These other influences, principally from land-use change and from pollution, are currently far stronger than climate change and may mask its effect.

1.1.4 Euro-limpacs

The key aim of Euro-limpacs was to further understanding of the potential effects of climate change on freshwaters focusing both on the direct physical and hydrological effects (i.e. changes in temperature and precipitation patterns) and on the interactions between climate and other stressors. It also examined the implications for monitoring and restoration and the definition of reference conditions under the Water Framework Directive. The results of these studies were used in modelling projections and providing the necessary guidance to inform management decisions.

The Key objectives of the Project included the following:

i) to improve understanding of how global change, especially climate change in its interaction with other drivers has changed, is changing and will change the structure and functioning of European freshwater ecosystems;

ii) to encapsulate this understanding in the form of predictive, testable models;

iii) to identify key taxa, structures or processes (indicators of aquatic ecosystem health) that clearly indicate impending or realised global change through their loss, occurrence or behaviour;

iv) to identify better approaches for the re-naturalisation of ecosystems and habitats in the context of global change that will lead to the successful fulfilment of the Water Framework Directive (WFD) in achieving good ecological status in freshwater habitats.

Euro-limpacs examined the effects of climate change on the ecology of lakes with reference to;

i) The direct effects of climate change;

ii) Climate change – hydrological/ land use interactions;

iii) Climate change – eutrophication interactions;

iv) Climate change – acidification interactions; and

v) Climate change – toxic substance interactions

This report will highlight output from the Project for each of these components separately before reviewing the implications for the application of the reference condition concept.

1.2 Direct effects of climate change on the status of lakes

Much of the work in Euro-limpacs concerned with the direct impacts of climate change on European freshwaters focused on physical and chemical responses rather than explicit impacts on ecological status. However, climate change impacts on physical and chemical conditions will clearly have consequences for ecological status.

In Euro-limpacs it was recognised that climate change affects the hydrological, physical, chemical and biological characteristics of all freshwaters, and is thus a key influence on element cycling (nutrients, major ions, dissolved organic carbon (DOC), organic pollutants, metals), food webs and biodiversity. One of the key questions in Eurolimpacs was focused on the likely changes to ecosystem structure and functioning that result from climate change that are independent of natural variability and the impact of other stressors.

A combination of time-series analysis, whole-lake experiments, palaeolimnology and modelling were used to assess natural lake ecosystem variability and sensitivity and the likely responses of lakes to future climate change. A series of separate studies examined;

(i) long-term direct climate change impacts on surface waters using long-term data series for water temperature and ice cover in relation to diurnal, seasonal and decadal trends in air temperature (Magnuson et al., 2000; Livingstone, 2003);

(ii) palaeolimnological evidence for climate effects;

(iii) climatic sensitivity of different types of lakes and their response to extreme events;

(iv) lake response to increased input of mixing energy using a whole-lake mixing experiment in Finland to simulate the predicted increase in mean geostrophic winds in northern Europe as a result of the northward shift of cyclone activity;

(v) integrated modelling of ecological thresholds at climatic extremes with a focus on the ecological response of small and medium-size lakes to climate change in areas of severe climate (i.e. in arctic-alpine and in semi-arid regions); and

(vi) the impact of climate change on deep and large lakes using coupled hydrophysical and ecological modelling.

Physical changes associated with warming such as hypolimnetic warming in large lakes (Dokulil et al., 2006) and decreasing ice cover (Magnuson et al., 2000) will subsequently affect the ecology of lakes and the ecological consequences of these impacts are already starting to be seen. These include changes in seasonality of phytoplankton (Catalan et al., 2002), extended growing season and increases in lake productivity (Blenckner et al.,2007), changes in the geographical range of taxa, e.g. Odonota (Hickling et al., 2005), and deleterious effects on cold stenothermal taxa (e.g. Griffiths, 2007).

1.2.1 Temperature

An increase in the temperature of lake hypolimnia can result in a greater risk of deep-water anoxia. Analyses of long-term temperature profile data from lake Zurich, Switzerland show how warming at all depths since the 1950's, particularly in the surface layers. This causes increases in thermal stability and a longer period of summer stratification (Livingstone, 2003). The summer of 2003 was exceptionally hot in central Europe and Lake Zurich experienced its highest recorded epilimnetic temperatures. Hypolimnetic temperatures were slightly lower than average, resulting in a highly stable water column. As a consequence hypolimnetic oxygen depletion exceeded the long-term mean by more than seven standard deviations. If those elevated temperatures were sustained over longer time periods (as predicted for the late 21st century (Schär et al. 2004)), the potential ecological consequences include the release of phosphorus from the sediments, possibly resulting in an increase in the intensity of algal blooms thus confounding management and restoration efforts to counter anthropogenic eutrophication.

The decoupling of trophic interactions is potentially one of the most severe consequences of climate warming in lakes. The timing of phytoplankton blooms affects competition within the plankton community as well as food-web interactions with zooplankton and fish. In Euro-limpacs a model-based analysis of Upper Lake Constance was conducted suggesting that, in a future warmer climate, the onset of the spring phytoplankton bloom will occur earlier in the year than it does at present (Peeters et al. (2007) due to the earlier occurrence of the transition from strong to weak vertical mixing in spring and of therefore the earlier onset of stratification. This effect is likely to be even stronger in lakes that freeze over during winter. According to model simulations, the shift in the timing of phytoplankton growth resulting from a consistently warmer climate (represented by a systematic increase of 4oC in air temperature) will be of greater magnitude than that resulting from a single unusually warm year. Therefore, analysis of the effects of long-term climate warming inferred from studies of inter-annual fluctuations may underestimate the effect of warming on aquatic ecosystems. In addition to the phenological changes in the growth of phytoplankton, climate warming is predicted to induce a change in the growth of Daphnia populations (Scheffer et al., 2001).

Following analyses of high altitude lakes across Europe, some common ecological thresholds emerged, related to lake size, physical characteristics, trophic state, water chemistry and fish occurrence. Two of these are of particular interest in terms of climate change: epilimnetic summer temperature of 8-10 ^{o}C and ice-cover duration of 180-195 days. Lakes crossing these thresholds in response to climate change are more likely to experience large changes in their biota, particularly chydorids and planktonic crustaceans (Catalan et al, 2009).

1.2.2 Ice cover

The seasonal ice-cover of lakes has significant ecological importance and is affected by air temperature, wind, snow depth, heat content of the water body and rate and temperature of potential inflows. As climate changes, and air temperatures, particularly in the winter, tend to increase, there will be significant changes to lake ice-cover.

Time series of ice phenology data from lakes in Eurasia and North America indicate later freezing and earlier melting of the seasonal ice cover. The average date of freezing and break-up have both advanced by about 6 days per 100 years across the Northern Hemisphere. An analysis of 54 Swedish lakes (Weyhenmeyer et al. 2005) showed that these trends were dependent on latitude with trends towards earlier melting substantially greater in warmer, southern Sweden than in the colder, northern regions.

1.2.3 Windspeed

Climate change scenarios predict increasing geostrophic winds by the end of the century. Changes to prevailing wind patterns may alter the input of mixing energy to lakes affecting overall heat balance and internal heat distribution. Increasing wind speeds are expected to increase the input of mixing. In Euro-limpacs whole lake manipulation experiments simulated increasing input of mixing energy and subsequent impact on the stratification and heat balance of lakes in Finland (Saloranta et al., 2009) and Norway (Lydersen et al. 2008). One consequence of the lowered thermocline was a change in oxygen stratification during the summer. The manipulation also affected nutrient levels (more so in the humic Finnish lake) and the phytoplankton communities (Arvola et al. in prep). The biomass of diatoms and non-flagellated green algae increased as well as the rate of change of the phytoplankton community in Finland. In

Norway the manipulation resulted in large changes in thermal properties with a deeper epilimnion, reduced stratification stability, autumn turnover occurring at high temperature and ice-on being delayed by several weeks. There was relatively little response in terms of the chemistry and biology. This may be due to the oligotrophic nature of the lake. However, there were some indications of the beginnings of change - planktonic chlorophytes and diatoms decreased, mixotrophic dinoflagellates increased and periphyton biomass increased.

1.2.4 Long-term climate variability

The variability in climate and in diatom assemblages over a 1,000-year period was investigated in Lake Kassjön in northern Sweden. Tree-ring inferred temperature data enabled the varved-sediment sequence in the lake to be analysed with respect to known temperature fluctuations between 500 Yrs BP to 500 Yrs AD, a period which is pre-cultural in this region. Results suggested that climatic variability was greater in the early part of the record during, and immediately after a short-lived cool period around 300 BC. This is reflected in the diatom data with a shift is species composition contemporaneous with the prolonged cooling event between 200 and 25 BC, with generally stable conditions either side of this event. Superimposed on this overall trend were rapid shifts in species composition which appeared to follow a regular 25-year cycle. Results have shown that substantial observed shifts in species abundances and diatom community composition are related to enhanced climatic variability. Altered species composition, notably increases in planktonic diatoms indicative of nutrient enrichment and higher DOC concentration, was associated with warmer temperatures and suggests altered catchment processes (e.g. generation of DOM within soils), i.e. indirect climate forcing. Significant direct climate effects were observed in the littoral zone (inferred from changes in benthic diatom composition) during short-term cold periods (Simpson & Anderson, 2009).

1.3 Interactions with hydromorphology

In Euro-limpacs studies of interactions between climate and hydromorphological / land use changes focused mainly on river ecosystems. For lakes, data from impoundments and oxbow lakes and existing sediment accumulation rate data from lakes across Europe were analysed to evaluate the role of climate and land-use change on lake sediment accumulation rates. The key research questions addressed were:

- How will the changing quantity and temporal variation of sediment load and discharge of tributaries influence large lakes including processes related to the accumulation of sediments in river deltas, water level fluctuations, aeration of deep water bodies and suspended matter intrusion in the pelagial and profundal regions of lakes?

- What is the role of climate and land-use change on lake sediment accumulation rates based on analyses of existing records and additional sediment cores taken within Eurolimpacs?
- What lake types are most susceptible to changes in sediment accumulation rate and, in particular, how susceptible are shallow lakes?

These studies did not directly address the consequences of changes on sediment accumulation rate or increases in suspended matter on ecological status.

1.3.1 Long-term water quality model investigations on deep lakes

Data on a number of hydrological and morphological parameters tributaries feeding into Loch Lomond (Scotland) and the Alpenrhein (Bodensee) were collected and analysed using the INCA model. Comparisons between measured sediment accumulation rates and computed river loads were undertaken. The two major lake tributaries investigated showed very different responses to simulated climate change. At the River Endrick, flowing into Loch Lomond the response is a two-fold increase in discharge and substantially higher transport of suspended matter into the loch. Predicted risk of flooding is almost three times that of today. The model runs on the Alpenrhein show changes in discharge patterns with stronger fluctuations and more peak discharges during winter. Aeration of the deep water in Bodensee will occur less frequently than currently observed. Due to higher temperatures in the inflowing river water the very fine suspended material will remain near the surface more frequently in both lakes in future.

1.3.2 Sediment Accumulation rates – the role of land use and climate change

Sediment accumulation rate (SAR) affects all aspects of lake ecosystem functioning. Influx of sediment to a lake reduces water depth resulting in changes to lake morphology, alteration of light regime, changes to physical and chemical stratification and increased resuspension and focussing. Indirect effects include impacts on plant distribution and growth and the alteration of biogeochemical dynamics (Punning et al 2006). If sediment deposition in shallow waters exceeds transportation downslope then sediments will accumulate in shallower zones and be permanently deposited in littoral areas (Engstrom and Swain 1986) allowing more macrophyte colonisation. Increased sediment in these areas also increases sediment resuspension which will have impacts on habitats and growth patterns of aquatic plants and the fauna dependent upon these. Fine sediment input, when delivered at elevated rates, is now recognised as a pollutant in its own right (Hatfield and Maher, 2008).

A widespread trend towards increasing SAR in many lakes over the last 100 – 150 years has been observed (e.g. Guilizzoni et al. 2001; Dearing and Jones 2003; Rose et al, 2011) primarily due to land-use practices, particularly in lowland lakes. Increases in SAR have also been observed at higher altitudes where catchment activities are limited and hence the causes more uncertain (Rose et al. 2011). While climate change may have a major impact on land-use in the future, at therefore SAR in lowland lakes, at upland lakes climate may play a more direct role. Temperature increases may result in greater productivity and therefore more autochthonous sediment production while elevated rainfall and increased frequency of extreme events (both summer droughts and winter storms) may increase erosion in catchments leading to elevated allochthonous sediment inputs. Future impacts will depend on soil type, vegetation and land-use but upland peats are already known to be experiencing increased levels of erosion (Coupar et al 1997) and this could be further exacerbated by continuing climatic changes.

In Euro-limpacs, sediment accumulation rate database was compiled (from over 250). Sites in the database were classified into classes using lake typology data. Temporal changes (rates, scales) in SAR for all lake types were identified in order to assess the types most ‘at risk’. An assessment of the reference condition concept for sediment accumulation rates was considered and reference SARs identified for some lake types. Factors driving contemporary bulk SAR and SAR change since 1850 in selected lake types was undertaken in order to assess likely impacts of future climate change. Most sediment cores in the SAR database showed surface SARs higher than “basal” (mainly 19th century) rates. Little change in SAR occurred prior to 1900 and most increases occurred in more recent periods (1950 – 1975 and post-1975). This indicates a general acceleration in SAR in European lakes during the second half of the twentieth century. Lowland lakes, especially large ones, are generally the most susceptible to SAR increases. It is considered that climate change may play a progressively more important role in driving SAR in the future (Rose et al., 2011).

1.4 Interactions with eutrophication

The eutrophication of inland waters is now probably the most widespread problem in freshwater ecosystems and the most obvious symptoms appear in lakes. In Euro-limpacs, the key hypothesis was that increased temperature will interact with continued high nutrient loading to increase the severity of eutrophication symptoms. The consequences of increases in temperature on nutrient cycling include: (i) changes in the growth and respiration of organisms, (ii) enhanced oxygen consumption and increased nutrient release from sediments; (iii) life-history impacts such as shorter lifespan and earlier reproduction; and (iv) changes in phenology and trophic dynamics which potentially may result in a mismatches between consumer demand and prey availability. These temperature-induced changes are likely to interact strongly with existing increased nutrient flows and create new problems for freshwater biota, or exacerbate existing ones (Blenckner et al. 2006; Mooij et al. 2005, Jeppesen et al. 2007, 2009).

Euro-limpacs used several approaches to examine climate-nutrient interactions, including space-for-time comparisons, field and mesocosm experiments, palaeolimnology and modelling. The key questions addressed were:

- Do nutrients structure ecosystems in different ways under current and anticipated future climatic conditions?
- How might changing climate interact with increased nutrient supply to alter ecosystem processes?
- Will changing climate aggravate eutrophication symptoms?
- Can the effects of climate change be distinguished from those of eutrophication?
- Are there lessons to be learnt from the past to understand future problems better?
- Can we mitigate negative effects of climate change on ecosystems in terms of enhanced eutrophication?

1.4.1 Spatial surveys

Euro-limpacs assessed the effects of a warming climate on the symptoms of eutrophication using field experiments in Uruguay and Denmark and mesocosm tanks in Europe (see below). These were designed to address whether warming may result in (i) significant fish impacts littoral trophic structure; (ii) truncation of trophic cascades; and (iii) deleterious effects on the role of submerged plants in maintaining clear water. Differences between the structure of communities associated with plant beds in lakes in Uruguay and Denmark supported the first two hypotheses (Meerhoff et al, 2007a, b). The littoral food-web was more complex and less hierarchically structured in subtropical lakes and fish communities exhibited higher diversity, greater density and biomass, less piscivory and widespread omnivory, smaller individual size and stronger association with the submerged plants than in the temperate lakes. Fish communities in the warm lakes were dominated by omnivorous cyprinodontids, whereas somewhat larger cyprinids and percids dominated in the temperate lakes.

The temperate lakes had higher taxon richness and significantly greater densities of plant-associated macroinvertebrates with higher densities of predators, grazers, and collectors. Cladoceran species richness, density and body size were also significantly higher in the temperate lakes. It has been argued that macrophyte growth will be stimulated by climate warming (Scheffer et al. 2001) but these and other analyses indicate a lower probability of macrophyte dominance in warm lakes (Kosten et al., 2009). Additionally, higher dominance of benthivorous fish foraging in the sediment may enhance internal nutrient loading following increases in lake temperature. This in turn may accelerate eutrophication and lead to higher and prolonged dominance of cyanobacteria which are highly sensitive to increases in temperature.

In a future warmer European climate, assuming species will migrate northwards, major changes in trophic structure and ecological status are to be expected (Jeppesen et al. 2007). These changes are likely to include higher dominance of zooplanktivorous and omnivorous fish. Enhanced predation on zooplankton has also been observed in warmer lakes with a decrease in the average size of cladocerans and copepods with increasing temperature (Jeppesen et al. 2009). With smaller zooplankton species, grazing on phytoplankton is likely to decline. Comparative experimental studies provide further evidence of reduced grazer control in warm lakes in comparison with similar temperate lakes (Meerhoff et al. 2007a; 2007b).

The size structure of fish populations also changes latitudinally, with greater proportions of small fish in warm lakes. Higher-latitude fish species are often larger and grow more slowly, mature later and have longer life-spans. Traits can vary even within species along these gradients (Blanck & Lamouroux 2007).

One of the key questions in Euro-limpacs was whether nutrients structure ecosystems in different ways under current and anticipated future climatic conditions? There is a clear change in trophic structure in lakes along the climate gradient from simple, often elongated food-webs in cold climates to truncated webs in warmer systems with a higher degree of omnivory. With increasing temperature, European lakes are likely witness significant impacts on phytoplankton, zooplankton and macrophyte populations with implications for ecological status and biological assessments, particularly where there are barriers to migration. There will certainly be a deviation from notional reference conditions.

1.4.2 Mesocosm studies

Experimental warming of mesocosm tanks in the UK suggest that warming exacerbates symptoms of eutrophication (Feuchtmayr et al., 2009; Moran et al. 2009). While a temperature increase of 3ºC combined with low nutrient loading results in a limited response, with a 4ºC rise and nutrient loadings matching those in many European lowlands at present the effects include increased phosphorus loading from the sediments, deoxygenation, reduced fish biomass, reduced plant diversity and species richness, an increase in warm-water exotics, and predominance of free-floating plants. However, one of the perceived symptoms of advanced eutrophication, the disappearance of submerged plants did not occur. The consequences of warming/deoxygenation for fish are severe, except for sticklebacks which are resilient and more tolerant of reduced oxygen concentrations than most other European species. In the UK, only tench (*Tinca tinca*), crucian carp (*Carassius carassius*), and the common carp (*Cyprinus carpio*) are more tolerant. Analysis of the oxygen balance of the mesocosm tanks suggested that respiration rates increased markedly following warming compared with photosynthetic rates. The effect also occurred in response to nutrient loading and could imply a positive feedback of warming on carbon dioxide release (Moss, 2009).

The mesocosm experiments were concerned with the effect of climate change on turbid phytoplankton-dominated lake ecosystems, a key issue for restoration. The assumption that warming would exacerbate the switch from plant-dominated to turbid systems was not supported by the experimental results. Although warming increased many symptoms of eutrophication in both the Danish and UK experiments, it sometimes had no effects and occasionally reduced them. The nature of the responses varied widely. Indeed in the current UK experiment, heating has favoured plants, and despite high nutrient loads has not led to turbid conditions. The starting conditions, intrinsic chaotic dynamics and interactions of nutrient loading and temperature increase make precise predictions of the future difficult.

1.4.3 Palaeolimnological, statistical and process-based modelling to disentangle climate and nutrient signals

In Euro-limpacs several complimentary approaches were used in an attempt to disentangle the effects of nutrient enrichment and climate change, and assess interactions between the two. These included statistical analysis of long-term monitoring data (e.g. Ferguson et al. 2008), process-based modelling of sites where historical catchment and lake data are available (e.g. Elliott & May 2008) and palaeolimnological reconstruction from remains of biota preserved in lake sediments (e.g. Manca et al. 2007). There was evidence of ecological responses to changes in both nutrient levels and climate at a number of case study lakes.

Lago Maggiore, Italy

In most cases the eutrophication signal tends to dominate any climate signal. However, in Lago Maggiore (northern Italy), there is evidence of increased temporal variation in zooplankton communities following extreme meteorological events and changes in fish predation may represent a response to increased temperatures (Manca et al. 2007). Studies of subfossil cladoceran data, long-term contemporary data series and historical information suggest the lake went through a eutrophication phase until from 1940s to 1980 followed by oligotrophication, which has recently been partly counteracted by increased warming. Meteorological events detected in the sediment also provided evidence that eutrophication tends to override climate signals. The study showed that a combined palaeo-neolimnological approach can be a powerful tool for elucidating past changes in the trophic dynamics of lakes and the interaction with climate induced changes, not least when high resolution sediment records are available.

Loch Leven, UK

A combination of methods was applied to Loch Leven, the largest shallow lake in Great Britain, where significant changes in both the climate and nutrient availability have been recorded (Carvalho & Kirika 2003). A period of eutrophication and subsequent recovery coincides with a period when there has been a measurable impact of climate change on the lake. Winter ice cover has reduced spatially and temporally, spring air temperatures and winter rainfall has significantly increased (Ferguson et al. 2008). The reductions in nutrient loading have led to significant decreasing trends of soluble reactive phosphorus concentrations. Winter nitrate concentrations have however, decreased, probably due partly to the significantly increased winter rainfall. Chlorophyll a concentration has decreased in spring but increased during the rest of the year

(Ferguson et al. 2009). Daphnia numbers have also increased in winter and spring (Ferguson et al. 2007; 2009). The negative relationship between chlorophyll and water temperature at Loch Leven in spring suggests an indirect response to higher spring temperatures, probably related to greater zooplankton production and grazing.

The phytoplankton community model PROTECH (Phytoplankton RespOnses To Environmental Change; Reynolds et al. 2001) was used to investigate the impacts of changing water temperature and nutrient loading on the phytoplankton in Loch Leven (Elliott & May 2008). Change in water temperature had relatively little effect on biomass and species diversity compared to changes in nutrient loading. Phytoplankton response varied according to the way in which nutrient loading changed. While increasing P alone resulted in a large increase in total chlorophyll a concentration and in Anabaena (Cyanobacteria) abundance, simultaneously increasing loads of phosphate and nitrate resulted in higher Anabaena densities at lower nutrient concentrations. It is suggested that Anabaena, which is a nitrogen-fixer, is able to exploit the available P better than other phytoplankton species when nitrogen levels are low.

The palaeolimnological study at Loch Leven (Bennion et al., 2011) related the sedimentary diatom record to nutrient and climate pressures using information from long-term data sets of water quality, climate and planktonic diatoms. The core data indicate an enrichment from c. 1800–1850, probably due to agriculture in the catchment, with a more marked phase since c. 1940–1950. This was caused by increased phosphorus inputs from sewage treatment works, land drainage and a woollen mill. While the recent diatom plankton remains are dominated by taxa associated with nutrient-rich conditions, compositional shifts since the mid-1980s suggest that reductions in nutrients from catchment sources may have resulted in partial recovery. This agrees well with long-term monitoring water chemistry and phytoplankton data. On a decadal-centennial scale, the eutrophication signal in the sediment record eclipses any evidence of climate as a control on the diatom community. At an inter-annual scale however, there are several changes in species composition in the recent fossil record that may be attributed to climatic controls. The study highlights the value of a palaeolimnological approach, particularly when coupled with long-term data sets, for developing understanding of environmental change at a range of temporal scales.

The Loch Leven analyses show that the lake has been slow to recover from eutrophication and that temperature has had both positive and negative effects on the plankton community. The study highlights the complexity of lake responses to changes in nutrient regimes and climate and, despite advances in analytical methods, the difficulty of unravelling their effects.

Piburger See, Austria

Euro-limpacs examined palaeolimnological and contemporary limnological data from Piburger See (Eastern Alps, Austria) to reconstruct trophic conditions since the late

19th century and assess changes in phytoplankton biomass and species composition in relation to environmental changes over this period (Thies et al., 2011). The sedimentary pigment and diatom record revealed moderate eutrophication during the 20th century, followed by a slow re-oligotrophication since the mid-1980s following lake restoration. Additionally epilimnetic temperature for Piburger See was reconstructed using air temperature records. A pronounced increase during the mid-1940s and since the late-20th century promoted both algal growth and changes in species composition. Climate scenarios predict substantial warming for this region by the end of the 21st century particularly during the growing season. The predicted change in lake water temperature and thermal dynamics represents a key driver of change for the trophic and ecological status of Piburger See in the future (Thies et al., 2011).

Esthwaite Water, UK

In Euro-limpacs a long-term monitoring programme on phytoplankton and physicochemical characteristics of Esthwaite Water (since 1945) was used to assess the effects of climate and nutrients on a lake ecosystem (Dong et al., 2011). The lake experienced nutrient enrichment from the early 1970s, mainly as a result of inputs from a local sewage treatment plant. Air temperature and rainfall are highly variable with increasing trends after 1975. Diatom analyses showed that fossil diatoms exhibited distinct compositional change in response to the nutrient enrichment. Multivariate statistical analyses showed that winter soluble reactive phosphorus (SRP) was the most important factor controlling the diatom assemblages for the whole monitoring period. Air temperature had little effect on the diatom assemblages when nutrient levels were low prior to 1975. As nutrient concentrations increased during the eutrophication phase climate became more important in regulating the diatom community, although SRP was still the major controlling factor. The relative importance of climate and nutrients varies according to timescale with climate contributing little to diatom dynamics at an annual or decadal scale.

Euro-limpacs set out to answer a series of questions about the combined effects of warming and eutrophication using a range of approaches and techniques. The results obtained in Euro-limpacs gave partial answers to these questions.

- ***Do nutrients structure ecosystems in different ways under current and anticipated future climatic conditions?***

This question was addressed using comparative studies of warm and temperate systems. There are clear changes in trophic structure in lakes along this climate gradient from simple, elongated food-webs in temperate systems to truncated webs in warmer lakes. The effect of increasing nutrients also differs between climate regions. In temperate lakes shifts often occur from high proportions of piscivorous fish, few and large plankti-benthivorous fish, high abundance of zooplankton and clear water often with macrophytes, to a turbid state with dominance of small plankti-benthivorous fish and phytoplankton. In warmer areas, lakes subject to both low and high nutrient loading are often dominated by numerous small omnivorous fish that exert a high predation pressure on zooplankton. These systems can have clear water when nutrient loading is low but are extremely vulnerable to increases in nutrient levels because the top-down effect of zooplankton is weaker than in temperate lakes due to the higher predation on zooplankton by fish.

- ***Will changing climate interact with increased nutrient supply to alter ecosystem processes?***

There is evidence that some processes (e.g. deoxygenation, decomposition and denitrification) are influenced both by nutrients and warming. However, the interaction between these is complex and variable, and there are discrepancies about how the various system components and the systems as a whole are affected. Generally there is likely to be: (i) higher internal loading of phosphorus in response to higher temperatures, more prolonged stratification in deep lakes, increased sedimentation rates as phytoplankton becomes more abundant and grazing by zooplankton is reduced; (ii) possible loss of submerged macrophytes and a shift from benthic to pelagic dominated systems and a reduction in biodiversity in shallow lakes; (iii) higher nutrient and carbon turnover and higher productivity, though perhaps unchanged or reduced net ecosystem production.

There is also evidence that nitrogen, which is viewed as equally as important as phosphorus in freshwater systems (Elser et al. 2007), may have counterintuitive effects, for example by inhibiting decomposition, but in some cases interacting with temperature to change the structure of aquatic plant communities in ways that will give more problems, such as increases in nuisance free-floating plants. Other evidence points to temperature driven rapid expansion in exotic species of plants and fish, such as carp which thrive as more sensitive fish struggle to survive.

Will changing climate aggravate eutrophication symptoms?

The space-for-time studies and controlled experiments in ponds and lakes suggest that climate warming will exacerbate symptoms of eutrophication. However, the effects will be complex and will vary depending on initial conditions and location. Shifts in trophic structure with warming result in greater risk of eutrophication symptoms, such as algal blooms, and higher risk of cyanobacterial dominance in larger lakes and filamentous algae in shallow lakes and streams. However, no evidence to date suggests that macrophyte-dominated clear-water lakes will shift to a turbid state. Other factors such as increased salinity, raised water levels, changes in fish communities, mechanical damage or damage by vertebrate grazers or toxins to invertebrate grazers or the plants themselves will generally be involved.

- ***Can we mitigate negative effects of climate change on ecosystems in terms of enhanced eutrophication?***

There is considerable scope for combating eutrophication symptoms aggravated by global warming, in particular by taking measures to reduce external nutrient loading to freshwaters beyond those already implemented or planned. Such measures could include: (i) less intensive land use in catchments with sensitive freshwaters to reduce diffuse nutrient inputs; (ii) re-establishment of riparian vegetation to buffer nutrient transfers to streams and rivers and improve in-channel structures to increase retention of organic matter and nutrients; (iii) improved land management to reduce sediment and nutrient export from catchments; (iv) improved design of sewage works to cope with the consequences of flood events and low flows in receiving waters; and (v) more effective reduction of nutrient loading from point sources and, for N, from the atmosphere.

1.4.4 Conclusion

Generally it is apparent that warming will exacerbate many, though not necessarily all, symptoms of eutrophication. Three key problems in answering the questions posed here emerge from the numerous studies undertaken in Euro-limpacs and elsewhere. Firstly, responses are complex and varied depending on the specific context. As a result there is a great deal of uncertainty about which particular measures should be taken in particular situations. A precautionary approach is recommended. Secondly, evidence hints at biological feedback mechanisms that may result in increased respiratory production of carbon dioxide and possibly nitrous oxide (N_2O), and methane (CH_4). This might mean that the physical models that underpinning climate change predictions made by the IPCC (2007) are severe underestimates. Finally, with increasing world population, pressure to grow more food in tandem with the expansion of crops for biofuel will probably lead to further increased nutrient inputs and an intensification of eutrophication problems in receiving freshwaters.

1.5 Interactions with acidification

Ecological damage resulting from acidification has included loss of salmon and trout populations and changes in the species composition of invertebrate, aquatic macrophyte and algal communities over large regions of Europe and eastern North America. Following dramatic reductions in S deposition in both Europe and North America surface waters showed the first signs of recovery in response to lower levels of acid deposition in the 1990s. Impacted lakes and streams are becoming less toxic for fish and other aquatic organisms (Monteith et al. 2005), but there is still a long way to go before recovery is complete.

However, there is evidence that climate change can affect the chemical and biological recovery of freshwaters from acidification. Long-term, seasonal and episodic changes in climate all potentially affect a variety of processes in catchments and surface water bodies. Warming may increase mineralization rates in soil organic matter releasing nutrients such as nitrogen currently stored in the catchment. These can subsequently reach the surface waters in runoff. The most biologically damaging acidification effects often occur during acidic episodes. These typically coincide with meteorological extremes, such as droughts (Dillon et al. 1997), storm events (Hindar et al. 1994) or snowmelt. Episodic acidification is more likely to affect streams than lakes which exhibit greater buffering capacity at this temporal scale. Future climate conditions in Europe are predicted to be generally warmer, wetter in the north but drier in the south, and stormier in all areas with more frequent extremes.

The priority for Euro-limpacs was to understand chemical responses of acid waters to climate change and then predict probable biological and ecological response. The focus was on how climate change might delay recovery of aquatic ecosystems damaged by acidification. Survey data from acid-impacted areas of Europe and eastern North America were used together with long-term datasets (30+ years) to link variations in acid deposition and climate on water chemistry and biology. The main objective was to determine the effects of long-term, seasonal and episodic climate change on the recovery of acidified freshwaters.

1.5.1 Effects on aquatic biota

Sensitive aquatic biota are vulnerable as surface waters become toxic due to elevated concentrations of inorganic Al and H^+. Climate change can affect the concentrations of these toxic chemical components. Climate change can also have direct effects on aquatic biota. For example, salmon migration is dependent on water temperature and discharge. Euro-limpacs focused on the relationships between climate change and chemical recovery as this is still an area of considerable uncertainty. There were a number of studies examining the ecological aspects of this relationship. Hardekopf et al. (2008) found that in a warmer climate, the recovery of benthic invertebrates streams will be hampered by continued release of sulphate (and acid) from the soil. The effects of drought on benthic invertebrates were also investigated (Gilbert et al. 2008). Drought acts as a disturbance mechanism that simplifying benthic communities and, reducing biodiversity. The studies of acid episodes under future scenarios of climate change and acid deposition point to increased frequency and severity. Kroglund et al. (2008) indicate that this will lead to poorer conditions for populations of salmon. A similar conclusion was reached by Kowalik et al. (2007) with respect to invertebrates in British streams. However, these studies did not include an assessment of lake ecosystems.

As temperatures increase, lakes in high latitudes or at high altitudes may cross a threshold at which they are no longer is ice-covered in the winter. These systems will then be subject to circulation rather than thermal stratification. In acidified lakes could lead to acid snowmelt in the spring mixing with the entire lake rather than be restricted to a 1-m thin layer beneath the ice. There is evidence that such acidic layers may be the limiting factor with respect to recruitment of lake-spawning fish species, such as lake trout in Canada (Gunn & Keller 1984) and brown trout in Norway (Barlaup et al. 1998).

Climate change is a confounding factor in that it can exacerbate or ameliorate the rate and degree of acidification and recovery, chemical as well as biological. The lack of recovery following deposition reductions may be the result of the confounding influence of climatic variations. Extreme climatic events, such as droughts, cause extreme responses that can offset biological recovery process, and slow down progress towards a stable ecosystem. Management efforts to restore ecological status at acidified sites need to take such interactions into consideration.

1.6 Interactions with trace metals and persistent organic pollutants

Persistent organic pollutants (POPs) and some trace metals (e.g. mercury, cadmium and lead), are released into the atmosphere by a range of urban, industrial and agricultural processes. Once emitted these pollutants are dispersed widely. Once they reach surface water bodies (directly deposited or via catchment runoff) they can enter the food web where they bioaccumulate and become toxic to aquatic and terrestrial organisms. Although many toxic substances are now banned or restricted, many persist, particularly in soils and sediments where they have accumulated over time. These ‘legacy’ pollutants may eventually be re-mobilised and taken up by aquatic biota (Catalan et al., 2004; Vives et al., 2005). High concentrations of metals and POPs in the tissue of fish in arctic and alpine lakes (Grimalt et al., 2001; Vives et al., 2004) are evidence of their mobility in the atmosphere and their concentration in cold regions (Fernandez and Grimalt, 2003). The potential consequences of climate change on these factors and therefore on water quality and biota were examined in Euro-limpacs. The central hypothesis was that future climate change will influence the distribution patterns and mobility of organic pollutants and toxic metals (lead, cadmium, mercury) in freshwater systems and lead to changes in the uptake and accumulation of these substances in freshwater food chains.

1.6.1 Increases in temperature

Temperature influences most of the physicochemical properties and processes that determine the environmental behaviour of chemical compounds. Variations in temperature can thus affect the dynamics, transport and fate (bioaccumulation, bioavailability, biodegradation, and above all, environmental persistence and incorporation into trophic chains) of contaminants in the environment, particularly in the aquatic environment. The process of accumulation via condensation affects remote and high mountain regions (Grimalt et al. 2001; Vives et al. 2004). In other words, the industrialized countries have not only exported part of their pollution abroad, they have also transferred part of it to what were previously the best preserved areas of the industrialized world.

Previous studies indicate that the most contaminated lakes are those which are furthest from pollution sources (i.e. cities and factories). This my appear counterintuitive. However, what is observed is a net transfer of pollutants to remote ecosystems due to a process of evaporation (i.e. dilution) and subsequent condensation (i.e. concentration). Hence, the effects of POPs on ecosystems are not diluted; they simply move from one location (warm) to another (cold). This also applies to compounds with very different applications such as DDE and PCBs.

Research on mountain lake food-webs provides further clues on the physical-chemical processes leading to the accumulation of these compounds in organisms. Organochlorine (OC) composition in water, chironomids, terrestrial insects, cladocerans, molluscs, cyanobacteria and fish (brown trout) has been investigated in Lake Redon (Pyrenees). Evidence suggests that the distribution of these compounds does not reach equilibrium within the life span of the food web organisms (ca. 1 year).

Once these compounds are introduced into the environment, temperature becomes a determining factor in their distribution. Increases in temperature have been particularly pronounced in high latitudes and mountain regions and these can be expected to have resulted in a redistribution of contaminants accumulated in these areas. High-mountain zones are inherently important, representing the most remote ecosystems in Europe. Lakes in these regions provide highly important water resources for human use, constituting the headwaters of river systems. Ensuring low levels of water contamination is a prerequisite for maintaining the ecological status of these systems.

Accumulations of these compounds have resulted in toxic effects on the organisms living in remote sites (Grimalt et al., 2010). Euro-limpacs highlighted evidence of exposure to PCBs among brown trout in European mountain lakes (Grimalt et al., 2010). This suggests that POP redistribution as predicted by global warming projections may have significant effects on the physiology of the exposed fish populations even at remote sites.

1.6.2 Mercury

While mercury is similar in many respects to the organic compounds discussed above (e.g. semi volatility, persistence, toxicity) it differs in the importance of the different forms of mercury existing in the environment. In air, elemental mercury vapour is predominant while oxidised divalent compounds are the most common in water, soils and sediments. Generally, methylmercury accounts for a very small fraction but as this species is highly toxic and prone to bioaccumulation, it is the most important from environmental and health perspectives.

Increased temperatures will alter mercury cycling because the rates of transformation between chemical species (e.g. oxidation, reduction, methylation) and the rates of transport between compartments (e.g. exchange between air and surfaces or water and sediments) are temperature dependant. Very little is known about the overall impacts of temperature on mercury cycling. Increased oxidation rates of atmospheric mercury may occur, which would result in increased deposition. However, this may be counterbalanced by increased volatilization of elemental mercury from land and water. Increased temperatures may lead to increased rates of methylation of inorganic mercury but again, the rate of demethylation may also be enhanced. Increased temperatures at high latitudes where cold conditions currently inhibit methylation and mercury mobility may be of particular concern.

1.6.3 The effects of temperature

The IPCC (2007) predicts that precipitation will increase in northern Europe and decrease in the Mediterranean zones by 10 to 20% due to climatic change. These changes, together with increases in the frequency of extreme events will influence the transport and distribution of pollutants as well as their impact on aquatic environments.

Future decreases in precipitation would probably reduce deposition of volatile OCs such as HCH, HCB and congeners of PCBs, DDEs and DDTs. Remobilization of accumulated pollutants will be a problem with increased rainfall or more frequent extreme precipitation events, particularly where increased temperature results in the disappearance of permanent snow in the mountains. Erosion in the catchments will be greater and POPs and metals will be more easily mobilized from the soil. Re-mobilization of metals as a result of increased soil erosion has been invoked to explain the continued high concentrations of Hg and Pb in Scottish lake sediments (Yang et al. 2002). Studies in Scotland concludes that catchment soil erosion is the main mechanism for transfer of trace metals to the lake water, while leaching may play an additional minor role. Consequently, any climate changes which may exacerbate soil erosion will increase metal inputs to lakes negating the effects of emissions reductions (Rose et al., in press).

In the boreal forests of northern Europe, climate change may lead to increased methylmercury concentration in fish. Many lakes in Scandinavia already have mercury levels in fish exceeding health guidelines making them unsuitable for human consumption. Climate models predict increases of winter precipitation in these regions which may lead to higher groundwater levels and more water flowing through organic-rich soil horizons where a large fraction of the soil-bound mercury is accumulated, potentially causing direct mobilization of mercury and methylmercury.

In Euro-limpacs, manipulation of precipitation and hydrology at Gårdsjön, an experimental lake site in south-west Sweden, has shown increases in both total mercury and methylmercury in run-off water. The transport of total mercury was found to be proportional to the increases in run-off amounts whereas the relative increase in methylmercury was larger than the relative increase in water transport. Increased soil wetness therefore enhanced methylmercury formation. The results of these experiments are consistent with the future scenarios indicating that changing climate may lead to increased loadings of methylmercury to aquatic ecosystems in areas where increased precipitation is expected.

The impacts of volatile heavy metals and POPs are much more difficult to decipher than those of habitat change, acidification or eutrophication. Their effects on biology are largely unknown and difficult to trace, because they are generally sub-lethal. The Water Framework Directive requires that all inland and coastal waters within defined river basin districts should reach good status by 2015 through the establishment of environmental objectives and ecological targets for surface waters. More recently a ‘daughter directive’ aimed at protecting groundwater has been adopted and a further daughter directive has been proposed which seeks to reduce pollution of surface water (rivers, lakes, estuaries and coastal waters) by pollutants on a list of priority substances which pose a threat to or via the aquatic environment. Therefore there is an urgent need to gain an insight into the main processes reducing water quality and ecosystem health in these headwater catchments, to identify which processes associated with toxic compounds are the most deleterious and to better understand the mechanisms of transport and accumulation within, and between, the atmosphere, catchment soils, lakes and biota. This knowledge is essential for the effective implementation of adequate prevention, mitigation and remediation strategies.

1.7 Summary of potential threats to ecological status from climate change and indicators to monitor these

Euro-limpacs considered the many complex cause-effect chains that will be driven by climate change. These will be directly and/or indirectly influenced by temperature and precipitation and will be linked by numerous interacting environmental parameters. The biological response, at species level, will be less predictable than the response of water chemistry or hydrology. However, biotic parameters such as species richness, community composition or functional diversity can integrate the complex responses of freshwater ecosystems to a variety of stressors including climate change. Under the Water Framework Directive monitoring programmes are mainly designed to detect the effects of previously dominant stressors such as eutrophication, organic pollution, acidification or hydromorphological degradation. Climate change is not specifically incorporated in the Water Framework Directive, although as Euro-limpacs has indicated, climate impacts on European freshwaters are likely to become more pronounced in future. Euro-limpacs was tasked with identifying a series of indicators for the effects of climate change on freshwater ecosystems. Indicator here is defined as a simply detectable signal of ecosystem change. Indicators are reflections of complex chemical, hydrological, morphological, biological or functional parameters, or processes, influenced by climate change and which are relatively simple to monitor.

Under the Water Framework Directive emphasis is placed on biological indicators to assess ecological status and a number of organism groups (phytoplankton, macrophytes, benthic invertebrates and fish) are monitored for this purpose. As noted previously, the impact of climate change has not been considered specifically in the Water Framework Directive, yet almost all indices used to monitor ecological status will be affected by climate change. In future, climate change impacts will be among the most important pressures, on freshwater ecosystems particularly in marginal regions such as those at high latitude and altitude and surface waters in semi-arid areas of Europe. Therefore there is a need to develop simple indicators to assess current impacts and which could be integrated into existing assessment systems. With climate change impacts expected to vary among cold, temperate and warm ecoregions, different sets of indicators may be required. Euro-limpacs identified a potential set of indicators for lakes in cold, temperate and warm ecoregions (Table 1.1). Most of these indicators can be accommodated within existing routine monitoring programmes and, in many cases, simple physico-chemical measurements are most appropriate.

Table 1.1 Direct and indirect impacts of climate change on lakes. Category: ecosystem component being affected by direct or indirect climate change effects. Response: describes how the variables change under the stressor considered. Indicator: a judgemental selection of the variables that most clearly reflect climate change. c, t, w: variable relevant in cold (c), temperate (t) and warm (w) ecoregions. (from Hering et al., 2009)

Category		**Response**	**Indicator**	**Justification of indicator**	c	t	w
Hydrology	Ice cover	Higher air and thus higher water temperature leads to a shorter ice cover period. The relationship between air temperature and timing of lake ice-breakup shows an arc cosine function. This nonlinearity results in marked differences in the response of ice-breakup timing to changes in air temperature between colder and warmer regions.	Ice cover duration, timing of ice-breakup, ice thickness.	Ice cover duration is simple to monitor, e.g. by remote sensing.	x	(x)	
	Stratification	Higher temperatures result in earlier onset and prolongation of summer stratification. As a result, changing mixing processes occur and systems may change from dimictic to warm monomictic. A lack of full turnover in winter might lead to a permanent thermocline in deeper regions.	Duration of summer stratification as reflected by water temperature	Water temperature well reflects the status of lake stratification.	x	x	(x)
	Water level	Increased temperature and decreased precipitation in conjunction with intensive water use will decrease water volumes. This will lead to water level imbalances and in many cases to the complete loss of water bodies.	Lakes surface	Easy to monitor by remote sensing.	(x)	(x)	x
Physico-chemistry	Oxygen depletion	High temperatures will stimulate phytoplankton growth, which will lead to oxygen depletion of profundal habitats.	Oxygen concentration of the bottom water in summer	The parameter is easy to record and often incorporated into routine water chemistry monitoring.	(x)	(x)	x

Category		**Response**	**Indicator**	**Justification of indicator**	c	t	w
	Sulphate concentration	With less precipitation in El Nino years and resulting droughts, stored reduced S in anoxic zones (wetlands) are oxidised during drought, with subsequently high sulphate export rates. Elevated sulphate concentrations in lakes will be the result.	Sulphate concentration	Directly reflecting the responding parameter; often incorporated into routine water quality monitoring	x	(x)	
	DOC	Rising temperatures in combination with declining acid deposition cause increasing DOC concentrations.	DOC	Incorporated into routine water quality monitoring	x	(x)	
	Acidification effects on phytoplankton	Acidification pulses occur due to draught (El Nino). Acidification pulses will cause changes in phytoplankton richness and biomass.	pH; biotic acid indices	pH is easy to record and often incorporated in water chemistry monitoring. As pH varies seasonally and daily, biotic indices are often more stable.	x		
	Salinity	Warmer winters cause extreme rainstorms and heavy sea-salt deposition, which might affect water chemistry.	Acidifying substances	These parameters are easy to record and often incorporated into routine water chemistry monitoring.	x		x
	Total Organic Carbon (TOC) run-off patterns	Warmer winters produce higher levels of run-off TOC release with subsequently increasing TOC water concentrations.	TOC levels and/or absorbance (water colour).	Water TOC concentrations reflect changes in run-off and input of allochtonous material.	x		
Primary production	Water temperature effects on phytoplankton	Increasing water temperatures lead shifts from a dominance of diatoms and cryptophtes to cyanbacteria. This effect is especially pronounced at temperatures > 20°C, since cyanobacteria (especially large, filamentous) and green algae are favoured at higher temperatures.	Phytoplankton biomass and composition, cyanobacterial algal blooms	The shift in community composition gives information about the response of biota to changed lake characteristics as water temperatures. Phytoplankton community composition is routinely monitored for the Water Framework Directive.	x	x	(x)

Category		Response	Indicator	Justification of indicator	c	t	w
	Water temperature effects on macrophytes	Inter-annual variation in water temperature result in deeper macrophyte colonisation, greater wet weight biomass, and an increase in whole lake biomass.	Water temperature	The parameter is easy to record and often incorporated into routine monitoring programmes.		x	
Secondary production	Water temperature effects on zooplankton	Higher water temperature leads to shifts in zooplankton community composition. Higher, earlier population growth rates of *Daphnia* and earlier summer decline occurs due to higher spring temperatures. As a result, higher *Daphnia* biomass leads to earlier phytoplankton suppression and a shift from a dominance of large-bodied to smaller species.	Zooplankton biomass and composition, size classes	The response of zooplankton (although not monitored for the Water Framework Directive) might be a good indicator for changes food-web dynamics due to temperature increase.	(x)	x	(x)
	Water temperature effects on cold water fish	Higher water temperatures (especially in the epilimnion) lead to the progressively reduction of thermal habitats for e.g. *Salvelinus namaycush*. As a result, cold water species will disappear from littoral areas in spring and summer. Furthermore, higher water temperatures will reduce reproduction success of cold water species and increase parasitic and predator pressure on the egg and young life stages.	Summer water temperature or air temperature	Water temperature is easy to measure, but even air temperature reflects warming up of mixed layer temperature.	x	x	
	Spread of alien species	Higher temperatures often favour alien fish, macrophyte or macroinvertebrate species.	Share of alien species in the community	This parameter can often be inferred from routine monitoring for the Water Framework Directive.	(x)	x	X

Category		Response	Indicator	Justification of indicator	c	t	w
Food webs	Water temperature effects on food webs	Increased water temperature generates principal shifts in food webs. As cyprinid planktivorous fish species are supported, large zooplankton species are suppressed and grazing intensity is reduced.	Proportion of planktivorous and piscivorous fish species; proportion of large and small zooplankton species	Food web structure is well reflected by these two parameters. The share of large zooplankton species determines the effects on phytoplankton, the share of planktivorous species determines the effects on zooplankton.	x	x	X

1.8 Climate change: Defining reference conditions and restoring freshwater ecosystems

As noted, attempts to restore aquatic ecosystems under the Water Framework Directive requires that freshwaters should be maintained at or returned to good ecological status, defined as ‘slightly’ different from the pristine or reference state. Both the biodiversity and functioning of ecosystems need to be restored to a more natural or reference state. This may entail removing or mitigating the causing of degradation, but may also require more active restoration management (e.g. physical reconstruction of or habitat alteration.

To assess ecological status and to determine whether restoration efforts have been successful knowledge of the baseline conditions that occurred prior to the human-induced stress is required. Thus reference conditions are needed; (i) to understand how the current condition differs from the ecological target/reference condition; (ii) to determine what factors have been degraded and by how much; (iii) to identify the drivers of the observed change; and (iv) to decide what steps are needed to restore the ecosystem to the desired condition.

However, defining the ‘reference state’ is difficult and is likely to become moreso as climate change increasingly affects the structure and functioning of ecosystems. Euro-limpacs considered how climate might affect or confound the use of reference conditions in ecological assessment, recognising that a reference condition is not a static state, but changes over time. The concept of a dynamic reference condition concept can be used to modify restoration targets in systems where changing climate may shift baseline conditions beyond those to which it can reasonably be expected to be restored.

Euro-limpacs compared different methods for establishing reference states. The initial objective was to understand the inherent variability that might be associated with the use of different methods to establish reference conditions. Secondly, the Project sought to determine how climate change might affect perception of contemporary reference conditions or baselines, and hence influence interpretation of restoration.

Many approaches are used to establish reference conditions. In areas where land use has not drastically altered the landscape the use of survey data is common since the approach, by using space for time substitution, encompasses natural variability. However, in many areas across Europe, the landscape has been extensively altered over centuries and hence reference conditions, or even relatively minimally disturbed cannot adequately be determined using space-for-time approaches. Models and hindcasting provide alternative approaches. Relationships between response and predictor variables can be used to predict the expected reference condition (e.g. community composition or palaeo-reconstruction of water chemistry and biota) in the absence of stress (e.g. Wright 1995). The use of palaeoreconstruction and contemporary time-series data (depending on the length of the record) may capture the dynamic nature of aquatic ecosystems. However, these often only provide information on a single population or assemblage of organisms, and, until recently, have seldom been used to reconstruct the elements of whole communities or ecosystems. Expert judgment can be employed to assess many different types of information to provide a more holistic reference condition. This approach is rarely used to establish reference condition in isolation due to potential sensitivity, bias and inaccuracy, but may strongly complement other methods.

Euro-limpacs considered two main approaches to establishing reference conditions in lakes.

1.8.1 Typology- and model-based approaches.

The role of biogeographical factors in determining species distribution patterns, and the use of spatial typologies for partitioning natural variability are recognised for some time (e.g. Hawkins & Vinson 2000; Johnson et al. 2007). Research has confirmed the importance of regional and local scale variables for predicting the composition of aquatic habitats but comparatively little work has been done on the efficacy of a priori classification systems for predicting biotic assemblages. Euro-limpacs, confirming findings from earlier studies, Johnson (unpublished), found that latitude, altitude and catchment size were important predictors of invertebrate assemblages in boreal streams (e.g. Hawkins et al. 2000; Johnson et al. 2004). These site-specific characteristics can also result in lag responses that differ among sites, resulting in high levels of uncertainty and confounding interpretation of the efficacy of restoration. Assessments of biological recovery from acidification, for example, often require the use holistic and multiple assessment approaches (Stendera and Johnson, 2008). A Euro-limpacs study of reference boreal lakes showed that communities did not fluctuate around a long-term mean, as expected, implying the influence of some other driver. One explanation 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.

There is evidence, however, that classifications based solely on landscape-scale predictors do not capture the fine-scale variability of aquatic communities. Site-specific predictors such as water chemistry also need to be included. Predictions based on continuous environmental and taxonomic data provide a more robust method for establishing reference conditions. Long-term datasets are also needed to better understand both the drivers of regional changes in chemistry and biology of aquatic systems and the direction and magnitude of changing baseline conditions. In addition, these and other studies (e.g. Johnson et al. 2007) support the contention that the scale of perturbation (e.g. local- vs region-scale drivers of change) and the scale of restoration (e.g. individual habitats within a stream or streams within a catchment or landscape) need to be considered to design robust and cost-effective restoration programmes.

1.8.2 Historical information and palaeolimnoloogical records

For some aquatic systems (e.g. European shallow lowland lakes) it is very difficult to find reference sites. Therefore historical information is required to determine the reference conditions. However, long term datasets are rare for most ecosystems, and where these do exist, monitoring programmes tend to have begun after disturbance has occurred and may not include all the variables of interest. For lakes however, palaeoecological analysis of the remains fossil remains of aquatic organisms preserved in sediment cores can provide historical information and hence to define reference conditions (Bennion & Battarbee 2007). The multi-indicator approach is a particularly powerful tool for determining site-specific reference conditions (e.g. Guilizzoni et al. 2006; Taylor et al. 2006; Bennion & Battarbee 2007). The ecological information within the lake sediments provides a sound basis on which to establish reference conditions and formulate management decisions such as the definition of restoration targets.

Palaeoecological applications are strengthened when used in tandem with historical datasets of sufficient length. In Euro-limpacs this approach was employed at Groby Pool, a small, shallow lake in England that has undergone nutrient enrichment over at least the last two centuries (Sayer et al. 1999; Davidson et al. 2005) and Loch Leven (see above). The combined historical, time series and palaeolimnological datasets for these two lakes provide a rare opportunity for a comparative study of the botanical record with the aquatic plant history as revealed by the sediment record. At both sites, the timing and nature of changes in the biology showed agreement between the two data sources. A clear succession in the aquatic flora over approximately the last 150 years was indicated. At Groby Pool the pollen record provided information on species that leave few macro-remains. There is inherent bias in both methods. Botanical surveys can be skewed towards rarities which are not captured by the sediment record (e.g. Zhao et al. 2006). Macrofossils in the sediment record tend to underestimate past species richness. However, at these sites there were also cases where taxa were absent from the old plant surveys but were present in the macrofossil data. Other problems were experienced due to patchy plant records, gaps in the historical record. Nevertheless, despite these uncertainties, two case studies show that macrofossils can be used on their own to provide a reliable record of the dominant components of the plant community. They demonstrate the value of combining methods to determine the ecological condition of the sites prior to impact.

Although palaeolimnological records provide a means for establishing reference conditions for lakes, the methods have inherent uncertainty. Although there is now increasing use of multiple methods, both direct (e.g. multiple groups of organisms) and indirect (e.g. different forms of inference), few studies have examined the use of different methods to better understand the inherent uncertainties. In Euro-limpacs Battarbee et al. (2005) assessed the relative accuracy of different approaches in reconstructing pH of a Scottish loch showing that the inferred reference pH in 1800 AD varied by less than an order of magnitude. The study showed that uncertainty can be reduced by increasing the size and representativeness of the calibration data-sets and by continued verification against observations from monitoring programmes. It is encouraging that different methods to establish reference condition were congruent, and also that model predictions agreed with contemporary monitoring data. The study demonstrates the efficacy of hindcasting methods for establishing the reference condition of lakes where no present-day spatial analogues exist. However, the modelling and time-series data also indicate substantial variability on decadal and yearly time scales, trends that are clearly the result of human-generated changes in surface water quality. More research is needed to assess how climate change affects our ability to detect degradation and recovery. The latter is particularly important with the context of the Water Framework Directive.

1.9 Global change and restoration

When restoring sites, connections to potential source populations and the dispersal abilities of key reference organisms are of critical importance. Delays in re-colonization of restored sites may hinder efforts to attain species composition characteristic of reference conditions. It has been argued that restoration should occur in a landscape context (i.e. where connections in the landscape are taken into account) (e.g. Verhoeven et al. 2008). The Operation Landscape Unit (OLU) approach, developed further in Euro-limpacs, considers how disrupted connections in the landscape may impede restoration success, and provides a tool for including crucial landscape connections in restoration planning.

Climate change may impact connections between sites and the dispersal abilities of species by. For example, the drying of ponds and shallow lakes, due to warmer and drier summers, will reduce ‘stepping stone’ connections between wetlands. Increased understanding of the effects of climate change on the connectivity among freshwater ecosystems is required to predict future impacts on the success of restoration measures. However, effects are likely to be highly specific per site and landscape, and will require landscape-scale predictions of climate change and detailed knowledge of the spatial configuration and connections in the landscape.

There remains a need to better quantify the uncertainties associated with different approaches to establish reference conditions. It is clear that spatial typologies (probably the most common approach used in implementing the WFD) are significantly poorer at partitioning biological variance than model-based approaches. There is also acknowledgement that the reference condition is not static or oscillating around long-term means, but showing monotonic climate-driven trends. Hence approaches that explicitly include interannual variability in weather and/or long-term trends in climate should be given greater consideration. 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 would be of interest.

1.10 OVERALL CONCLUSIONS

Euro-limpacs was designed to address the central question of how freshwater ecosystems will respond to future global change. An holistic approach was taken that embraced all surface freshwater types (lakes, rivers and wetlands) within an integrated catchment context, that covered a full range of spatial and temporal scales, and combined observational, experimental, palaeoecological and modelling methodologies. The outcomes of the Project included:

i) increased understanding of the effects of climate change, both directly and through its interaction with other key stressors, on the ecological status and functioning of European freshwaters;

ii) identified and evaluated restoration efforts to recover the historical losses and degradation which have occurred due to human impacts;

iii) developed approaches and identified priorities for dealing with the effects of future global change scenarios relating to climate and hydrology, land-use and nutrients, acidity and toxic substances.

iv) developed a unified system of ecological indicators for monitoring freshwater ecosystem health, and new methods for defining reference conditions and restoration strategies.

The main achievement of societal relevance is increased understand of how strategies for the sustainable management of freshwaters, for example, as required by the WFD, may need to be modified to take account of global, especially climate change. The results from Eurolimpacs provide a foundation for future research on the impacts of climate change on freshwaters and how these can be managed both within the current policy framework and as part of future management strategies. Subsequent projects such as WISER and REFRESH are further developing the themes and approaches from Euro-limpacs so that the scientific basis underpinning the management of freshwaters is strengthened and targeted appropriately.

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2. Assessing degradation and recovery pathways in lakes impacted by eutrophication using the sediment record

Responsible: Helen Bennion, Contributors: Ben Goldsmith and Gavin Simpson

2.1 Introduction

Most lakes throughout the world have been modified to some extent by human activity. Excessive nutrient and organic matter loading resulting in eutrophication has affected numerous waterbodies, most notably since the mid-twentieth century associated with the intensification of agriculture and expansion of populations connected to sewage treatment works (Battarbee et al., 2011). The consequent high algal biomass leads to filtration problems for the water industry, oxygen depletion, recreational impairment, loss of biodiversity, fish mortality, and decline or loss of submerged plants.

Efforts to restore enriched systems have increased over the last few decades and there are now numerous examples of lakes in recovery. Point-source control at sewage treatment works has been particularly effective at reducing external nutrient loads. Nutrient pollution from diffuse agricultural sources has proved more difficult to control as it is dispersed over large areas. Nevertheless restoration schemes that promote use of buffer strips, good agricultural practice and wetland regeneration have all contributed to the reduction of nutrient loading from agricultural sources (Sharpley et al. 2000). In deep, well flushed lakes, eutrophication is often reversed by the reduction in phosphorus (P) inputs alone, such as in Lake Washington, USA, where P concentrations fell dramatically, phytoplankton biomass declined and there were sustained increases in transparency following effluent diversion and treatment (Edmondson & Lehman, 1981). However, in shallow lakes internal P loading can delay recovery and external P reduction is often combined with other management measures such as dredging or biomanipulation (Søndergaard et al., 2007). Whilst there are many individual success stories, there remains considerable uncertainty about whether restoration targets can be achieved and over what timescales one might expect to see improvement. Recovery may be a slow process as biotic communities tend to exhibit hysteresis and time-lags, and thus ecosystems take time to re-adjust to reduced stress (e.g. Yan et al., 2003; Johnson & Angeler, 2010). In an analysis of long-term datasets from 35 restored lakes, Jeppesen et al. (2005) showed that internal nutrient loading delayed recovery, but in most lakes a new equilibrium for total P (TP) was reached after 10-15 years. Furthermore, new pressures, especially from global warming, may counter restoration strategies. Climate change in combination with land use changes is anticipated to cause increased nutrient loading in lakes, and may increase the frequency and intensity of harmful algal blooms. Longer growth seasons, higher water temperature and more turbid conditions may amplify this problem (Jeppesen et al., 2010). Thus the expectation that ecosystems can be returned, following remediation efforts, to conditions prior to enrichment may be a naive one and managers and policy makers may have to accept that "shifting baselines" will limit the ability to meet restoration targets (Duarte et al., 2009; Bennion et al., 2011a).

Legislative programmes are now in force to reduce pollution and restore aquatic ecosystems to good health in many regions of the world. In Europe, the Water Framework Directive (WFD) with its aim to restore waters to at least good status, has increased the need for effective restoration programmes for all lakes. Within the WFD, ecological status is based on the degree to which present day conditions deviate from those expected in the absence of significant anthropogenic influence, termed reference conditions. Consequently there has been a wave of research aimed at defining reference conditions and development of tools for estimating deviation from them. Lake sediment analysis provides unique insights into the history of freshwater ecosystems giving evidence for the nature and timing of ecosystem change, and providing a record of human impact that can be indispensible in developing strategies for ecosystem management (Bennion et al., 2011a). Palaeoecological methods can reveal pre-impact conditions and identify any signs of recovery, and have played a key role in the WFD (Bennion & Battarbee, 2007), particularly in determining pre-enrichment reference conditions and degree of eutrophication (Bennion et al., 2004). Diatom records have proved especially valuable in this respect, largely due to their sensitivity to shifts in trophic status (Bennion & Simpson, 2011; Bennion et al., 2011b). As many restoration programmes progress there is great potential to employ a combination of limnological and sediment records to track recovery using the pre-eutrophication baseline as a benchmark (Battarbee et al., 2005).

This paper employs palaeoecological techniques to examine the degree of impact and recovery in thirteen European lakes that have been subject to eutrophication. Changes in the diatom assemblages in sediment cores from the study lakes are assessed in response to enrichment and subsequent reduction in nutrient loading. The response of several metrics is explored including percentage plankton, diversity, community composition and diatom-inferred TP (DI-TP) concentrations. The extent to which the diatom assemblages are approaching or deviating from reference conditions is explored using ordination and dissimilarity scores. The key questions being addressed are: i) Do the observed changes reflect degradation and recovery?, ii) Is the recovery pathway simply a reversal of the degradation pathway?, and iii) Can the degree of degradation be quantified?

2.2 Methods

2.2.1 Study sites

The thirteen study sites are located in European lowland catchments and represent a range of lake types in terms of lake area, depth and trophic status (Table 2.1). For data analyses, the sites have been classed as either deep, stratifying or shallow, non-

Table 2.1 Summary characteristics of the thirteen study sites

Site name	**Core code**	**Country**	**Alt**	**Lake Area**	**Max Depth**	**Current mean TP**	**Lake type**	**Management actions**
			m asl	**km^2**	**m**	**µg l^{-1}**		
Barton Broad	BART1	England	2	0.77	1.5	74	Shallow, non-stratifying	Reduced external P loading since late 1970s; sediment removal to reduce internal P-loading from 1995-2000
Lake Bled	BLED3	Slovenia	475	1.5	32.0	20	Deep, stratifying	Sewage effluent diversion in 1982
Bosherston Lily Pond Central	BOSHC1	Wales	2	0.34	2.0	20	Shallow, non-stratifying	Sewage diversion since 1984, bypass pipeline construction in 1992
Esthwaite Water	ESTH1	England	65	1	15.5	28	Deep, stratifying	Reduced P loading since 1986 but internal loading issues and fish farm present until 2009
Gjersjoens	GJER-NIVA	Norway	40	2.4	64.0	15	Deep, stratifying	Sewage effluent diversion in 1971
Kiełpińskie	KIEP2009	Poland	120	0.61	11	105	Deep, stratifying	Decrease in fertiliser use and change in land use in early 1990s
Loch Leven	LEVE11	Scotland	106	13.7	25.5	53	Shallow, non-stratifying	Reduced P loading since 1985 but internal loading issues
Lidzbarskie	LIDZ2009	Poland	128	1.22	25.5	66	Deep, stratifying	Decrease in fertiliser use and change in land use in early 1990s
Llangorse Lake	LLAN3	Wales	156	1.4	9.0	118	Shallow, non-stratifying	Sewage diversion in 1981 and 1992
Marsworth Reservoir	MARS91	England	115	0.1	4.0	476	Shallow, non-stratifying	Sewage part-diversion and improved sewage treatment works in mid 1980s
Mill Loch	MILL1	Scotland	55	0.11	16.8	92	Deep, stratifying	Exact restoration measure and timing unknown
Mjøsa	core B	Norway	123	362	453.0	4	Deep, stratifying	Improvements to sewage treatment works in late 1970s
Rumian	RUMI2009	Poland	152	3.06	14.4	75	Deep, stratifying	Decrease in fertiliser use and change in land use in early 1990s

stratifying, in order to explore whether these lake types respond differently to nutrient reduction measures. All of the sites have experienced eutrophication within the last ~100 years and have either seen a reduction in external nutrient loading from sewage treatment works since the 1970s and 1980s or, in the case of the three Polish lakes, have received less diffuse pollution from the early 1990s as a result of national changes in fertiliser and land use.

2.2.2 Sediment core collection and analyses

A sediment core was collected from the open water area of each lake as part of several different previous studies and, therefore, coring methods and analytical resolution vary from site to site. However, at least ten samples from each core, spanning the last ~200 years, were analysed for diatoms using standard methods (Battarbee *et al*., 2001). A minimum of 300 valves were counted from each sample using a research microscope with a 100x oil immersion objective and phase contrast. Krammer & Lange-Bertalot (1986-1991) was the principal flora used in identification. The diatom data are expressed as percentage relative abundances.

Chronologies for the cores included in this study were determined using radiometric methods and/or spheroidal carbonaceous particle (SCP) analysis. For radiometric analysis sediment samples were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay using the methods of Appleby *et al.* (1986). ^{210}Pb chronologies were calculated using either Constant Rate of Supply (CRS) or Constant Initial Concentration (CIC) dating models (Appleby & Oldfield, 1978), based on the method best suited to the data. SCP analysis followed the methods described by Rose (1994) and Rose & Appleby (2005).

2.2.3 Data analysis

The degree of floristic change in the diatom assemblages between the bottom sample and every other sample in the core was assessed using the squared chord distance (SCD) dissimilarity coefficient (Overpeck *et al*., 1985) implemented in C2 (Juggins, 2003). The dissimilarity scores range from 0 to 200 whereby 0 indicates that two samples are exactly the same and 200 that they are completely different. This provides a measure of deviation from the reference assemblage. It is generally considered that a shift from benthic to planktonic dominance occurs with eutrophication (Vadeboncoeur *et al*., 2003). Hence, the percentage of planktonic taxa versus non-planktonic taxa was calculated for each sample to assess whether this provides a useful metric for assessing diatom response to degradation and recovery. The Hill’s N2 diversity score (Hill & Gauch, 1980) was also calculated to explore whether the diversity of the diatom assemblage shifts in line with enrichment and recovery.

Principal components analysis (PCA), an indirect ordination technique, was used to analyse the variance downcore within the diatom assemblages using C2 (Juggins, 2003). The technique helps to identify the main points of compositional change within complex species-rich data sets. The sample scores for PCA axis 1 are shown. Where scores between two neighbouring samples in the core differ markedly this indicates that the assemblages have undergone substantial change between these two points in the core.

A diatom-TP transfer function was applied to the diatom data to reconstruct the trophic status of each site. Reconstructions of DI-TP were produced using either i) a training set of 56 relatively large, deep lakes (> 10 m maximum depth) from Scotland, Northern Ireland, Cumbria, southern Norway and central Europe with annual mean TP concentrations ranging from 1-73 µg TP L^{-1} and a median value of 22 µg TP L^{-1} (Bennion *et al*., 2004); the best model was generated with simple weighted averaging and inverse deshrinking (ter Braak & van Dam, 1989); this model has a coefficient of determination (r2) between observed and inferred values of 0.75 and a root mean squared error of prediction (RMSEP based on the jack-knifing cross validation method) of 0.25 $\log_{10}$ µg TP L^{-1}, or ii) a Northwest European training set of 152 relatively small, shallow lakes (< 10 m maximum depth) with a median value of 104 µg TP L^{-1} and a RMSEP of 0.21 $\log_{10}$ µg TP L^{-1} for the weighted averaging partial least squares two-component (WA-PLS2) model (Bennion *et al*., 1996). All reconstructions were implemented using C^2 (Juggins, 2003). The training set containing the greatest percentage of taxa present in the fossil samples was selected, which resulted in the shallow lake training set being used for the shallow, non-stratifying lakes and the deep lake model being used for the deep, stratifying lakes.

The PCA scores on axis 1 and 2 of each core are also displayed passively on a covariance matrix of samples from the modern diatom-TP training sets described above, with logTP as a supplementary environmental variable. The logTP values are represented by generalized additive model (GAM) contours. The plots allow the direction of floristic change at each site and its relation to TP to be visualised. The sample and species scores are plotted in ordination biplots to illustrate the degree to which the recovery trajectories follow back along the enrichment trajectories. The analysis was implemented in Canoco (ter Braak & Smilauer, 2002).

2.3 Results

2.3.1 Dissimilarity scores

The dissimilarity scores between core bottom and other samples in each core indicate that all sites have experienced deviation from reference condition (core bottom sample) over the period represented by the cores (Figure 2.1). All sites, with the exception of Lakes Kielpinskie and Lidzbarskie where the patterns are less clear, exhibit progressive deviation from the reference sample during the period prior to nutrient reduction, indicating gradual compositional change with enrichment. The diatom assemblages of some sites, most notably the deep lakes, show signs of returning towards the reference flora following reduction of nutrient load. This is most apparent in Lake Bled, Gjersjoen, Mill Loch, and Mjoesa. Nonetheless most are still far from reference condition with high dissimilarity scores ranging from 38 to 157 between the core top and bottom samples.

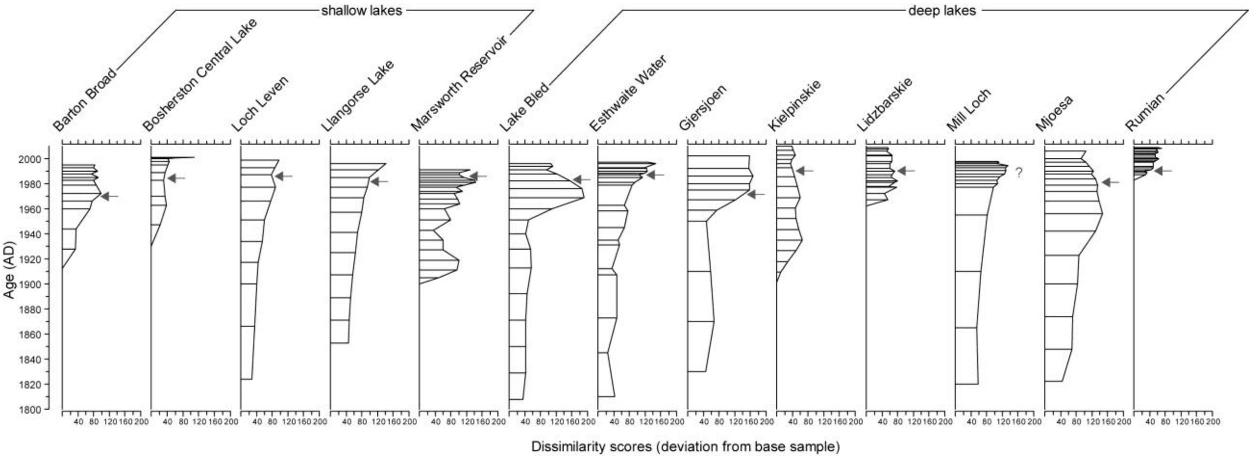

Figure 2.1 Dissimilarity scores for the thirteen study sites (timing of nutrient reduction is shown by the arrow) (degree of floristic change in the diatom assemblages between the bottom sample and every other sample in the core)

2.3.2 Percentage plankton and diversity

In four of the five shallow lakes (Barton Broad, Loch Leven, Llangorse Lake and Marsworth Reservoir) the % plankton increases with enrichment but does not decline during the recovery phase (Figure 2.1). In the other shallow lake, Bosherston Lily Pond, the % plankton stays low throughout the record. In the deep lakes % plankton was high throughout the cores (generally > 60%) but in Esthwaite Water, Gjersjoen, Mill Loch and Mjoesa slight increases in the planktonic component were observed with enrichment. Only in Mjoesa, and to a lesser extent in Esthwaite Water, was a slight decline in % plankton seen in the recovery period. Shifts in diatom diversity with enrichment and recovery were difficult to discern (Figure 2.3). Nonetheless, a slight decrease in Hill's N2 diversity scores was observed in eight lakes (Barton Broad, Bosherston Lily Pond, Loch Leven, Marsworth Reservoir, Kielpinskie, Lidzbarskie, Mill Loch and Mjoesa) prior to the introduction of management measures. A subsequent increase in diversity following restoration was seen only in Barton Broad and Mjoesa.

2.3.3 Ordination and transfer functions

The PCA axis 1 scores show that all sites experienced marked, though gradual, shifts in diatom composition during the eutrophication phase. However, only five sites (Marsworth Reservoir, Lake Bled, Gjersjoen, Mill Loch and Mjoesa) return towards an assemblage similar to that prior to enrichment following reduction in nutrient loading as indicated by a clear reversal in PCA axis 1 scores (Figure 2.4). The data suggest that for the remaining lakes the diatom flora following nutrient reduction exhibits a degree of change but that this shift is not towards the same assemblage as that present before enrichment.

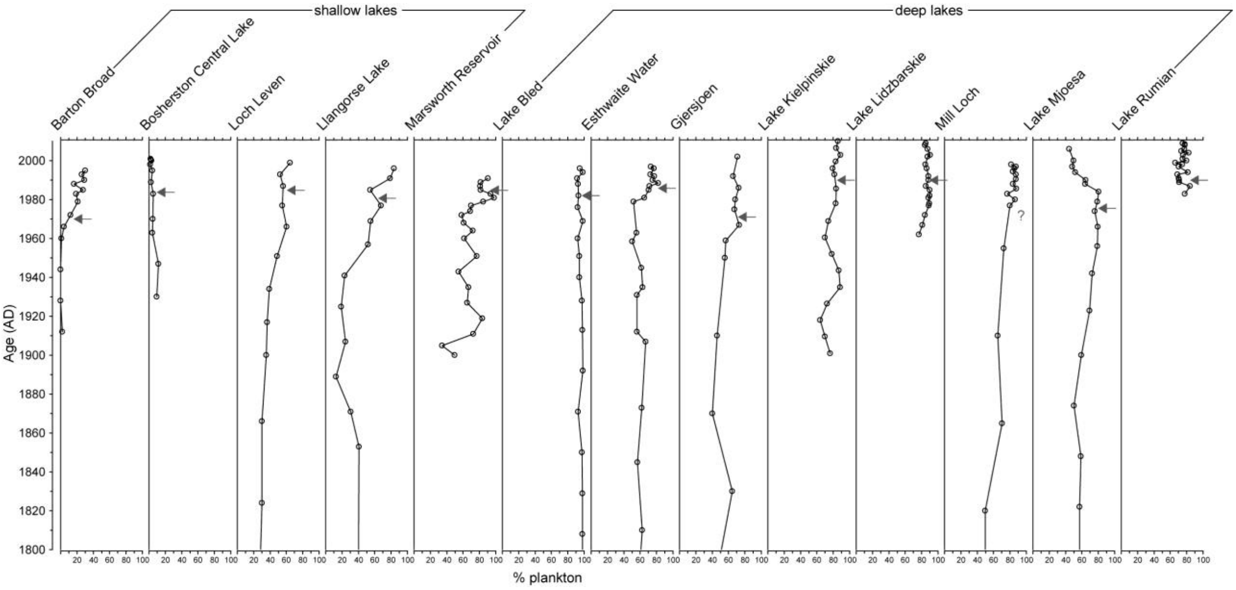

Figure 2.2 Percentage plankton in the thirteen study sites (timing of nutrient reduction is shown by the arrow)

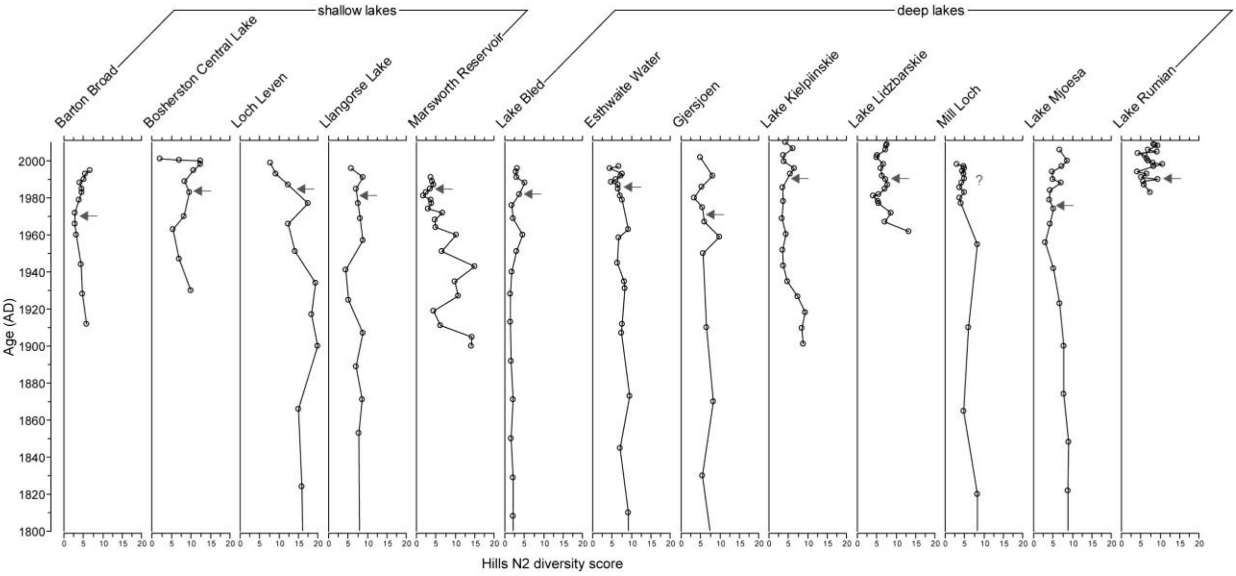

Figure 2.3 Hill's N2 diversity score in the thirteen study sites (timing of nutrient reduction is shown by the arrow)

The diatom transfer functions infer an increase in TP concentrations in eight of the study lakes during the enrichment period (Figure 2.5). Of the shallow lakes, a clear signal was not seen in Barton Broad, Bosherston Lily Pond or Llangorse Lake, and of the deep lakes a clear increase was not apparent in Gjersjoen or Kielpinskie. However, the diatom transfer functions infer a decline in TP concentrations following a reduction in nutrient loading at 12 of the 13 study lakes, the exception being Kielpinskie where a decrease in DI-TP concentrations is not clearly seen (Figure 2.5). This suggests that at these 12 sites there have been compositional changes towards taxa associated with lower nutrient concentrations following the nutrient reductions. In the case of Kielpinskie, the shifts in the diatom assemblages were subtle and have resulted in no major change in DI-TP values in recent years.

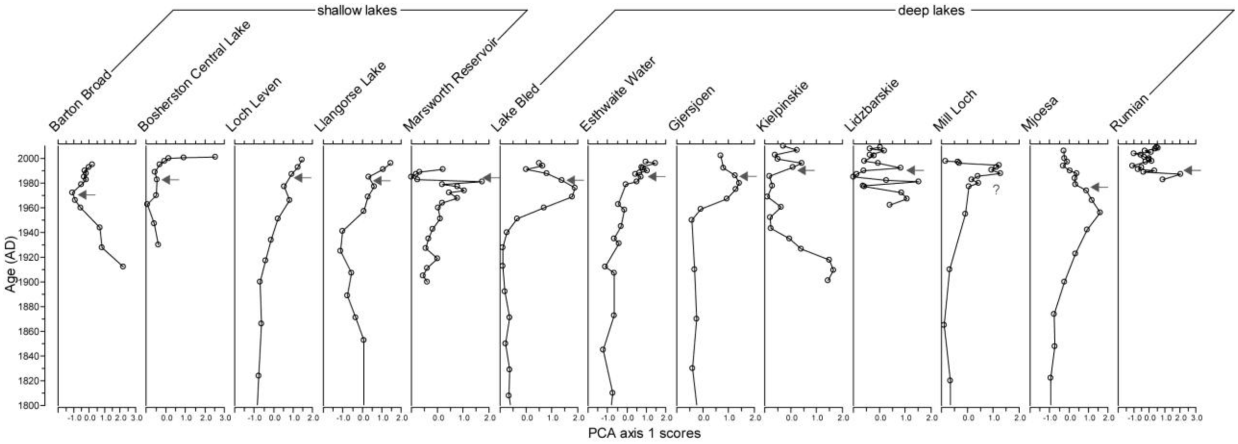

Figure 2.4 PCA axis 1 scores for the thirteen study sites (timing of nutrient reduction is shown by the arrow)

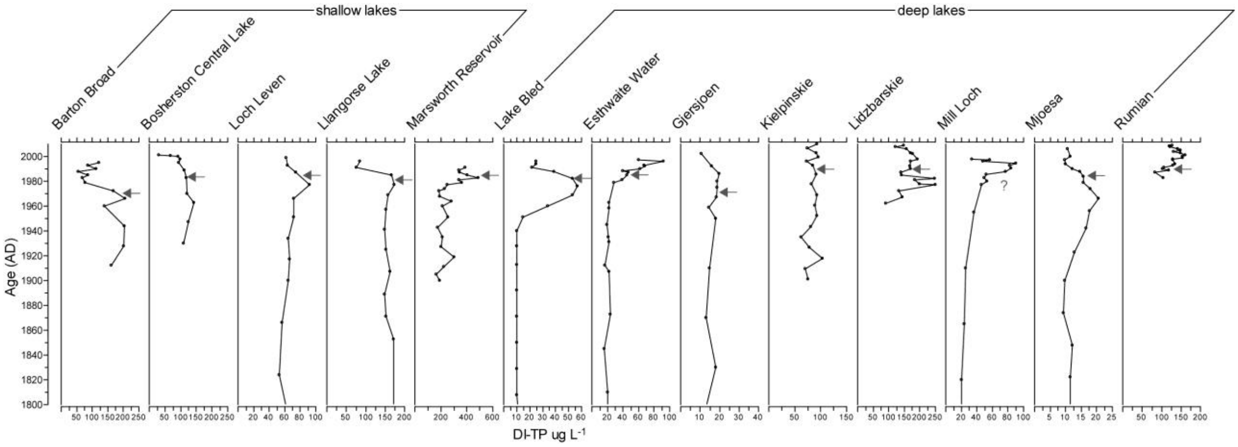

Figure 2.5 Diatom-inferred TP (DI-TP) reconstructions for the thirteen study sites (timing of nutrient reduction is shown by the arrow)

When the deep lake cores are plotted passively on a PCA covariance matrix of the large, deep lakes training set samples with logTP as a supplementary environmental variable (Table 2.2, Figure 2.6 A-C) the core samples generally move from the upper right of the plot towards the lower left during the enrichment period, following the direction of increasing TP concentrations in the training set. A reversal is seen in Lake Bled, Gjersjoen, Mill Loch, and Mjoesa where samples move back towards the upper right following a reduction in nutrient loading. This reverse pattern is not seen in Esthwaite Water. Nor is a clear pattern observed for the three Polish lakes: at Kielpinskie samples move from right to left but there is no subsequent reversal, at Lidzbarskie there is no clear direction of change in the lower part of the record but there is a slight move back to the right in the upper core, and at Rumian there are slight shifts from right to left and back again. The core trajectories reflect changes in the composition of the diatom flora with taxa associated with lower nutrient concentrations located on the right of the diagram (e.g. *Achnanthes* spp., *Brachysira* spp., *Cymbella* spp., *Eunotia* spp., oligotrophic *Cyclotella* spp. and *Tabellaria flocculosa*), those more typically found in

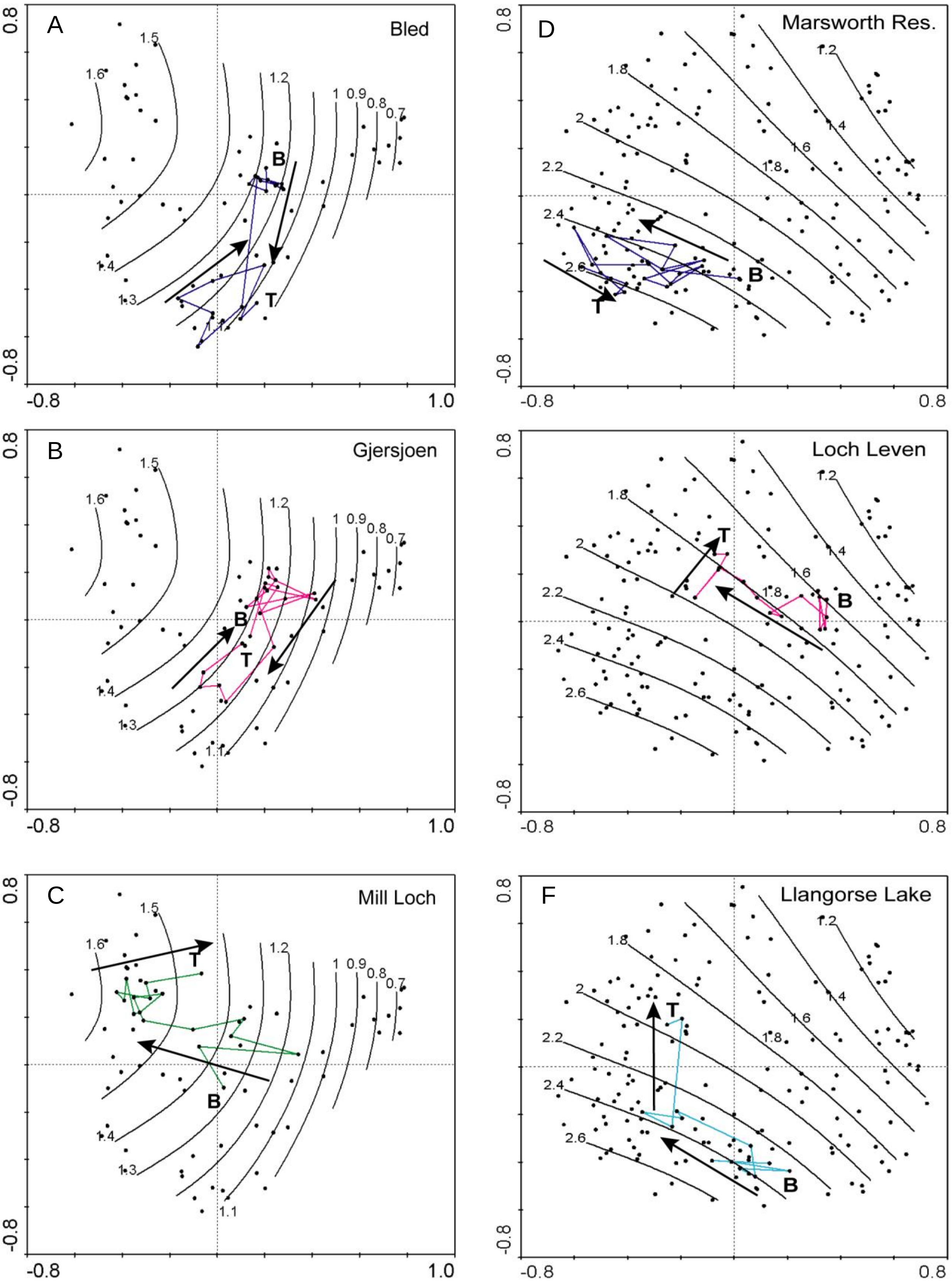

Figure 2.6 Examples of deep lake (A-C) and shallow lake cores (D-F) plotted passively on a PCA covariance matrix of training set samples with logTP as a supplementary environmental variable (logTP values, µg l^{-1}, represented by GAM contours). The direction of change over time is shown by the arrows (T = core top and B = core bottom)

waters with intermediate nutrient concentrations located on the lower left (e.g. *Aulacoseira subarctica*, *Aulacoseira granulata*, *Asterionella formosa*, *Fragilaria crotonensis* and *Cyclotella radiosa*) and those commonly seen in nutrient-rich conditions located on the upper left of the plot (e.g. *Cyclostephanos dubius*, *Stephanodiscus hantzschii*, *Stephanodiscus parvus*) (Figure 2.7).

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Total variance**
Species-environment correlations	0.686	0.277	0.129	0.459	
Cumulative % variance of species data	16.1	28.0	36.0	42.7	
Cumulative % variance of spp-env relation	58.1	65.2	66.2	77	
Sum of all canonical eigenvalues					0.130

Table 2.2 PCA results for the eight deep lake cores plotted passively on a covariance matrix of training set samples with logTP as a supplementary environmental variable (inter-sample distances, divide by SD, centre by species, 208 total samples,178 total species, 56 active samples, 152 passive samples, 139 active species)

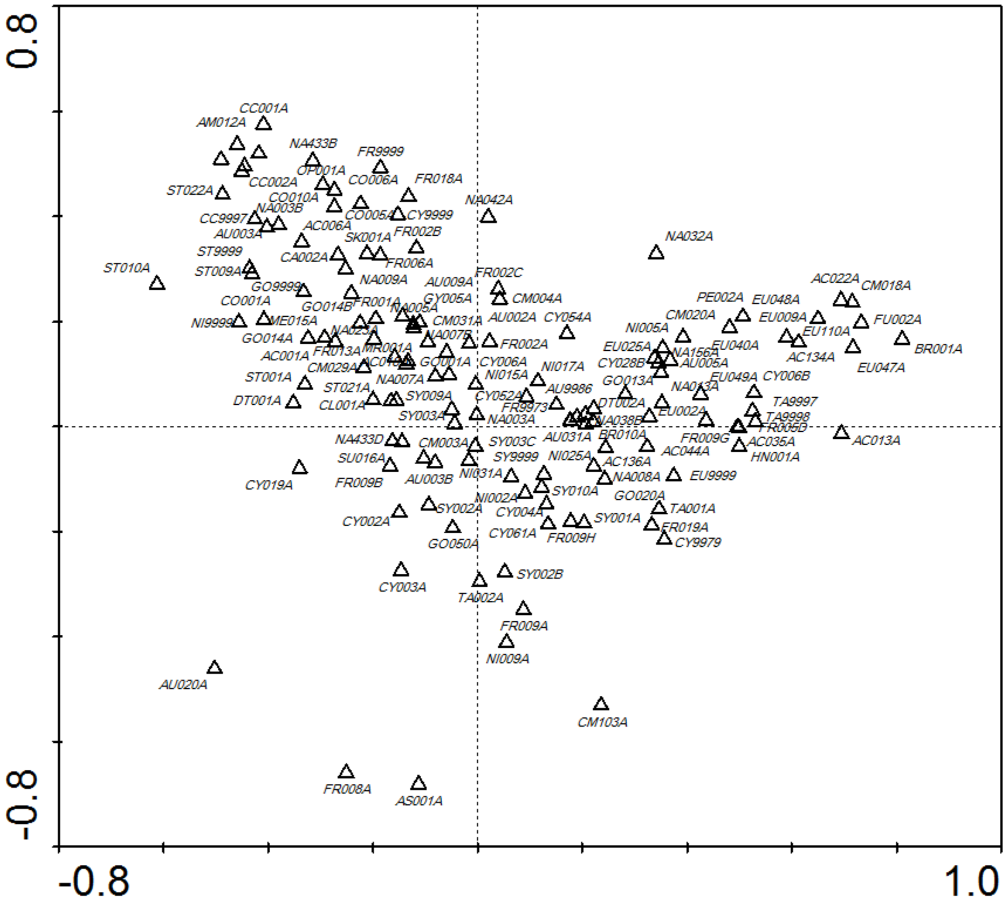

Figure 2.7 Deep lake cores - species plot on a PCA covariance matrix of training set samples (see Appendix 1 for diatom codes and names)

Similarly, when the shallow lake cores are plotted passively on a PCA covariance matrix of the shallow lake training set samples with logTP as a supplementary environmental variable (Table 2.3, Figure 2.6 E-G) the core samples of all five lakes move from the right of the plot towards the left during the enrichment period, following the direction of increasing TP concentrations in the training set. A clear reversal is apparent only at Marsworth Reservoir following nutrient reduction, while a slight move back towards the right of the diagram is seen at Loch Leven. At Barton Broad, Bosherston Lily Pond, and Llangorse Lake, the upper core samples move to a new position within the ordination space but do not obviously track back along the enrichment trajectory. As for the deep lakes, the core sample shifts during the eutrophication phase largely reflect a move from taxa associated with relatively nutrient poor conditions located to the right of the diagram (e.g. *Achnanthes* spp., *Cymbella* spp., *Eunotia* spp., oligotrophic *Cyclotella* spp. and *Tabellaria flocculosa*) to those taxa typically found in nutrient rich waters located to the left of the plot (e.g. *Cyclostephanos dubius, Cyclostephanos tholiformis, Stephanodiscus hantzschii, Stephanodiscus parvus*) (Figure 2.8).

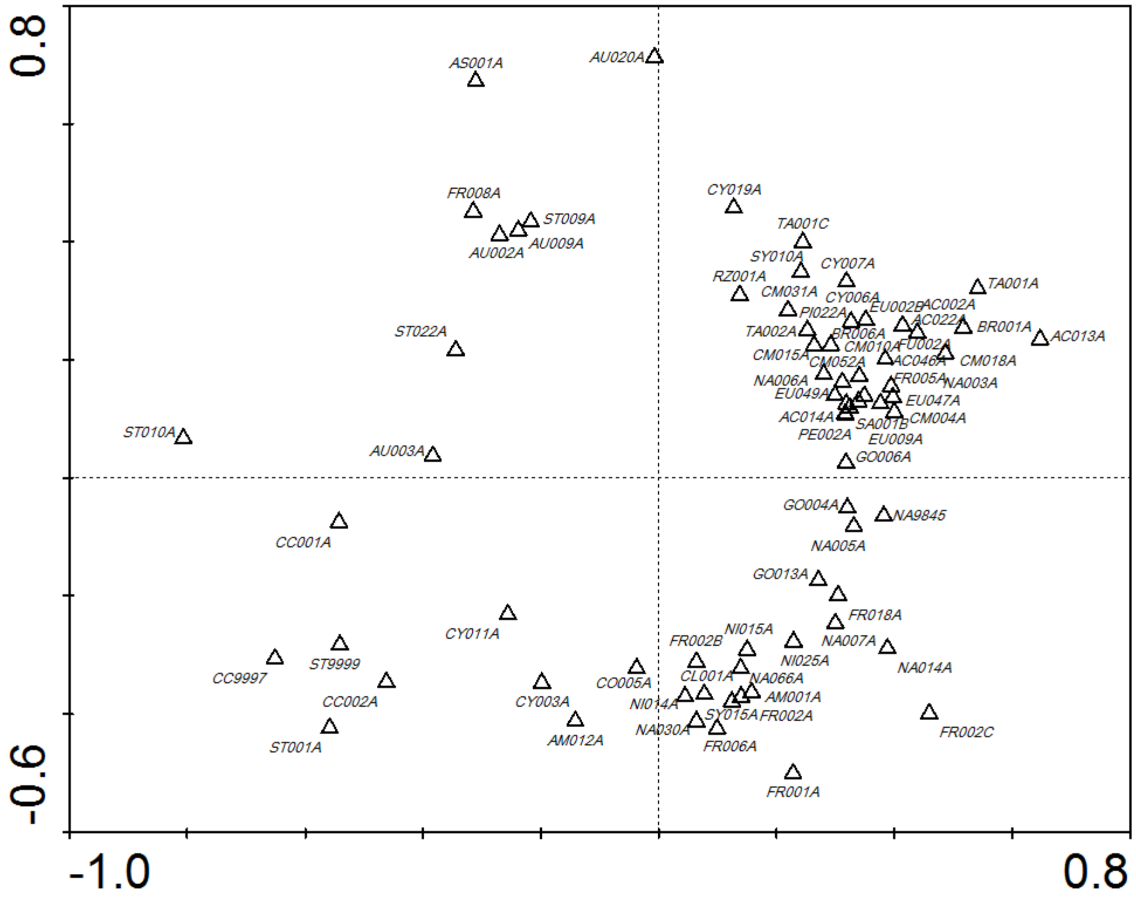

Figure 2.8 Shallow lake cores - species plot on a PCA covariance matrix of training set samples (see Appendix 1 for diatom codes and names)

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Total variance**
Species-environment correlations	0.598	0.608	0.055	0.208	
Cumulative % variance of species data	15.4	26.6	32.9	39.0	
Cumulative % variance of spp-env relation	54.0	94.2	94.4	97	
Sum of all canonical eigenvalues					0.102

Table 2.3 PCA results for the five shallow lake cores plotted passively on a covariance matrix of training set samples with logTP as a supplementary environmental variable
(inter-sample distances, divide by SD, centre by species, 225 total samples, 317 total species, 152 active samples, 73 passive samples, 298 active species)

2.4 Discussion

2.4.1 Diatom response to changes in nutrient loading

One of the challenges for ecologists wishing to track environmental change is to find biological indicators that are sufficiently sensitive to the pressure gradient of interest. Here, a range of diatom metrics were explored as diatoms are sensitive to changes in water quality and are particularly good indicators of lake nutrient concentrations (Hall & Smol, 2010). The most striking changes were observed in diatom composition and were effectively summarised by the ordination (PCA axis 1) and dissimilarity (SCD) scores. The data demonstrate that progressive deviation from the reference condition (here defined as the assemblage at the bottom of the core) occurred at all sites during the eutrophication phase. These shifts were gradual rather than abrupt, reflecting a process of relative decline in taxa associated with low nutrient concentrations and their replacement with taxa typically found in more nutrient rich waters. The ordination plots illustrate that whilst the reference conditions of the 13 study lakes are site specific there are some common patterns in compositional change with shifts from a flora composed of *Achnanthes* spp., *Brachysira* spp., *Cymbella* spp., *Eunotia* spp., oligotrophic *Cyclotella* spp. and *Tabellaria flocculosa* to one composed of *Aulacoseira subarctica*, *Aulacoseira granulata*, *Asterionella formosa*, *Fragilaria crotonensis* and *Cyclotella radiosa* as enrichment progresses and, in the most nutrient-rich cases, to an assemblage composed of small centric taxa such as *Cyclostephanos dubius*, *Stephanodiscus hantzschii* and *Stephanodiscus parvus.* These same shifts have been observed in numerous European lakes during periods of increased nutrient loading (e.g. Bennion *et al*., 2004; 2011b) and, therefore, provide a useful indication of ecological change associated with eutrophication.

The shifts in diatom composition following reduction in nutrient loading are more equivocal. A clear reversal towards the reference flora is seen only in four of the deep lakes, Lake Bled, Gjersjoen, Mill Loch and Mjoesa, and to a lesser extent in Marsworth Reservoir, a shallow lake, in terms of both the dissimilarity and PCA axis 1 scores. As for the degradation phase, the compositional changes are gradual rather than sudden suggesting that ecological recovery may take several years to decades. Indeed even these five lakes do not exhibit a return to the pre-enrichment flora over the 20-30 year period since remedial measures were introduced, as dissimilarity scores between the core bottoms and tops remain relatively high, and the core trajectories illustrate that the recent assemblages have not yet returned to those observed in the lower cores (Figure 2.6 & Figure 2.8). The data for these five lakes suggest that, whilst the diatoms have responded to nutrient reduction and are heading back along the eutrophication pathway, they still have some way to go before they reach reference condition.

For the remaining lakes, the diatom response during the ‘recovery’ period is more difficult to discern. At Esthwaite Water, P loading from a local sewage treatment works was reduced in 1986 but nutrients derived from catchment runoff, a fish farm established in 1981 and sediment P release have negated any potential reduction in lake nutrient concentrations (Bennion *et al*., 2000) and thus biological recovery is not apparent. For the three Polish lakes (Kielpinskie, Lidzbarskie, Rumian) which are relatively deep, stratifying waterbodies, the reversal towards former assemblages is less striking than for the other deep sites. This may be because there have been no specific restoration measures taken to reduce point sources of nutrients, and any decrease in nutrient loading is due to the reduction of fertilizer use and changes in land use in the catchments caused by the significant economic changes in the country in the early 1990s. Diatom response is, therefore, very recent and appears to be relatively subtle.

The Loch Leven data point to partial recovery of the diatom flora, namely an increase in *Aulacoseira subarctica* relative to *Stephanodiscus* taxa since the mid-1980s, as a result of a catchment management plan introduced in 1985. Long term datasets for the loch show that P concentrations have declined markedly but the trend was non-linear with a slight increase in the early 1990s caused by P recycling from the sediments (Carvalho *et al*., 2012). Additionally agriculture in the Leven catchment remains a significant diffuse source of nutrients to the loch as much of the land is used for arable farming, and rural septic tanks also contribute to the P load. The sediment record suggests that those diatom taxa lost during enrichment have not yet returned, most likely because nutrient concentrations remain too high (Bennion *et al*., 2011c). Likewise, at Barton Broad there is little evidence of any recovery in the diatom assemblages. In spite of a substantial reduction in the amount of P entering the rivers from sewage treatment discharges and a consequent progressive decline in lake TP and chlorophyll *a* concentrations since the late 1970s and early 1980s, the reduction in epilimnetic TP was slow due to the continued release of P from the sediments (Phillips *et al*., 1999; 2005). Barton Broad, therefore, remains dominated by phytoplankton with almost no submerged macrophyte growth and it is perhaps not surprising that the diatoms show minimal response.

At the other two shallow lakes (Bosherston Lily Pond and Llangorse Lake) there are compositional changes in the diatoms following remediation efforts but the diatom floras do not appear to revert back towards those seen prior to enrichment but rather move towards a different assemblage. At Llangorse Lake, the effluent from the local sewage treatment works was diverted from the lake in 1981, with a second smaller input diverted in 1992. While the lake appears to be recovering following the remedial measures taken (Bennion & Appleby, 1999), the diatom community in the upper samples is dominated by planktonic forms that were not previously abundant in the record (namely *Aulacoseira subarctica*, *Aulacoseira ambigua* and *Cyclotella radiosa*) and has not yet returned to the *Fragilaria* spp. dominated assemblage seen prior to enrichment. At Bosherston Lily Pond monitored total phosphate concentrations have exhibited a decline since 1981 following various interventions including diversion of sewage since 1984 and construction of a bypass pipeline in 1992 (Davidson *et al*., 2002). The principal change in the diatom assemblages from this time, most notably since the early 1990s, has been a shift in life-forms with an overall increase in epiphytic taxa relative to benthic taxa. Interpretation of the diatom species shifts is difficult owing to the subtle nature of the changes and the uncertainties regarding the factors which determine the composition of non-planktonic communities. Nevertheless, changes in the nutrient concentrations, shifts in habitat availability and plant community structure and alterations in grazing pressures are all possible explanations (Davidson *et al*., 2002). The importance of both top down and bottom up mechanisms, the role of the trophic cascade, interactions between the pelagic and littoral environments, the potential for alternative stable states (Scheffer *et al.,* 1993), and the numerous pathways of P recycling must all be considered in order to fully understand how shallow lake ecosystems might respond to changes in nutrient loading. It is important to bear this complexity in mind when attempting to interpret the findings for the shallow lakes in the present study.

In addition to community composition, the response of several other metrics to changes in nutrient loading was explored. Firstly, the percentage of planktonic taxa in the assemblages was calculated. The data suggest that this may be a useful metric for tracking enrichment in shallow lakes as a shift towards higher percentage of plankton was apparent with increased nutrient loading in four of the five shallow sites. An increase was less obviously seen in the deep lakes where percentage of planktonic taxa was generally high throughout the records. The shift from benthic to planktonic production associated with eutrophication in shallow waterbodies has been well documented (e.g. Vadeboncoeur *et al*., 2003). Benthic algae often become light limited as planktonic forms become more abundant, and as submerged macrophytes are lost so too are potential habitats to support epiphytic taxa. However, a subsequent decline in the planktonic component of the diatom assemblages following nutrient reduction was not evident, indicating that there is a degree of resilience in the systems and the diatom flora does not automatically revert back to that seen prior to enrichment.

Secondly, diatom diversity, expressed as Hill's N2 diversity scores, was estimated. A decrease in diversity during the eutrophication phase was observed in eight lakes. This conforms to the general expectation that waters with low nutrient concentrations are associated with high diversity while conversely nutrient-rich waters favour fast-growing, competitive species thereby excluding less aggressive, more specialist ones, resulting in reduced diversity (Dodson *et al*., 2000; Mittelbach *et al*., 2001). However, there was an increase in diversity corresponding with the recovery phase in only two of the study lakes, suggesting that, as for percentage plankton, there is no immediate response of diatom diversity to a reduction in nutrients. Finally, DI-TP estimated from existing diatom transfer functions was trialled as a metric. Increases in DI-TP were observed in eight lakes during the enrichment period while a decline in DI-TP was seen in 12 lakes following remediation. Hence this metric, which essentially reflects shifts in diatom composition, appears to have some potential for tracking recovery. Nonetheless, several studies have highlighted the shortcomings of the transfer function technique in certain situations, and this is particularly well documented for shallow lakes where non-planktonic taxa dominate the diatom assemblages. Problems include the influence of factors such as light, substrate and top-down factors, in addition to water chemistry on the distribution of these taxa and their wide tolerance to nutrient concentrations, making them poor indicators of lake trophic status (e.g. Anderson *et al*., 1993; Bennion, 1995; Bennion & Appleby, 1999; Sayer, 2001; Bennion *et al.* 2001).

2.4.2 Degradation versus recovery pathways

Our 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. Duarte *et al*. (2009) examined four coastal systems demonstrating that they failed to return to the reference status upon nutrient reduction. Explanations for failure included alternative nutrient sources, internal loading, shifts in limiting nutrients, co-limitation effects of nutrients and light, and decreased filter-feeder activity. Similarly, Palmer *et al.* (2007) showed that riverine communities do not necessarily show the anticipated and desired signs of recovery and indeed that recovery may lead to endpoints very different from the original undisturbed state. Lake ecosystems have also been reported to follow convoluted trajectories following nutrient reduction, with internal loading, changes in food webs, the impacts of climate change, and 10–15-year time lags proposed as the causes for the complex lake trajectories observed (Jeppesen *et al*., 2005). Our palaeoecological data accord with these studies highlighting that whilst in some cases the diatom recovery trajectories do appear to track back along the degradation pathway, in others (particularly shallow lakes) either little sign of recovery is evident or the assemblages follow a new trajectory owing to the host of factors discussed above.

Most of the existing studies on recovery pathways are based on long-term datasets but for the majority of freshwater ecosystems monitoring activities are rather short-term and do not sufficiently account for long time periods required for restoration. The longer timeframe afforded by the sediment record thus lends itself well to studies of lake recovery and by extending back several decades or even centuries is valuable for defining the reference condition against which degree of recovery can be assessed. Nonetheless, palaeoecological data are not without their limitations and in this study it is perhaps the relatively low resolution of the data for the recovery period (i.e. at some sites only two or three samples correspond to the period since nutrient reduction) that is the greatest weakness. Hence, a combination of long-term datasets and palaeolimnological approaches provides a particularly powerful tool for assessing timescales of ecological change (Battarbee *et al*., 2005; Bennion *et al*., 2011c; Dong *et al*., 2011).

2.4.3 Management implications and factors confounding recovery

Several of the study lakes exhibit signs of ecological recovery in terms of reversal in their diatom assemblages but even these are slow to do so and the assemblages are still far from reference conditions as much as two to three decades since management measures were taken to reduce nutrient loads. This has major implications for the WFD which requires waterbodies to be restored to at least good status, initially by 2015, in that the effects of any measures that have recently been introduced could take several decades to be seen. Perhaps even more importantly the data suggest that for some lake systems the assemblages following remedial action may not return back down the degradation pathway at all and, therefore, reference conditions are unlikely ever to be achieved. The key message arising from the case studies examined here is that for the most part managers are advised to isolate the main source(s) of nutrients and then wait. In most of our study lakes, the main point source of nutrients, principally P, has been the key focus of management efforts. However, in recent decades diffuse nutrient sources have become relatively more significant than urban wastewater pollution and losses from agricultural land are now the biggest challenge. There has been a growing literature on the need to reduce nitrogen (N) loads as well as P in order to reverse eutrophication, particularly in shallow lakes with moderate P levels where high summer N concentrations stimulate algal growth and cause loss of submerged plants (e.g. Jeppesen *et al*., 2007). Indeed, a recent assessment of nutrient sources to Llangorse Lake, one of the shallow lakes in this study, revealed the importance of reducing N inputs if restoration targets are to be met (May *et al*., 2010).

The role of climate change in exacerbating the symptoms of eutrophication and confounding recovery efforts cannot be ignored. Climate change is predicted to result in higher water temperatures, shorter periods of ice-cover and longer summer stratification (Jeppesen *et al*., 2010). Models suggest that lakes with long residence times may experience higher P levels in the future under warmer temperatures (Malmaeus *et al.,* 2006) and shallow lakes may be particularly susceptible. Ecological consequences might include earlier appearance of spring blooming phytoplankton and increased proportions of cyanobacteria. In some systems, negative effects may be compensated by greater predation pressure by zooplankton which is known to be positively temperature dependent. However, fish activity may also increase in warmer temperatures thereby reducing zooplankton populations through increased predation

(Moss *et al*., 2003). In addition, changes in mixing may influence the availability of nutrients in the photic zone and higher temperatures may enhance sediment-P release, whilst higher winter precipitation is likely to enhance nutrient loss from cultivated fields (see Battarbee *et al*. 2008 for a review).

An examination of the role of climate change in explaining the shifts in the diatom assemblages of the 13 lakes is beyond the scope of this study. However, detailed studies on two of the lakes, Esthwaite Water (Dong *et al*., in press) and Loch Leven (Bennion *et al*., 2011c) have attempted to explore the ways in which nutrients and climate interact on decadal and inter-annual timescales to affect the diatom communities. Dong *et al.* (in press) conclude that while nutrients have been important during the entire 60-year investigation period, air temperature has become a controlling factor in recent decades during a period when nutrient availability was relatively high. Bennion *et al.* (2011c) showed that at an inter-annual scale the diatom data for Loch Leven exhibit high variability, yet there are several changes in species composition in the recent fossil record that may be attributed to climatic controls. In both of these studies the presence of *Aulacoseira granulata* and *Aulacoseira granulata* var. *angustissma* seems to coincide with warmer temperatures. Such investigations contribute to a better understanding of the effects of multiple environmental drivers on aquatic ecosystems but equally illustrate the complexity of ecosystem response to synchronous changes in nutrients and climate, and the difficulty of disentangling the effects of these interacting pressures.

Models that predict likely outcomes of climate change on nutrient regimes will play a vital role in improving our understanding of future lake response and in guiding management decisions (e.g. Whitehead *et al*., 2006). Whilst sediment records cannot be used in a predictive capacity, they provide an opportunity to validate hindcasts derived from dynamic models (Anderson *et al.,* 2006). They should, therefore, play an increasingly important role in assessing uncertainty associated with future predictions. Conceptual models based on the DPSIRR scheme, i.e. the ‘Driver-Pressure-State-Impact-Response-Recovery chain’, as adopted in the EU WISER project, will also be important for providing guidance on the ecological effectiveness of restoration measures (Feld *et al*., 2010). In the context of the present study, the key Drivers are urbanisation and agricultural intensification, the Pressure is eutrophication, the State is trophic status and nutrient concentrations, the Impact explored is that on one of the algal groups, diatoms, in terms of community composition, functional groups and diversity, the Response is nutrient load reduction principally by management of sewage effluent but also by good agricultural practice in some instances, and the Recovery relates to shifts in the structure of the diatom assemblages. The study illustrates, therefore, that palaeoecology is a valuable tool for populating conceptual models of this kind.

2.5 Conclusions

In terms of the original questions posed we can conclude that the observed changes in the diatom records do reflect both the degradation and the recovery process. The latter has reached a different stage in each of the study lakes and is more clearly seen in the deep lakes where the diatom assemblages have started to revert back toward those seen prior to enrichment. In shallow lakes factors such as internal loading and top down control may influence the recovery process and in this study, whilst the assemblages of several shallow lakes were replaced by ones associated with lower productivity following remediation, they did not track back along the enrichment pathway. It can, therefore, be concluded that the deep stratified lakes tend to follow a more predictable recovery pathway than the shallow lakes. Nevertheless, the recovery process has a long way to go in all cases as the present assemblages remain very different from those seen in the pre-enrichment samples. Dissimilarity and ordination scores can be used to quantify the deviation from reference condition.

The study highlights the important role that paleolimnological approaches can play in establishing a benchmark against which managers can evaluate the degree to which their restoration efforts are successful. The centennial to decadal timescale adopted here provides the critical temporal context to inform the difficult decisions that emerge for the management of enriched waterbodies. We recognise that this study is based only on diatom responses and our inferences about biological recovery may therefore be biased, especially as diatoms are arguably one of the most sensitive groups in the system and have short response times relative to other assemblages such as macrophytes and fish. Assessments using multiple assemblages are required to evaluate wider ecosystem responses to environmental stressors, hence multi-proxy palaeoecological techniques have an important role to play in future studies of degradation and recovery pathways.

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Appendix 1 List of diatom taxa included in the analyses with codes and names

Code	Name	Code	Name	Code	Name
AC001A	Achnanthes lanceolata	CC001A	Cyclostephanos dubius	DP003A	Diploneis oculata
AC002A	Achnanthes linearis	CC002A	Cyclostephanos invisitatus	DP007A	Diploneis oblongella
AC004A	Achnanthes pseudoswazi	CC9997	Cyclostephanos [cf. tholiformis]	DP012A	Diploneis marginestriata
AC005A	Achnanthes calcar	CL001A	Cymatopleura solea	DP065A	Diploneis parma
AC006A	Achnanthes clevei	CM002A	Cymbella turgida	DT001A	Diatoma elongatum
AC008A	Achnanthes exigua	CM003A	Cymbella sinuata	DT002A	Diatoma hyemale
AC013A	Achnanthes minutissima	CM004A	Cymbella microcephala	DT002B	Diatoma hyemale var. mesodon
AC014A	Achnanthes austriaca	CM006A	Cymbella cistula	DT004A	Diatoma tenue
AC018A	Achnanthes laterostrata	CM010A	Cymbella perpusilla	DT021A	Diatoma mesodon
AC022A	Achnanthes marginulata	CM013A	Cymbella helvetica	EP001A	Epithemia sorex
AC023A	Achnanthes conspicua	CM014A	Cymbella aequalis	EP007A	Epithemia adnata
AC028A	Achnanthes saxonica	CM015A	Cymbella cesatii	EP9999	Epithemia sp.
AC030A	Achnanthes sumara	CM017A	Cymbella hebridica	EU002A	Eunotia pectinalis pectinalis
AC032A	Achnanthes hungarica	CM018A	Cymbella gracilis	EU002B	Eunotia pectinalis var. minor
AC034A	Achnanthes suchlandtii	CM020A	Cymbella gaeumannii	EU002K	Eunotia pectinalis var. ventricosa
AC035A	Achnanthes pusilla	CM022A	Cymbella affinis	EU003A	Eunotia praerupta var. praerupta
AC042A	Achnanthes detha	CM029A	Cymbella ehrenbergii	EU004A	Eunotia tenella
AC044A	Achnanthes levanderi	CM031A	Cymbella minuta	EU008A	Eunotia monodon
AC046A	Achnanthes altaica	CM033A	Cymbella hustedtii	EU009A	Eunotia exigua exigua
AC049A	Achnanthes ploenensis	CM038A	Cymbella delicatula	EU011A	Eunotia rhomboidea
AC134A	Achnanthes helvetica	CM047A	Cymbella incerta	EU019A	Eunotia iatriaensis
AC136A	Achnanthes subatomoides	CM048A	Cymbella lunata	EU020A	Eunotia meisteri
AC156A	Achnanthes amoena	CM050A	Cymbella subaequalis	EU021A	Eunotia sudetica
AC9999	Achnanthes sp.	CM052A	Cymbella descripta	EU025A	Eunotia fallax
AM001A	Amphora ovalis	CM086A	Cymbella leptoceros	EU029A	Eunotia valida
AM004A	Amphora veneta	CM103A	Cymbella silesiaca	EU040A	Eunotia paludosa
AM012A	Amphora pediculus	CM9999	Cymbella sp.	EU047A	Eunotia incisa
AM013A	Amphora inariensis	CN001A	Cymbellonitzschia diluviana	EU048A	Eunotia naegelii
AN009A	Anomoeoneis sphaerophora	CO001A	Cocconeis placentula	EU049A	Eunotia curvata
AP001A	Amphipleura pellucida	CO001B	Cocconeis placentula var. euglypta	EU056A	Eunotia minutissima
AS001A	Asterionella formosa	CO005A	Cocconeis pediculus	EU070A	Eunotia bilunaris
AU002A	Aulacoseira ambigua	CO006A	Cocconeis diminuta	EU107A	Eunotia implicata
AU003A	Aulacoseira granulata	CO009A	Cocconeis thumensis	EU110A	Eunotia minor
AU003B	Aulacoseira granulata v. angustissima	CO010A	Cocconeis disculus	EU9999	Eunotia sp.
AU004A	Aulaoseira lirata	CO9999	Cocconeis sp.	FR001A	Fragilaria pinnata
AU004D	Aulacoseira lirata var. alpigena	CY002A	Cyclotella pseudostelligera	FR002A	Fragilaria construens
AU005A	Aulacoseira distans	CY003A	Cyclotella meneghiniana	FR002B	Fragilaria construens var.binodis
AU005B	Aulacoseia distans var. nivaloides	CY004A	Cyclotella stelligera	FR002C	Fragilaria construens var. venter
AU005K	Aulacoseira distans var. lacustris	CY006A	Cyclotella kuetzingiana	FR002D	Fragilaria construens var. exigua
AU005L	Aulacoseira distans var. humilis	CY006B	Cyclotella kuetzingiana v. planetophora	FR003A	Fragilaria bicapitata
AU009A	Aulacoseira islandica	CY007A	Cyclotella glomerata	FR005A	Fragilaria virescens
AU010A	Aulacoseira perglabra	CY009A	Cyclotella ocellata	FR005D	Fragilaria virescens var. exigua
AU010B	Aulacoseira perglabra var. floriniae	CY010A	Cyclotella comensis	FR006A	Fragilaria brevistriata
AU014A	Aulacoseira nygaardii	CY011A	Cyclotella atomus	FR008A	Fragilaria crotonensis
AU020A	Aulacoseira subarctica	CY016A	Cyclotella arentii	FR009A	Fragilaria capucina
AU022A	Aulacoseira subborealis	CY019A	Cyclotella radiosa	FR009B	Fragilaria capucina var. mesolepta
AU028A	Aulacoseira tenella	CY028B	Cyclotella distinguenda v. unipunctata	FR009G	Fragilaria capucina var. rumpens
AU031A	Aulacoseira alpigena	CY052A	Cyclotella rossii	FR009H	Fragilaria capucina var. gracilis
AU9986	Aulacoseira cf. subarctica type 2	CY054A	Cyclotella krammeri	FR010A	Fragilaria constricta
AU9999	Aulacoseira sp.	CY061A	Cyclotella gordonensis	FR011A	Fragilaria lapponica
BA001A	Bacillaria paradoxa	CY9979	Cyclotella [cf. comensis]	FR013A	Fragilaria oldenburgiana
BR001A	Brachysira vitrea	CY9999	Cyclotella sp.	FR014A	Fragilaria leptostauron
BR006A	Brachysira brebissonii	DE001A	Denticula tenuis	FR016A	Fragilaria heidenii
BR010A	Brachysira neoexilis	DE003A	Denticula kuetzingii	FR018A	Fragilaria elliptica
CA002A	Caloneis bacillum	DP001A	Diploneis ovalis	FR019A	Fragilaria intermedia

Appendix 1 continued

Code	Name	Code	Name	Code	Name
FR059A	Fragilaria radians	NA040A	Navicula hoefleri	NI013A	Nitzschia triblionella
FR063A	Fragilaria robusta	NA042A	Navicula minima	NI014A	Nitzschia amphibia
FR065A	Fragilaria leptostauron	NA045A	Navicula bryophila	NI015A	Nitzschia dissipata
FR9999	Fragilaria sp.	NA050A	Navicula clementis	NI017A	Nitzschia gracilis
FU002A	Frustulia rhomboides	NA055A	Navicula graciloides	NI018A	Nitzschia dubia
GO001A	Gomphonema olivaceum	NA056A	Navicula cuspidata	NI020A	Nitzschia angustata
GO003A	Gomphonema angustatum	NA057A	Navicula elginensis	NI020B	Nitzschia angustata var. acuta
GO003B	Gomphonema angustatum var. productum	NA063A	Navicula trivialis	NI023A	Nitzschia scalaris
GO004A	Gomphonema gracile	NA064A	Navicula exilis	NI025A	Nitzschia recta
GO006A	Gomphonema acuminatum	NA065A	Navicula gastrum	NI026A	Nitzschia romana
GO010A	Gomphonema constrictum	NA066A	Navicula capitata	NI028A	Nitzschia capitellata
GO011A	Gomhonema subclavatum	NA071A	Navicula bacillum	NI031A	Nitzschia linearis
GO013A	Gomphonema parvulum	NA079A	Navicula pseudolanceolata	NI033A	Nitzschia paleacea
GO014A	Gomphonema intricatum	NA080A	Navicula slesvicensis	NI042A	Nitzschia acicularis
GO014B	Gomphonema intricatum var. pumilum	NA082A	Navicula muralis	NI043A	Nitzschia inconspicua
GO018A	Gomphonema longiceps	NA083A	Navicula frugalis	NI044A	Nitzschia intermedia
GO020A	Gomphonema affine	NA084A	Navicula atomus	NI046A	Nitzschia sigmoidea
GO029A	Gomphonema clavatum	NA095A	Navicula tripunctata	NI053A	Nitzschia acuta
GO050A	Gomphonema minutum	NA101A	Navicula jaagii	NI063A	Nitzschia agnita
GO9999	Gomphonema sp.	NA109A	Navicula opportuna	NI072A	Nitzschia bremensis
GY001A	Gyrosigma attenuatum	NA113A	Navicula acceptata	NI076A	Nitzschia calida
GY005A	Gyrosigma acuminatum	NA114A	Navicula subrotundata	NI127A	Nitzschia subcapitellata
GY017A	Gyrosigma macrum	NA124A	Navicula molestiformis	NI171A	Nitzschia subacicularis
GY020A	Gyrosigma parkeri	NA128A	navicula schoenfeldii	NI195A	Nitzschia supralitorea
GY9999	Gyrosigma sp.	NA133A	Navicula schassmannii	NI196A	Nitzschia palaeo var. debilis
HN001A	Hannaea arcus	NA144A	Navicula utermoehlii	NI198A	Nitzschia lacuum
ME013A	Melosira arenaria	NA152A	Navicula lapidosa	NI199A	Nitzschia angustatula
ME015A	Melosira varians	NA156A	Navicula leptostriata	NI201A	Nitzschia graciliformis
MR001A	Meridion circulare	NA166A	Navicula submuralis	NI9999	Nitzschia sp.
NA001A	Navicula tuscula	NA168A	Navicula vitabunda	OP001A	Opephora martyi
NA002A	Navicula jaernefeltii	NA400A	Navicula glomus	OP008A	Opephora olsenii
NA003A	Navicula radiosa	NA402A	Navicula gottlandica	PE002A	Peronia fibula
NA003B	Navicula radiosa var. tenella	NA429A	Navicula hustedtii	PI005A	Pinnularia major
NA005A	Navicula seminulum	NA433B	Navicaul ignota var. anglica	PI007A	Pinnularia viridis
NA006A	Navicula mediocris	NA433D	Navicula ignota var. acceptata	PI015A	Pinnularia abaujensis
NA007A	Navicula cryptocephala	NA512A	Navicula minisculoides	PI018A	Pinnularia biceps
NA007B	Navicula cryptocephala var. veneta	NA590A	Navicula pseudoventralis	PI022A	Pinnularia subcapitata
NA007E	Navicula cryptocephala var. intermedia	NA669A	Navicula suchlandtii	PI023A	Pinnularia irrorata
NA008A	Navicula rhyncocephala	NA675A	Navicula tenelloides	PI030A	Pinnularia acoricola
NA009A	Navicula lanceolata	NA676A	Navicula tenera	PI9999	Pinnularia sp.
NA013A	Navicula pseudoscutiformis	NA742A	Navicula duerrenbergiana	PL050A	Pleurosigma salinarum
NA014A	Navicula pupula	NA743A	Navicula subrhyncocephala	PL9999	Pleurosigma sp.
NA016A	Navicula indifferens	NA744A	Navicula pseudoanglica	RA9999	Rhaphoneis sp.
NA021A	Navicula cincta	NA745A	Navicula capitoradiata	RC001A	Rhoicosphenia abbreviata
NA022A	Navicula halophila	NA768A	Navicula reichardtiana	RH001A	Rhopalodia gibba
NA023A	Navicula gregaria	NA9845	Navicula cryptotenella type	RZ001A	Rhizosolenia longiseta
NA024A	Navicula oblonga	NA9999	Navicula sp.	SA001A	Stauroneis anceps
NA025A	Navicula mutica	NE012A	Neidium glaberrimum	SA001B	Stauroneis anceps var. gracilis
NA027A	Navicula viridula	NI002A	Nitzschia fonticola	SA003A	Stauroneis smithii
NA028A	Navicula scutelloides	NI003A	Nitzschia denticula	SA006A	Stauroneis phoenicenteron
NA029A	Navicula gracilis	NI005A	Nitzschia perminuta	SA012A	Stauroneis kriegeri
NA030A	Navicula menisculus	NI006A	Nitzschia sigma	SK001A	Skeletonema costatum
NA032A	Navicula cocconeiformis	NI007A	Nitzschia hungarica	ST001A	Stephanodiscus hantzschii
NA037A	Navicula angusta	NI008A	Nitzschia frustulum	ST009A	Stephanodiscus alpinus
NA038B	Navicula arvensis var. maior	NI009A	Nitzschia palea	ST010A	Stephanodiscus parvus

Appendix 1 continued

Code	Name
ST015A	Stephanodiscus binderanus
ST021A	Stephanodiscus minutulus
ST022A	Stephanodiscus neoastraea
ST9999	Stephanodiscus sp.
SU001A	Surirella angusta
SU002A	Surirella ovata
SU002C	Surirella ovata var. crumena
SU004B	Surirella biseriata var. bifrons
SU005A	Surirella linearis
SU006A	Surirella delicatissima
SU016A	Surirella minuta
SU073B	Surirella brebisonni var. kuetzingii
SY001A	Synedra ulna
SY001C	Fragilaria ulna var. danica
SY002A	Synedra rumpens
SY002B	Synedra rumpens var. familiaris
SY003A	Synedra acus
SY003B	Synedra acus var. radians
SY003C	Synedra acus var. angustissima
SY004A	Synedra parasitica
SY008A	Synedra pulchella
SY009A	Synedra nana
SY010A	Synedra minuscula
SY015A	Synedra tabulata
SY017A	Synedra radians
SY9999	Synedra sp.
TA001A	Tabellaria flocculosa
TA001C	Tabellaria flocculosa var. asterionelloides
TA002A	Tabellaria fenestrata
TA9997	Tabellaria flocculosa short
TA9998	Tabellaria flocculosa long
TE001A	Tetracyclus lacustris
TE9999	Tetracyclus sp.
TH016A	Thalassiosira guillardii
UN9995	Unknown centric
UN9999	Unknown sp.

3. Identifying nutrient and climate impacts on diatom dynamics in Loch Leven from recent sediment records

Responsible: Helen Bennion[1], Contributors: Laurence Carvalho[2], Carl Sayer[1], Gavin Simpson[1] & Juliane Wischnewski[3]

[1]Environmental Change Research Centre, Department of Geography, University College London, Gower Street, London WC1E 6BT, UK.

[2]Centre for Ecology & Hydrology (Edinburgh), Bush Estate, Penicuik, EH26 0QB, UK.

[3]Alfred Wegener Institute for Polar and Marine Research, Telegrafenberg A43, 14473, Potsdam, Germany.

3.1 Introduction

Eutrophication, principally caused by phosphorus (P) and nitrogen (N) from agriculture, industrial waste and domestic sewage, remains one of the foremost environmental issues threatening the quality of surface waters (Smith, Joye & Howarth, 2006). Many lakes have been subject to nutrient loading over relatively long (centuries, decades) timescales (e.g. Bradshaw, Rasmussen & Odgaard, 2005) but over the last decade or so efforts to better manage and restore enriched systems have increased (e.g. Jeppesen et al., 2007; Søndergaard et al., 2007) and there are now numerous examples of lakes in recovery (Anderson, Jeppesen & Søndergaard, 2005). Current attempts to mitigate eutrophication could be frustrated, however, by the influences of a changing climate (Battarbee et al., 2005; Jeppesen et al., 2007, 2010). At present, the effects of climate change on lake ecosystems are poorly understood. It is often assumed, for example, that rising global temperatures will lead to deterioration in water quality because phytoplankton will become more abundant and warm-water associated cyanobacteria will begin to dominate lake ecosystems. Experimental studies on phytoplankton growth rates and seasonal community successions certainly appear to support this possible outcome (Reynolds, 1984; Moss et al., 1997). However, other studies have shown that the reproductive and grazing rates of zooplankton are affected by changes in temperature (Hanazato & Yasuno, 1985). This suggests that warming could also significantly increase the grazing effect of the zooplankton community on the phytoplankton. If so, the net effect of an increase in water temperature could be lower, rather than higher, phytoplankton abundances. Changes in other meteorological parameters, such as wind speed, incident solar radiation and precipitation, may also have an influence. For example, increases or decreases in precipitation affect the nutrient supply from the catchment and flushing rate (Bailey-Watts et al., 1990).

The potential confounding effect of climate change on remediation efforts is of particular concern to the implementation of the EU Water Framework Directive (WFD) (European Union, 2000). Under this Directive, all Member States must achieve good ecological status in lakes with a surface area of >0.5 km^2 by 2015. If the definition of good ecological status is based simply on historical reference conditions that do not take the effects of climate change into account, Member States may be faced with water quality targets that are impossible to achieve. In order to improve our understanding of how climate change will affect water quality in the future, we need a better knowledge of how this pressure has modified lake ecosystems in the past. This information is contained within existing historical and palaeolimnological records, but it is difficult to extract because many lakes (especially in populated lowland regions) that have been affected by climate change have also experienced changes in nutrient input over a similar timescale. The examination of long-term limnological and climate records may provide a means of disentangling the effects of nutrient enrichment and climate change, and assessing interactions between the two.

This paper focuses on Loch Leven (Kinross, Scotland) and explores the potential of a palaeolimnological approach, in combination with long time series, to assess the impacts of nutrients and climate on a range of timescales from several centuries to seasons. A well documented eutrophication history and existence of comprehensive limnological (spanning the last forty years) and palaeolimnological datasets for the site provides a rare opportunity for examining ecological responses to enrichment and recovery. Further, the latter have occurred over a period when there has been a measurable impact of climate change on the loch. In particular, over the last 30 years, winter ice cover has become less frequent and less extensive, spring air temperatures have increased markedly and winter rainfall has significantly increased (Ferguson et al., 2008; Carvalho et al., in press). Studies considering limnological (e.g. Bailey- Watts et al.,1990; Carvalho & Kirika, 2003) and palaeolimnological (e.g. Haworth, 1972; Bennion, Fluin & Simpson, 2004; Salgado et al., 2010) data have been published previously, but the data have not been integrated to provide a more comprehensive picture of how lake ecosystem structure and functioning are impacted by, and recover from, nutrient pressures. Furthermore, to date such data have not been used to examine how climate and nutrients may interact. The use of sediment records can potentially provide a temporally integrated, longer-term view of ecological dynamics at the site than can be provided by the monitoring data alone, whilst the long-term monitoring data series can be used to identify trends and relationships among variables recorded at a seasonal timescale which is less accessible to palaeolimnology (Battarbee et al., 2005).

Loch Leven has been a particular focus for diatom-based palaeoecological studies (Haworth, 1972; Bennion et al., 2004). Diatoms (unicellular, siliceous algae: Bacillariophyceae) are one of the most widely used biological groups in palaeolimnological studies for tracking environmental change (e.g. Battarbee et al., 2001). They are sensitive to changes in water quality and are particularly good indicators of lake nutrient concentrations (Bennion, Juggins & Anderson, 1996; Hall & Smol, 2010). Here, we present diatom data analysed at a high resolution from a recent sediment core, in combination with existing diatom records from previous cores and long-term datasets of phytoplankton, nutrient and climate variables, to track environmental change at a range of temporal scales.

3.2 Methods

3.2.1 Site details

Loch Leven is a large, shallow lake (lake area 13.3 km^2, mean depth 3.9 m, maximum depth 25.5 m), in lowland Scotland (56° 12'N, 3° 22' W; altitude 107 m) (Figure 3.1). The loch has a well documented history of eutrophication and subsequent recovery following the implementation of a catchment management plan in the late 1980s and early 1990s. This resulted in a 60% reduction in the external load of phosphorus (P) to the loch over the period 1985 to 1995 (from ~20 t y^{-1} to ~8 t y^{-1}), largely attributed to effluent control from a local woollen mill (D'Arcy, 1991) and improvements to local sewage treatment facilities (Bailey-Watts & Kirika, 1987, 1999). Diffuse P loads from agricultural sources contributed approximately 3.5 t TP y^{-1} to the load reduction.

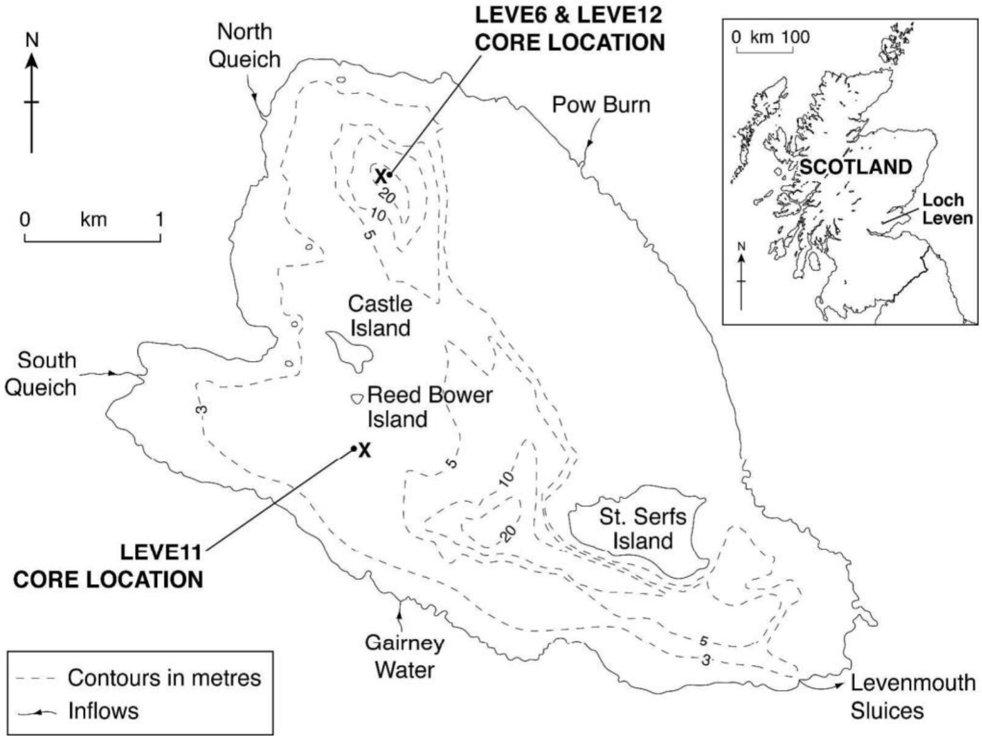


Figure 3.1 Map of Loch Leven showing coring locations

3.2.2 Long-term datasets

The lake has been monitored weekly to fortnightly since 1968 and significant changes in both climate variables and nutrient availability have been recorded over this period (Carvalho & Kirika, 2003; Ferguson et al., 2008; Carvalho et al., in press). Sampling for water chemistry and phytoplankton was carried out by boat from a mid-basin area, using a weighted polythene tube, providing an integrated water sample from the surface to a depth of around 25 cm from the sediment (usually around 3.5 m depth).Samples were stored and analysed using standard methods as described in Bailey-Watts & Kirika (1999). There are gaps in the phytoplankton record for the years 1983,1984, 1986, 1987, 1991 when samples were not collected. Additionally, a horizontal phytoplankton net (53 µm mesh) tow sample was collected on each occasion to provide information on the dominant algae. As part of the present study, a subset of 34 of these samples, covering the period from 1996-2005, were analysed for diatom composition using standard procedures (Battarbee et al., 2001) to provide information on the seasonality of the dominant species and to facilitate comparison with the sedimentary diatom records. Three to four phytoplankton samples, representing the main diatom growing seasons of each year, were chosen for analysis. Prior to diatom slide preparation, samples stored in formaldehyde were centrifuged (1500 rpm for 3minutes) and rinsed in distilled water four times. Counts were carried out at x1000magnification using a Leitz Ortholux II microscope. The main diatom floras used for taxonomic identification were Krammer & Lange-Bertalot (1986, 1988, 1991a, b). At least 200 valves of centric diatoms and 100 valves of *Aulacoseira* spp. were counted for each sample.

As a result of the catchment management plan, P concentrations in Loch Levendeclined from an annual mean in excess of 100 µg total P (TP) L^{-1} in the early 1970s to 33 µg TP L^{-1} in 2008, which meets the water quality target of 40 µg TP L^{-1} annual mean for restoring the ecological health of the loch set by the Loch Leven Area Management Advisory Group (LLAMAG, 1993). The declining trend was non-linear, however, with a rapid decline in concentrations in the early 1970s thought to be largely due to the return of Daphnia to the lake in 1970 after an absence of 15-20 years (Gunn et al., in press), a slight increase in the early 1990s caused by P recycling from the sediments (Carvalho et al., in press), and another rapid decline in 2007 and 2008. Significant reductions in soluble reactive P (SRP) concentrations, a decline in May chlorophyll a concentrations and an increase in spring Secchi disc depth have also been recorded in the last two decades (Carvalho et al., in press). Low SRP concentrations of <10 µg L^{-1} are generally now present from February through to June (Carvalho et al., in press). Indeed Fozzard et al. (1999) and May & Carvalho (2010) have reported signs of positive ecological change in the loch following the reduction of point sources of P, including lower algal abundances, increased water clarity, increases in macrophyte abundance in some years, and an increased diversity and abundance of invertebrates.

Daily air temperatures and rainfall measurements in the Loch Leven catchment have been recorded from 1968 to present at a meteorological station near the shore of the lake. The data have been used to calculate monthly averages for key climate variables for each calendar year. Additionally mean air temperature and total rainfall values have been calculated for spring, summer, autumn and winter periods to assess seasonal changes in climate. Data gaps were filled using estimations based on regression equations relating monthly weather data at Loch Leven with monthly records from the Royal Air Force base at Leuchars, 44 km north-east of Loch Leven (http://www.metoffice.gov.uk/climate/uk/stationdata/).

Analysis of trends in the climate data from 1968-2007 have revealed that air temperature displays a highly significant, increasing linear trend in spring and significant, and increasing trends in autumn and winter (Carvalho et al., in press). Winter rainfall has exhibited a significant increasing trend over the monitoring period although all seasons showed high variability in rainfall. Notably the years 1990, 1995 and 2000 had particularly wet winters and 1976, 1996 and 2006 were particularly dry winters (Carvalho et al., in press). Given that the most significant changes were seen in spring air temperatures and winter rainfall, these variables are used in the current study for assessing climate influence over observed shifts in the fossil diatom assemblages.

3.2.3 Sediment records

Three cores were collected from the loch: i) a short (33 cm) gravity core (LEVE6) was taken on 24 June 1997 from the North deep basin at a water depth of 23 m, ii) a 90 cm mini-Mackereth core (Mackereth, 1969) (LEVE11) was taken on 5 May 1999 at a water depth of 4 m near to Reed Bower Island, and iii) a 94 cm mini-Mackereth core (LEVE12) was taken on 1 June 2005 from the North deep basin at a water depth of 23 m (Figure 3.1). The cores LEVE6 and LEVE11 were extruded in the laboratory at 1 cm intervals and core LEVE12 was sliced throughout at 0.25 cm contiguous intervals. Cores LEVE11 and LEVE12 were radiometrically dated using standard gamma assay procedures (Appleby et al., 1986; Appleby, Richardson & Nolan, 1992) and chronologies were calculated based on ^{210}Pb using the constant rate of supply model (Appleby & Oldfield, 1978).

Selected sub-samples from each core (19 samples from LEVE6, 16 samples from LEVE11 and 61 samples from LEVE12) were prepared and analysed for diatoms using standard procedures (Battarbee et al., 2001). At least 300 valves were counted in each sample using a Leitz research microscope at x1000 magnification and phase contrast. Principal floras used in identification were Krammer & Lange-Bertalot (1986, 1988, 1991a, b), as before. The small centric taxa *Stephanodiscus parvus* Stoermer & Hakansson and *Stephanodiscus minutulus* (Kütz.) Cleve & Moller were merged into *Stephanodiscus parvus/minutulus* owing to difficulties in splitting them consistently using light microscopy. All slides are archived at the Environmental Change Research Centre. Diatom data are expressed as percentage relative abundances for all cores. All diatom taxa shown in subsequent figures are listed in Appendix 1.

Summary groups were used to aid ecological interpretation of the diatom data and for comparison with the monitoring data. Thus, all diatoms were grouped by their habitat (planktonic vs. periphytic) and plankton species were summarised variously as *Aulacoseira* spp., unicellular centrales (genera *Cyclotella*, *Cyclostephanos* and *Stephanodiscus*) or 'oligotrophic *Cyclotella'* (*C. comensis* Grun. in Van Heurck, *C. aff. comensis*, *C. cyclopuncta* Håkansson & Carter, *C. ocellata* Pant., *C. kuetzingiana* var*. planetophora* Fricke in A. Schmidt, *C. rossii* Håkansson, *C. glomerata* Bachm. and *C. stelligera* (Cleve & Grun. in Cleve) Van Heurck). Species were also partitioned by their typical seasonal response in a temperate lake into i) those taxa frequently dominant in late winter-spring and autumn-early winter (January-May and October-January) when the water column is cooler and ill-illuminated ('springautumn' taxa), and ii) those often dominant in summer (May-September) when the water is warmer and subject to strong illumination through longer day lengths ('summer' taxa) (Appendix 1). Categorisation of each species was achieved by reference to published seasonality studies in which diatom taxonomic resolution was high (Kiss & Padisák, 1990; Köhler & Nixdorf, 1994; Gosselain, Descy & Everbecq,1994; Reynolds & Irish, 2000; Sayer & Roberts, 2001) and importantly was also informed directly by the available phytoplankton records for Loch Leven (e.g. Bailey-Watts, 1988; Bailey-Watts et al., 1990; and see Figure 3.2). Given the opportunistic nature of diatom algae (Reynolds, 1984) and the inherent temporal variability of environmental controls it is recognised that exact seasonal categorisation of species is impossible. Indeed where conflicting reports of diatom seasonality arose, or where no specific favoured season could be identified a species was divided between the two groups on a 50:50 basis.

Cluster analysis was performed on the full diatom dataset from LEVE12 to identify the major zones in the diatom profile using CONISS (Grimm, 1987), implemented by TILIA and TILIAGRAPH (Grimm, 1991). CONISS is a program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. The high resolution of diatom counts for LEVE12 resulted in multiple samples (up to four) for some years. For comparison with the monitoring data and to remove noise, annual mean diatom composition data were generated by averaging the counts for all samples from a single year.

The diatom data from LEVE12 for the period 1969-2005 were compared with measured hydrochemical and climatological data using principal components analysis (PCA). PCA, an indirect ordination method, was used in preference to constrained techniques such as redundancy analysis (RDA) and canonical correspondence analysis (CCA) as our aim was to extract the main components of variation in the diatom record, not those components that were restricted to be linear combinations of the available environmental data. Previous trend analysis had identified that the most significant changes were in spring air temperatures and winter rainfall (Carvalho et al., in press), consequently these two variables were selected for assessing climate influence over observed shifts in the fossil diatom assemblages, while annual mean TP provided the most complete dataset for assessing response to changes in nutrient concentrations.

Prior to analysis the diatom data were transformed using the Hellinger method of Legendre & Gallagher (2001) such that the resulting PCA represents Hellinger distance between samples rather than Euclidean distance. Measured hydrochemical and climatological data were fitted into the ordination space described by the first two principal components of the diatom data by projecting biplot vectors. This provides a linear representation of the individual variables within the ordination space and allows for easy comparison among the three selected variables. However, in unconstrained ordinations this linear representation may not be ideal as there is no reason to assume a priori that relationships between the variables and the ordination space will be linear. To address this issue, we used additive models to fit response surfaces for each variable to the two-component ordination space. A smooth 2-d function of the sample scores on PCA axes one and two was generated using thin-plate splines and used to model the individual measured hydrochemical and climatological variables in turn. The degree of smoothness in the thin-plate spline was estimated by generalised cross validation. Ordinations and response surfaces were produced using the R statistical language (version 2.11.1-patched revision 52767; R Development Core Team, 2010) and function 'ordisurf' in the vegan package (version 1.17-4; Oksanen et al., 2010).

We rejected partial constrained ordination as a means of measuring the effects of the three variables on diatom composition change for several reasons. Chief among these was that RDA and CCA fit axes that are linear functions of environmental variables and we did not wish to make such a limiting assumption. Furthermore, partial ordination provides a single measure of the magnitude of effect for each environmental variable for the whole data set; here we are interested in developing a more fine-grained assessment of the effects of the three environmental variables to investigate periods in the sediment core when species compositional shifts were related to the environment. The method of Simpson & Anderson (2009) would have provided a more direct assessment of the relative effects of the three variables plus identification of the timing of the effects. However, insufficient numbers of samples were available to justify the use of this more complex technique. Our indirect ordination followed by response surface modelling using an additive model is a sound compromise given our aims and the constraints of the available data.

3.3 Results

3.3.1 Seasonality of diatom plankton

Analysis of the 34 horizontal phytoplankton net tow samples, covering the period 1996-2005, provided useful information on the seasonality of the key diatom taxa in Loch

Leven (Figure 3.2). *Stephanodiscus parvus* and *Aulacoseira subarctica* peaked in winter to early spring. *Cyclotella radiosa* and *Asterionella formosa* reached highest relative abundances in winter. In contrast *Diatoma elongatum Aulacoseira granulata* and *Aulacoseira granulata* var. *angustissima* were most common in summer, and *Stephanodiscus hantzschii* forma *tenuis*, *Cyclostephanos invisitatus* and *Cyclotella pseudostelligera* bloomed in autumn. *Stephanodiscus hantzschii*, *Cyclostephanos tholiformis* and *Aulacoseira ambigua* appeared in all seasons, but were generally most abundant in autumn also.

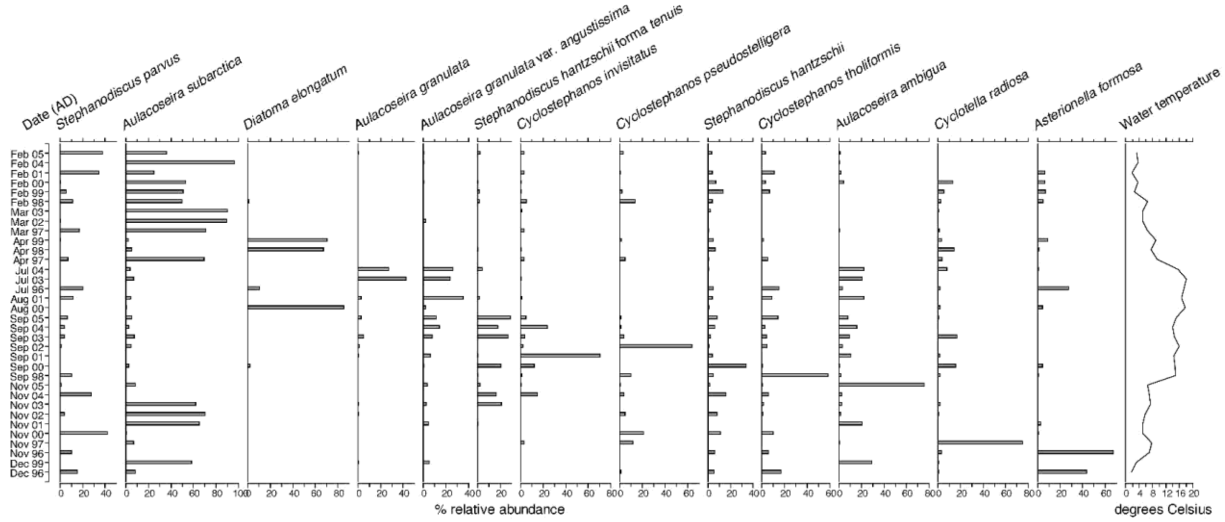


Figure 3.2 Seasonality of diatom taxa in the phytoplankton net tow samples 1996-2005. Samples are ordered by date (y-axis), species data are in % relative abundance and mean monthly water temperature is expressed in ^{o}C

3.3.2 Fossil diatom records

Diatom preservation was good throughout all cores with totals of 196, 198 and 164 taxa for cores LEVE6 (deep water, high resolution), LEVE11 (shallow water, low resolution) and LEVE12 (deep water, high resolution), respectively. Based on the radiometric dating results, LEVE11 covered the longest time period. Sediment accumulation rates of 0.12-0.15 cm yr^{-1} were estimated for this core for the period ~1930-1970, increasing gradually from this time to 0.33 cm yr^{-1} by 1990 (Figure 3.3). Dates below the base of unsupported ^{210}Pb were extrapolated back to ~1300 AD, using the constant accumulation rate for the 1930s. However, owing to uncertainties surrounding the chronology, extrapolated dates must be viewed with caution and dates have not been assigned to the lower section. A more reliable chronology was established for the upper 12 cm of the core which is estimated to represent the period from 1934 ± 14 to 1999. Marked changes in diatom community composition were evident in LEVE11 (Figure 3.4). Below approximately 20 cm (extrapolated date ~1850) assemblages were co-dominated by planktonic and periphytic taxa, the former being comprised of both ‘spring-autumn’ and ‘summer’ taxa. Common phytoplankters were *A. subarctica, C. radiosa, Tabellaria flocculosa* and ‘oligotrophic *Cyclotella*’. Periphyton assemblages consisted largely of small, ‘chain-forming’ taxa from the *Staurosira*, *Staurosirella*,

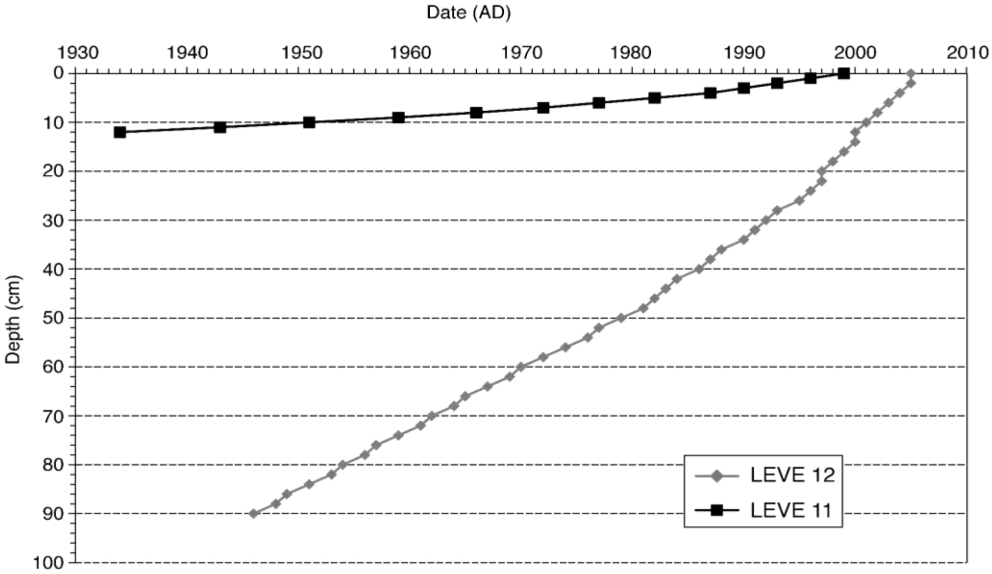


Figure 3.3 Depth-date profiles for Loch Leven cores LEVE12 (deep water) and LEVE11 (shallow water) based on the 210Pb constant rate of supply model (Appleby & Oldfield, 1978)

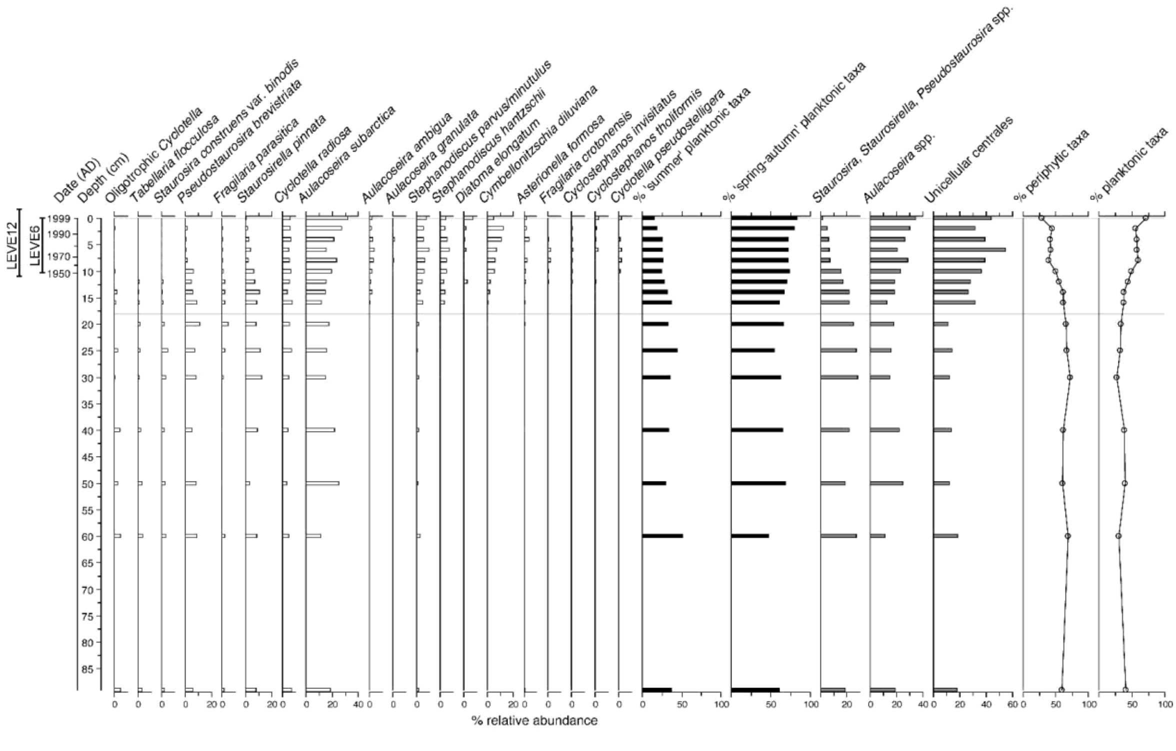


Figure 3.4 Summary diatom diagram of LEVE11. Diatom data are expressed as % relative abundance. The point of major compositional change is shown by the horizontal line and the approximate time periods covered by LEVE6 and LEVE12 are shown for comparison

Pseudostaurosira complex (formerly *Fragilaria* and termed so hereafter) and of species in the genera *Achnanthes*, *Amphora*, *Cocconeis* and *Navicula* (not shown). Above 20-15 cm there was an increase in the planktonic component, in particular small unicellular centrics (notably *S. parvus/minutulus* and *S. hantzschii*), together with A*. formosa, D. elongatum, Fragilaria crotonensis* and *A. ambigua.* Conversely, *T. flocculosa* and oligotrophic *Cyclotella* spp. sharply declined. This upper section also sees a shift towards increased dominance of taxa in the ‘spring-autumn’ group and a marked reduction in small *Fragilaria* taxa along with many other epiphytic and benthic taxa. By contrast, the epipsammic species *Cymbellonitzschia diluviana* appeared for the first time and steadily increased.

Based on a correlation of diatom assemblage changes, the undated core LEVE6 most likely corresponds to the upper 10 cm of LEVE11 (i.e. post-1950). It therefore affords a higher resolution record of Loch Leven’s recent past. Diatom shifts throughout LEVE6 were more subtle than in LEVE11 (Figure 3.5). Nonetheless, above 25-30 cm there were some important compositional changes including reductions in unicellular centrales, in particular *S. parvus/minutulus, S. hantzschii* and *C. pseudostelligera*, a decrease in *A. ambigua*, and an increase in *A. subarctica* and periphytic taxa (although not in small *Fragilaria* taxa). To a large extent these changes were evident in LEVE11 above 6 cm (dated 1977 ± 5), although a definitive correlation of levels is difficult to make.

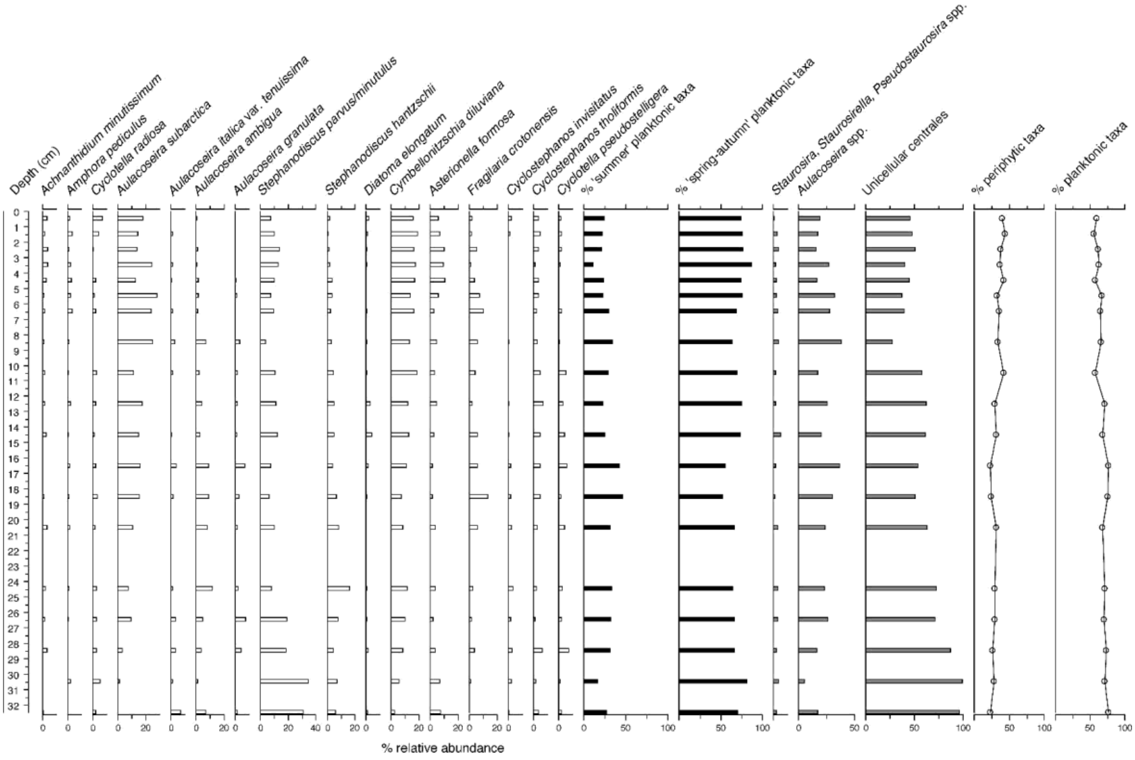


Figure 3.5 Summary diatom diagram of LEVE6. Diatom data are expressed as % relative abundance.

A yet higher resolution for the last 60 years is afforded by core LEVE12. Radiometric dating indicates that this core represents the period 1946 ± 14 to 2005 with rapid accumulation rates of 1-3 cm yr^{-1} (Figure 3.3). If our assumptions about the chronology of LEVE6 are correct then LEVE12 and LEVE6 represent a similar time period albeit with LEVE12 adding a further eight years to the top of the LEVE6 record (i.e. 1997- 2005) which spans the recovery period in lake P concentrations. Changes in diatom composition (Figure 3.6) and abundance (not shown) in LEVE12 were relatively subtle. As in LEVE6, planktonic taxa dominated the assemblages throughout the core

(70- 80%) and the community was composed of a large number of species with no single taxon dominating. The most notable shifts in the core were a decline in *A. granulata* var. *angustissima* and *S. parvus/minutulus* relative to *A. subarctica* after ~1970. The increase in the latter relative to S*. parvus/minutulus* was also observed in LEVE6 at ~25 cm. Other notable similarities between LEVE12 and LEVE6 include the expansion of *C. diluviana* which occurs in LEVE12 at ~1955 and in LEVE6 at 30 cm, and the low relative abundance of *A. ambigua* from ~1987 to ~1997 in LEVE12 and in the upper 8 cm of LEVE6, suggesting that there is some consistency in the two deep-water sediment records. The general decline in 'summer' diatoms in the 1980s- 1990s is evident in LEVE12 in accordance with their observed decrease in the upper parts of LEVE6 and LEVE11. However, in recent years there has been marked interannual variability in the diatom assemblages of LEVE12 with pulses of *A. ambigua, A. granulata* and *A. granulata* var. *angustissima* in 1986-87, 1998-1999 and 2003- 2004 resulting in peaks of 'summer' taxa in these years.

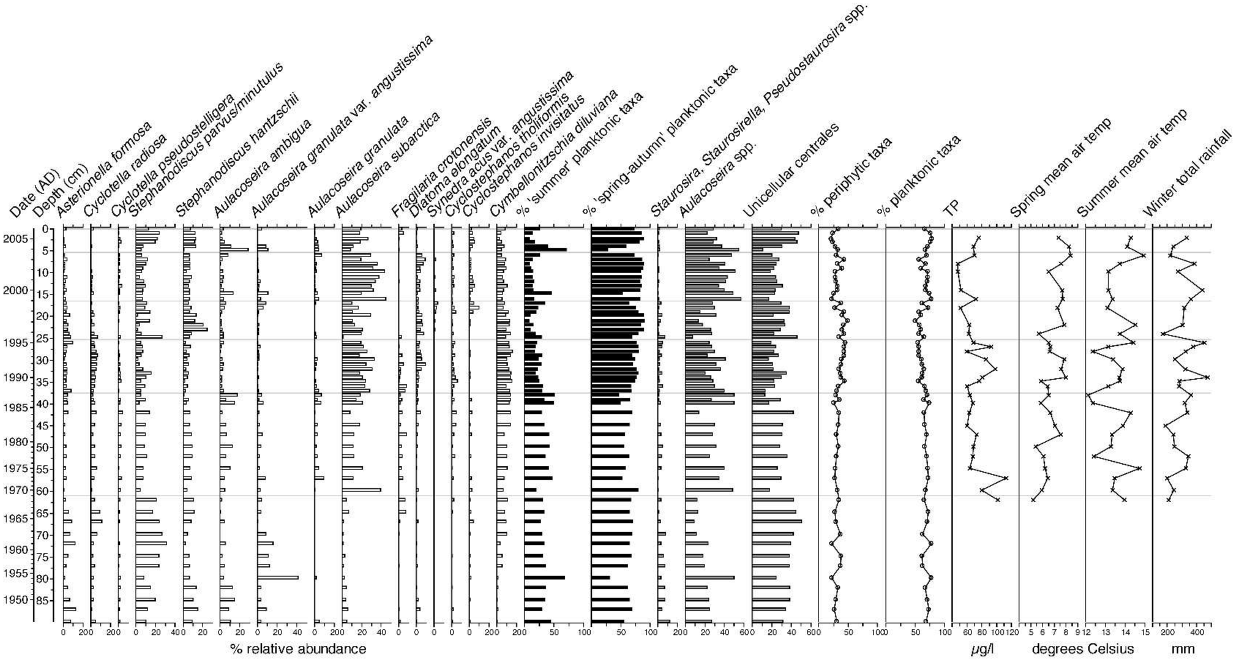
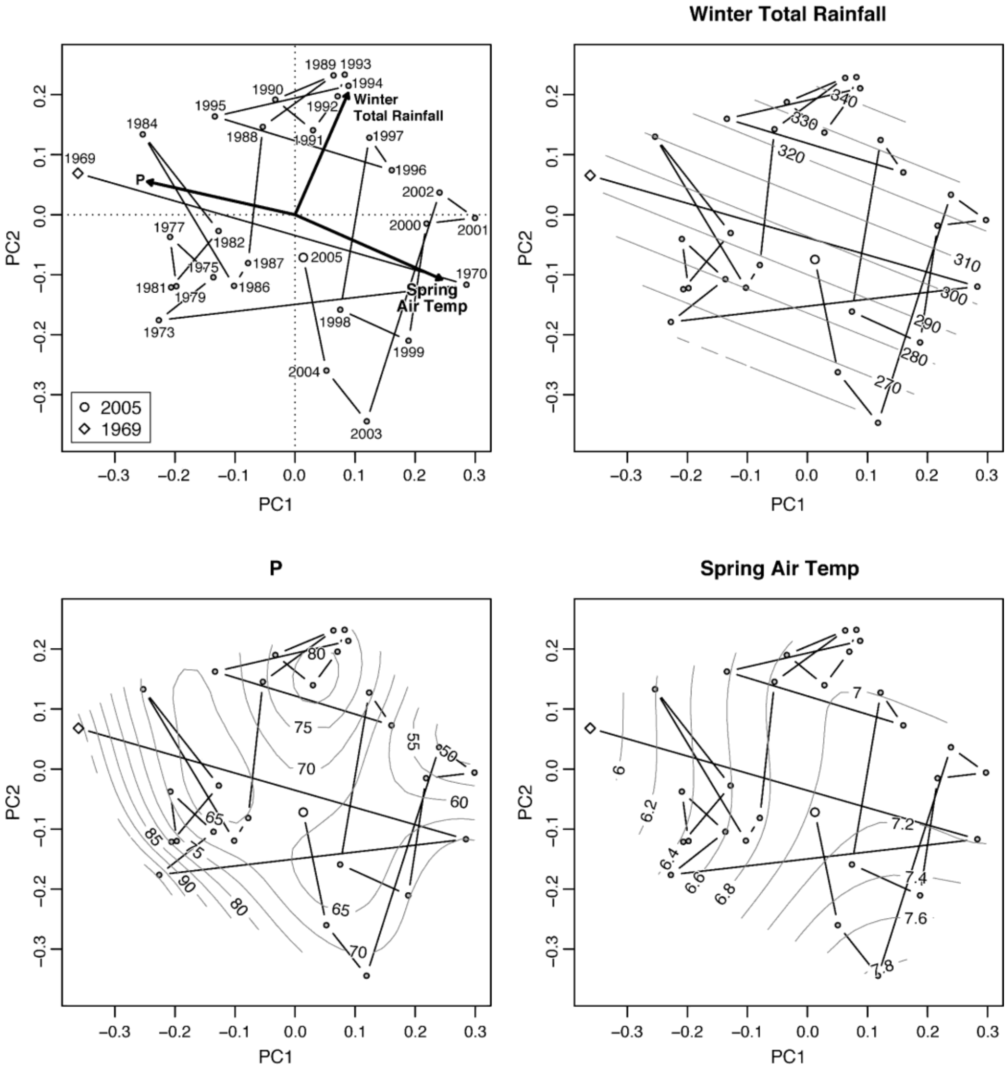


Figure 3.6 Summary diatom diagram of LEVE12. Diatom data are expressed as % relative abundance. The zones of compositional change are indicated by the horizontal lines (determined by CONISS). Measured environmental data (TP, Spring mean air temperature, Summer mean air temperature and Winter total rainfall) for 1969-2005 are shown.

3.3.3 Ordination

The ordinations with response surfaces for the three main variables, annual mean TP, spring air temperature and winter rainfall (Figure 3.7), show samples from 1969-1987 in LEVE12 (located on the left side of the plot) to be associated with the highest TP values and coolest spring air temperatures, with the exception of the 1970 sample which lies to the right of the diagram. The 1970 sample contained particularly high percentages of *A. subarctica* (40%) compared to neighbouring samples with abundances similar to those observed in samples from 2000-2003. The samples from 1988-1997 are located in the upper part of the plot associated with the highest winter rainfall values and intermediate TP, and the most recent samples from 1998-2005 are positioned to the right of the diagram associated with the highest spring air temperatures and lower TP. A total of 33% of the variance in the LEVE12 species data is captured on PCA axes one and two. The percentage of variance in each variable explained by the response surface of the PCA axis scores is 74, 12.1 and 36 for TP, winter rainfall and spring air temperature, respectively. Only the fitted response surface for TP was statistically significant (F = 2.569, P = 0.0339, df = 14.59).


Winter Total Rainfall

P

Spring Air Temp

Figure 3.7 Ordination of the 1969-2005 diatom data from LEVE12 with response surfaces for the three main environmental variables

3.4 Discussion

The various time periods represented by the three cores from Loch Leven allow us to assess environmental change at a range of temporal scales. The following discussion firstly explores the evidence for change at the decadal-centennial scale, and then examines the observed shifts seen at an inter-annual scale in the sediment record, in combination with the monitoring data, with a particular focus on the role of climate and nutrients as potential drivers of change.

3.4.1 Decadal-centennial scale

At the decadal-centennial scale, the palaeolimnological data reveal three main phases in the recent ecological history of Loch Leven: i) a pre-enrichment phase (pre ~1850), ii) an enrichment phase (post ~1850), and iii) a partial recovery phase (post ~1985).

Pre-enrichment phase (pre ~1850)

Core LEVE11 provides us with a long-term perspective on the ecological history of Loch Leven. The core is estimated to extend back ~700 years based on extrapolation of sediment accumulation rates. The early assemblages of Loch Leven were composed of a mixed planktonic and periphytic community with taxa found in circumneutral to slightly alkaline, oligotrophic to mesotrophic waters. The planktonic communities contained a mix of 'spring-autumn' and 'summer' taxa (e.g. Kiss & Padisák, 1990; Gosselain et al., 1994; Reynolds & Irish, 2000). Several periphytic species associated with benthic substrates (submerged macrophytes, sediments, stones) were present, indicating favourable light conditions and an important component of benthic primary productivity. There was no major change in the diatom assemblages until the ~20 cm level of LEVE11 (~1850), suggesting relatively stable conditions in the early part of the loch's history, although a higher resolution dataset for this period and analysis of variance is required to assess the degree of stability more fully.

The findings agree with an earlier study of the diatom history of Loch Leven's north basin (Haworth, 1972) where *Melosira italica* ssp. *subarctica* O. Mull. (now *A. subarctica*), *T. flocculosa* and oligotrophic *Cyclotella* taxa were observed along with small *Fragilaria* spp. and other periphytic taxa in the lower sections of a core. Furthermore, a recent study of plant macro-remains from a shallow-water core collected offshore from St. Serfs Island suggests a submerged macrophyte community associated with oligotrophic to mesotrophic waters during this era including *Isoetes lacustris* L. and *Lobelia dortmanna* L. (Salgado et al., 2010).

Enrichment phase (post ~1850)

The most marked change in the fossil diatom record occurred at around 20 cm in LEVE11 (~1850) with the appearance of planktonic taxa that had previously been in low abundance or had not been observed in the diatom record, namely *A. ambigua, S. parvus/minutulus, S. hantzschii,* and *C. pseudostelligera*. These taxa expanded from around 1940 to the core top (1999) in LEVE11. They are typically associated with nutrient-rich waters and occur in winter-spring and autumn suggesting a strengthening of the diatom bloom either side of the summer period. An increase in planktonic diatoms and turbidity in response to enrichment could have reduced the depth of light penetration thus reducing the habitat availability for benthic diatoms which decline during this period.

In accordance with our data, Haworth (1972) noted an appearance of *Melosira ambigua* (Grun. in Van Heurck) O. Mull. (now *A. ambigua*) and *S. hantzschii*, taxa indicative of enrichment, in the upper part of a core from the Northern basin of the loch. Although an accurate chronology was lacking for this core, it was concluded that there was evidence of early enrichment some time prior to 1816 AD followed by a subsequent more marked eutrophication phase. Furthermore, the post 1816 AD changes were thought to be associated with lowering of the lake level by 1.5 m in 1830 which resulted in an expansion of agriculture around the lake. The arrival of *Cymbellonitzschia diluviana* in LEVE11 and its expansion in both LEVE12 and LEVE6 perhaps reflects the shallowing of the lake as the lowering process may have brought more sandy sediment from the littoral zone to the core site. *C. diluviana* is a small, low-growing, epipsammic species which forms aggregates in the depressions of sand bars. It has the ability to stay firmly attached to sand grains, and can form resting stages that allow it to cope with wave action and changes in water level (Jewson, Lowry & Bowen, 2006). It is interesting to note, however, that despite the expansion of *C. diluviana* in our cores, there was no overall increase in periphyton, and indeed planktonic forms continued to dominate the assemblages. This suggests that the enrichment signal was sufficiently strong to over-ride the influence of lake level change on the diatom community. Nonetheless, a water level change of 1.5 m is not insubstantial and highlights the fact that there are multiple drivers of change and that Loch Leven’s pre-disturbance baseline in terms of water depth and benthic habitat has shifted.

Our core data provide evidence of enrichment of the loch starting initially in ~1850 with a more marked phase since ~1940-1950. The former is most likely attributed to nutrients from expanding agricultural practices in the catchment, and the latter with P inputs from sewage treatment works, land drainage and P-rich discharges from the woollen mill, considered to be a substantial point source of P (Holden & Caines, 1974). The enrichment trend inferred from the diatom record is supported by the long-term datasets which provide evidence of eutrophication, although the latter are limited in temporal extent as the monitoring programme did not start until 1968 and, therefore, post-dates the onset of enrichment. Nevertheless, available historical data record a decline in the extent of macrophyte beds since the late 1940s and cyanobacteria blooms as a regular feature on the loch since the 1960s (Fozzard et al., 1999).

Recovery? (post ~1985)

An increase in A. subarctica relative to *Stephanodiscus* spp. in all cores from ~1970s to 1980s suggests recent biological recovery from eutrophication. The phytoplankton monitoring data confirm that unicellular centrics, principally *Stephanodiscus* spp., produced extensive spring blooms in the 1960s and early 1970s and that these have shown two step-wise declines, along with a trend towards increasing cell size with larger species such as *Aulacoseira* spp. dominating over smaller unicellular centrics (Bailey-Watts, 1988; Bailey-Watts et al., 1990; Carvalho pers. comm.). The first decline, in the 1970s, coincided with the re-colonisation of *Daphnia*. These large zooplankton feed particularly efficiently on smaller algae, and thereby increased grazing pressure on the small centric diatoms (Bailey-Watts et al., 1990). The second decline, from the mid-1980s, however, is thought to be associated with nutrient reductions.

A considerable reduction in point sources of P from industrial and sewage effluents has been achieved since 1985 (May, Defew & Bennion, in press). However, agriculture in the Leven catchment remains a significant diffuse source of nutrients to the loch as much of the land is used for arable farming, and rural septic tanks also contribute to the P load. Nevertheless, Fozzard et al. (1999), May & Carvalho (2010) and Gunn et al. (in press) report signs of positive ecological change in the loch since the reduction of point sources of P, including lower algal abundances, increased water clarity, increased macrophyte colonisation depth, and an increased diversity and abundance of invertebrates. In line with these signs of improvement, a small increase in the periphytic taxa was observed in the cores from the mid-1980s. Whilst there appears to have been some recovery at the functional level, the sediment record suggests that those diatom taxa lost during enrichment, notably the oligotrophic *Cyclotella* spp., *T. flocculosa*, and the *Fragilaria* spp. have not yet returned. This may in part be due to the altered shoreline configuration and hence the shifting baseline which confounds attempts to return the flora to that seen in the past. It may also be that nutrient concentrations remain too high and indeed macrophyte abundance still remains low compared to pre-enrichment conditions.

The monitoring data show that chemical recovery of the loch has not followed a monotonic improving trend. The rapid decline in TP concentrations in the early 1970s (Figure 3.6) pre-dates the restoration programme and is again thought to be largely due to the return of *Daphnia* in 1970 following their disappearance, attributed to dieldrin poisoning (Morgan, 1970; Gunn et al., in press). The slight increase in measured annual mean TP in the early 1990s (Figure 3.6) arose due to increased P recycling from the sediments which compensated for reductions in the external nutrient load (Spears et al., 2007; Carvalho et al., in press). Changes in climate may also have played a role in driving observed recent changes in the loch and these are further discussed when examining finer scale variation in the diatom record (see below).

3.4.2 Inter-annual scale: variation in the diatom record over the last 40 years

The higher resolution diatom data for the recent period, provided by LEVE6 and LEVE12, show that the diatom flora has been dominated by planktonic, nutrient tolerant taxa for at least the last four decades. This is in accordance with plankton data which reveal a community of Aulacoseira taxa and unicellular centric diatoms, predominantly *S. parvus* and *S. hantzschii* with some *Cyclotella* and *Cyclostephanos* species (Bailey-Watts, 1988; Fig.2). A comparison of planktonic diatom composition in LEVE12 with that of phytoplankton records for the period 1996-2005 revealed a good match for the dominant taxa (Jeppesen et al., 2010). Indeed, both records exhibit a decline in *C. radiosa* and *A. formosa*, and more recently in *A. subarctica, A. granulata* and *D. elongatum*, and a relative increase in *F. crotonensis, S. hantzschii* and *S. parvus/minutulus*. This indicates that the core does reflect real compositional changes and suggests that the fossil assemblages are not just an artefact of variable dissolution or spatial variability induced by sediment mixing and bioturbation.

While there are consistencies in diatom changes recorded in all three cores (e.g. the *Stephanodiscus* decline in the upper part of the records), the assemblages exhibit high intra- and inter-annual variation which is also seen in the contemporary records. A detailed taxonomic analysis of diatom species in the spring maxima over 1968-1985 revealed no obvious temporal pattern in the occurrence of any species, with no species dominating for more than two years (Bailey-Watts, 1988). Indeed, in this respect Bailey-Watts et al. (1990) noted that “The hallmark of Loch Leven phytoplankton dynamics, which has been studied since 1967, is in its extraordinary inter-annual variability”. This high variability in the phytoplankton community in the sediment record confounds attempts to determine clear trends reflective of improving water quality. While there is evidence of partial recent recovery since the 1980s in the diatom record when viewed at a decadal scale (see above), it is difficult to extract a clear recovery signal from the higher resolution study of LEVE12 where initial signs of improvement in the late 1980s (e.g. increase in *Aulacoseira* spp. relative to unicellular centrales) are reversed in more recent years (2004-2005). This reversal of recovery was also evident in measured annual mean in-lake P concentrations which show that water quality varies from year to year with values of ~75 µg TP L^{-1} between 2003 and 2005 compared to ~50 µg TP L^{-1} in 2000.

While errors associated with the core chronology require that a degree of caution is exercised when comparing core and plankton data directly, these datasets can be explored to assess overall trends. Although the diatom data in LEVE12 are noisy over the last 37 years, some structure in the data is evident with apparent diatom responses to nutrient and climate variables. Of the 33% variance in the LEVE12 species data captured on PCA axes one and two, a large proportion can be related to TP and spring air temperatures, and to a lesser extent to winter rainfall. However, the small sample size and noisy data confound attempts to identify significant relationships for all but TP.

The samples from 1969-1987 comprised relatively high percentages of taxa typically associated with highly productive lakes, such as *A. ambigua, S. parvus/minutulus, S. hantzschii,* and *C. pseudostelligera*. The woollen mill did not cease using P-based materials until 1988 and reduction of nutrient loads from the sewage treatment works did not occur until the 1990s. Hence 1969-1987 marks one of the most productive periods in the history of the lake and the high P concentrations are likely to have been a key control over diatom assemblages. Additionally the data show that spring air temperatures in 1969-1987 were on average 1$_{o}$C lower than today and, therefore, temperature may also have played a role in influencing the diatom community. This highlights the problem of identifying the key controls on diatom dynamics and suggests that the measured variables are insufficient to capture the complexity of the multiple drivers.

The samples from 1988-1997 contained lower percentages of ‘summer’ taxa (*A. granulata, A. granulata* var. *angustissima* and *A. ambigua*) but higher amounts of ‘spring-autumn’ taxa (*A. subarctica*) than the 1969-1987 samples. Annual mean P concentrations remained relatively high in this period despite a reduction in external nutrient inputs, due to continued internal loading. However, winter rainfall values were at their highest during this ten-year period suggesting that the observed subtle species shifts may have been driven by climatic factors. Loch Leven has a characteristically variable oceanic climate and a large catchment, and hence rainfall exerts considerable influence on the loch. The amount of rainfall affects flushing rates which have been shown to affect the supply and dynamics of nutrients in Loch Leven, producing a highly variable water column and complex phytoplankton sequences (Bailey-Watts et al., 1990). A more rapid flushing rate in years of high winter rainfall may have favoured occurrence of *A. subarctica* over unicellular centrales as the former has resting stages and can, therefore, in spring quickly accumulate numbers from the sediments while the latter, which do not have this facility, may require a longer duration of low flushing rates to build up populations.

The samples from 1998-2005 saw a further increase in several of the ‘spring-autumn’ taxa (*A. subarctica, C. invisitatus*) but a decline in others typically associated with this season (*A. formosa*). Similarly there was a rise in the relative abundances of some of the ‘summer’ taxa (*A. ambigua* and *A. granulata* var. *angustissima*), with notably high percentages of these taxa in 1998-9 and 2003-4, but with decreases in others classed in the ‘summer’ group (*F. crotonensis, C. radiosa*). Ordination analysis suggests that these shifts may be associated with the decrease in annual mean P concentrations and/or the increase in spring air temperatures. Climate data from 1968 reveal an increasing trend in water temperatures, particularly during winter and spring (Carvalho & Kirika, 2003; Carvalho et al., in press). Given that nutrient reduction and climate warming have occurred over the same timescale at Loch Leven it is difficult to disentangle the relative ecological influence of these drivers. The long-term phytoplankton dataset for Loch Leven indicates that *Aulacoseira* spp. abundance is associated with years when winter SRP and spring silica concentrations are low and winter temperatures are high and conversely high unicellular centric abundance is associated with years when winter SRP is high and winter rainfall is low (Carvalho, unpublished data). The 1996-2005 dataset indicates that *A. granulata, A.*

granulata v. *angustissima* and *A. ambigua* generally bloom in late summer to early autumn and these taxa are known to tolerate warmer waters than A. subarctica (Lund, 1954) which tends to peak in late winter to early spring. Consequently, their higher abundances relative to *A. subarctica* may reflect changing climatic conditions, but in relation to different seasons and consequent effects on seasonal nutrient availability. Indeed 2003-4 saw spring temperatures of 8.4 and 8.2°C compared with an average of 7.6°C for 1998-2005. Reduced availability of silica for diatom growth may also be important as trend analysis reveals that soluble reactive silica concentrations for the first (1968-1977) and last (1998-2007) decade of monitoring have declined for all months of the year, leading to potentially limiting concentrations for diatom growth throughout the year (Reynolds, 2006). Diatoms have become the dominant algal group in the loch for much of the year (Carvalho, unpublished data) and hence the reduction in silica may be due to greater diatom uptake. Most probably a complex interaction between nutrient and climatic factors contribute to the observed shifts in the sedimentary diatom assemblages and a greater understanding of contemporary diatom ecology, especially at the species level, at a seasonal scale is required before high-resolution palaeo-records can be adequately interpreted.

3.5 Concluding remarks

Our study highlights the value of a palaeolimnological approach for developing an understanding of environmental change at a range of temporal scales and for tracking recovery. However, the study underlines the difficulty of deciphering a climate signal in sites where recent eutrophication and climate change have occurred over the same period. At the decadal-centennial timescale eutrophication is clearly the dominant force driving ecological change in Loch Leven and any climate effects seem to be overpowered by the enrichment signal. Ideally remote sites with little anthropogenic influence are required for extracting climate signals but these rarely have long-term monitoring data to help validate the trends inferred from the sediment record.

At an inter-annual scale it was not possible to establish the relative importance of climate and nutrients in explaining the diatom assemblages and indeed interactions between these variables make separation of their effects difficult. A study of this kind would ideally be undertaken at a site with varved sediments but such highly resolved sequences are rarely found in shallow lakes. The high intra- and inter-annual variability of the phytoplankton in Loch Leven relative to the signal also precludes detection of this climate signal at the fine scale. While nutrient and climate variables explained a moderate amount of the variation in the diatom assemblages, it is likely that small changes in local weather conditions, top-down control by fish and zooplankton, as well as chaotic and random factors have also played a role in controlling species composition. Nevertheless the strong influence of flushing rate on temperature regimes, external nutrient supply and in-loch nutrient dynamics suggests that, at an inter-annual scale, changes in species composition in the recent fossil record may be in part attributed to climatic factors. The study highlights the need for more autecological information on centric diatoms, particularly seasonality data, to better inform palaeoecological studies. The functional groups of Reynolds et al. (2002) would suggest that nutrients and light climate are likely to be key gradients for shifting between the unicellular and filamentous diatoms but information on the ecological preferences of individual diatom taxa in relation to temperature and flushing-rate is lacking.

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Appendix 1 List of diatom names with their authorities, and seasonal grouping for planktonic taxa (Sp-Au: spring-autumn taxa, Su: summer taxa, 50:50: divided between Sp-Au and Su groups on a 50:50 basis)

Achnanthidium minutissimum (Kutz.) Czarnecki	
Amphora pediculus (Kutz.) Grun.	
Asterionella formosa Hassall 1850	Sp-Au
Aulacoseira ambigua (Grun. in Van Heurck) Simonsen	Su
Aulacoseira granulata (Ehrenberg) Simonsen	Su
Aulacoseira granulata var*. angustissima* (O. Mull.) Simonsen	Su
Aulacoseira italica var*. tenuissima* (Grun. in Van Heurck) Simonsen	Sp-Au
Aulacoseira subarctica (O.Mull.) Haworth	Sp-Au
Cyclostephanos invisitatus Theriot, Stoermer & Hakansson, *comb. nov.*	Sp-Au
Cyclostephanos tholiformis Stoermer, Hakansson & Theriot	50:50
Cyclotella pseudostelligera Hust.	50:50
Cyclotella radiosa (Grunow) Lemmerman	Su
Cymbellonitzschia diluviana Hust*.*	
Diatoma elongatum (Lyngb.) Ag.	Sp-Au
Fragilaria crotonensis Kitton	Su
Fragilaria parasitica (W. Sm.) Grun. in Van Heurck	
Pseudostaurosira brevistriata (Grun. in Van Heurck) Williams & Round	
Staurosira construens var*. binodis* (Ehrenberg) P.B.Hamilton	
Staurosirella pinnata (Ehrenb.) Williams & Round	
Stephanodiscus hantzschii Grun. in Cleve & Grun.	Sp-Au
Stephanodiscus hantzschii forma tenuis (Hustedt) Hakansson & Stoermer	Sp-Au
Stephanodiscus parvus/minutulus	Sp-Au
Synedra acus var*. angustissima* (Grun. in Van Heurck) Van Heurck	
Tabellaria flocculosa (Roth) Kutz.	Su

4. Nutrients exert a stronger control than climate on recent diatom communities in Esthwaite Water: evidence from monitoring and palaeolimnological records

Responsible: Xuhui Dong[1&3], and Helen Bennion[1], Contributors: Stephen C. Maberly[2], Carl Sayer[1], Gavin L. Simpson[1] & Richard W. Battarbee[1]

[1]Environmental Change Research Centre, Department of Geography, University College London, Gower Street, London WC1E 6BT, UK.

[2]Centre for Ecology & Hydrology (Lancaster), Environment Centre, Bailrigg, Lancaster UK.

[3]State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing, China.

4.1 Introduction

Lakes are important resources for humans, not only for supplying drinking water but also for supporting other activities such as agriculture, industry and tourism. Nevertheless, lakes face a variety of environ- mental pressures that greatly threaten their ecological integrity (Vorosmarty et al., 2000). Lakes have under- gone substantial deviations from pristine conditions over the past few centuries (e.g. Bennion, Fluin & Simpson, 2004; Taylor et al., 2006; Bjerring et al., 2008). One key pressure is nutrient enrichment, which has received wide attention and continues to dominate the science and policy agenda (Bennion & Battarbee, 2007). Lakes have also experienced serious pressure from climate change, which in recent decades has proceeded at a rate beyond historical natural variability (IPCC, 2007; Battarbee & Binney, 2008). The changing climate may alter the structure and function of aquatic ecosystems directly, but may also exacerbate other environmental pressures such as eutrophication (George, Hurley & Hewitt, 2007; Whitehead et al., 2009; Jeppesen et al., 2010).

For the purposes of restoration and lake management, knowledge of how climate change will affect lake ecosystems and how it may interfere with nutrient dynamics is required (Jeppesen et al., 2010). To decipher the confounding effects of climate and nutrients on lakes, long-term monitoring data sets including ecological communities and environmental variables are needed. Such records are rare, however, or may lack consistency in methodology over different monitoring periods (Blenckner, 2005). Palaeolimnological records can augment the relatively short observed records to infer historical changes in lake ecosystems over longer timescales of several centuries or more (Smol & Cumming, 2000; Battarbee et al., 2005); nevertheless, they lack direct records of historical climate and nutrient changes and may also lack good chronological resolution. Given the clearly complementary strengths and weaknesses of monitoring and palaeolimnological records, they can be integrated to conduct research on separating climate and nutrient effects on lake ecosystems (Battarbee et al., 2005).

Esthwaite Water (54°21.56’N, 002°59.15’W) is a well- studied site where both long-term high-resolution monitoring and numerous palaeo-environmental studies based on sediment cores have been under taken (Bennion, Monteith & Appleby, 2000). Research initiated by the Freshwater Biology Association in

1945 and undertaken by the Centre for Ecology and Hydrology and its forerunners since 1989 offers a rare long-term and detailed record of key climate- and nutrient-related variables and biological communities (Maberly et al., 1994). Importantly, this monitoring record covers both oligotrophic (prior to 1970s) and eutrophic phases (post-1970s), whereas most other monitoring records capture only the nutrient enrichment phase (Battarbee et al., 2005). Consequently, this valuable record allows a direct comparison of the responses to climate forcing under different trophic conditions.

Given the complex interactions among environmental variables, statistical approaches have recently been developed to disentangle their relative effects. For example, variance partitioning (Borcard, Legendre & Drapeau, 1992) is used frequently to identify the major forcing variables and their relative effects on aquatic ecosystems over different spatiotemporal scales (e.g. Lotter & Birks, 1997; Hall et al., 1999; Quinlan et al., 2002; Bradshaw, Rasmussen & Odgaard, 2005; Kernan et al., 2009). This method, however, can estimate only the total effect of the various covariates over the time period of interest, not answering questions about when and where the various covariates may be driving change in the response variable(s) (Simpson & Anderson, 2009). To overcome this shortcoming, Simpson & Anderson (2009) employed a flexible and powerful statistical tool, additive modelling (Wood, 2006), to elucidate the critical questions of how much, and when, do the interacting factors affect the lake ecosystems.

By combining high-resolution diatom records from a sediment core and existing long-term monitoring data for Esthwaite Water, we employ both redundancy analysis (RDA) and additive models (AMs) to determine how climate and nutrients have affected the lake ecosystem over the period 1945–2004. First, RDA was used to identify the major factors driving diatom community changes and eliminate insignificant and redundant collinear variables. Second, RDA was used to calculate the independent effect of each factor that can explain the main patterns of diatom variation. Finally, an AM was employed to identify the relative importance of the main controls on the diatom community in greater temporal detail. Diatoms were selected since they have been widely used to indicate trophic changes (e.g. Sayer & Roberts, 2001; Bennion et al., 2004; Werner & Smol, 2005; Yang et al., 2008) or climate-induced changes in lakes such as temperature, extent of ice cover, stratification patterns and water depth (Battarbee, 2000; Smol & Cumming, 2000; Mackay, 2007). They can, therefore, act as useful indicators of ecological change driven by both climate and nutrients.

4.2 Methods

4.2.1 Site Description

Esthwaite Water is a small lake with maximum and mean depths of 15.5 and 6.4 m, respectively. It is located in the English Lake District, north-west England, where climate is significantly affected by fluctuations in the atmospheric pressure gradient, known as the North Atlantic Oscillation (NAO) (e.g. George, Maberly & Hewitt, 2004). The small catchment (17 km^2) of Esthwaite Water receives a high rainfall, with an annual average of 1350 mm. The lake has a short residence time of c. 90 days and stratifies from around late April to early October (Maberly et al., 1994). Currently, Esthwaite Water is eutrophic with a total P (TP) concentration of 28 $\mu g\ L^{-1}$ (mean of fortnightly data collected in 2008), and in recent decades, cyanobacteria have bloomed frequently. Nutrient loading to Esthwaite Water increased rapidly in the 1970s when a new sewage work was opened that discharged treated effluent into the main inflow (Talling & Heaney, 1988). Nutrient inputs continued to increase with the establishment of a fish farm (for rainbow trout) in the southern basin in 1981 and the consequent introduction of waste from cages to the system. From 1986, the phosphorus input from sewage was reduced by tertiary chemical treatment (Talling, 1999). Nevertheless, intensive human activities, particularly tourism in the catchment, have continued to exert pressure on the lake system in recent decades.

4.2.2 Long-term monitoring

Weekly or fortnightly water samples were collected for the analysis of physicochemical variables from 1945 to present. Integrated surface water samples (0–5 m) were collected using a weighted plastic tube (Lund, 1949). Chemical properties including soluble reactive phosphorus (SRP), nitrate (NO_3–N) and SiO_2 were measured according to standard methods (Sutcliffe et al., 1982; Heaney et al., 1988). Mean January (mid-winter) SRP concentration was used to indicate nutrient availability in this study because January SRP has been shown to provide the best measure of nutrient enrichment in the lake (Sutcliffe et al., 1982; Talling & Heaney, 1988).

Meteorological data used in this study, including air temperature (AirT) and rainfall, were obtained from two weather stations in the town of Ambleside, which is within 10 km of Esthwaite Water. The first station was operated between 1931 and 1970 and the second from 1965 to 2004. The two records, exhibiting similar range and variability, were combined to form a harmonised time series from 1945 to 2004 by taking average values for the period of overlapping measurements. Given that the NAO index is a good descriptor of regional climate forcing, winter and annual NAO index values (denoted as WNAO and ANAO, respectively) were obtained from the website maintained by the U.S. National Centre for Atmospheric Research (http://www.cgd.ucar.edu/cas/ jhurrell/indices.html) for further analysis.

4.2.3 Core extraction and radiometric dating

Two sediment cores were taken from the deepest area (c. 15 m) of Esthwaite Water as follows: (i) ESTH1, an 86-cm core was collected using a mini-Mackereth piston corer (Mackereth, 1969) in June 1995; (ii) ESTH7, a 65-cm core was collected using a percussion piston corer (Chambers & Cameron, 2001) in April 2006. ESTH1 was sliced at 0.5 cm throughout and ESTH7 was sliced at 0.25 cm in the top 30 and 0.5 cm intervals thereafter. Samples were subsequently stored in polyethylene bags at 4 °C in the dark.

Both cores were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay using ORTEC HPGe GWL series well-type coaxial low-background intrinsic germanium detector. ^{210}Pb chronologies were calculated using the constant rate of ^{210}Pb supply (CRS) model (Appleby & Oldfield, 1978). Full details of the age-depth model of ESTH1 are given in Bennion et al. (2000).

4.2.4 Diatom analysis and integration of sediment cores

Fossil diatoms in each sample from both cores were analysed following standard techniques (Battarbee et al., 2001). A minimum of 300 diatom valves were enumerated for each sample. Diatom identification followed Krammer & Lange-Bertalot (1986, 1988, 1991a,b) and Håkansson & Kling (1990). The fossil diatom data were expressed as relative abundance (in per cent).

Given the higher resolution of sediment accumulation for ESTH1 than ESTH7 during 1945 to 1991 and the consistency in the diatom records of the two cores, diatom records representing the period 1993–2004 in ESTH7 (2.5–8.5 cm) and 1945–1992 in ESTH1 (0.5–17 cm) were joined to obtain a record over 1945–2004 represented by the monitoring data. The integrated core was labelled ESTH9. To match fossil records with monitoring series, estimates of sediment ages were rounded to the nearest calendar year in the monitoring record. In cases where individual years included more than one fossil observation, an arithmetic mean of the observations was used (Bunting et al., 2007).

4.2.5 Ordination

Patterns of diatom community change were summarised using principal component analysis (PCA) of relative abundance data after Hellinger transformation (Legendre & Gallagher, 2001). The first two PCA axes were identified as explaining significant proportions of the variance in the species data when compared with those expected under the broken-stick distribution (Jackson, 1993). The scores of the two axes were retained as dependent variables for subsequent modelling.

Environmental variables SRP, NO_3–N, SiO_2, Si ⁄ P, N ⁄ P, Si ⁄ N, AirT, rainfall, winter NAO index and annual NAO index were transformed [$\log_{(x + 1)}$ for NO_3–N and SiO_2 and square-root transformation for all others] prior to RDA. After removing redundant environmental variables [indicated by variance inflation factors (VIF) above 20] by a primary RDA, a forward manual selection RDA and Monte Carlo permutation tests identified a minimal subset of environmental variables that explained significant proportions ($P < 0.05$) of the variations in the species data. Partial RDA was performed on the data set to partition the variance explained by each variable into a number of independent components (Borcard et al., 1992). RDA was implemented in the computer program CANOCO 4.5 (Ter Braak & Smilauer, 2002).

4.2.6 Additive models

An AM is a semi-parametric regression in which the sum of regression coefficients · explanatory variables of a linear regression is replaced by a sum of unspecified smooth functions of the explanatory variables (Hastie & Tibshirani, 1990). To allow correlation structures in the model residuals, we use a linear mixed-model representation of the AM (Simpson & Anderson, 2009). As the data represent a time series, we allow for autocorrelation in the residuals by introducing a continuous-time, first-order autoregressive process [CAR(1)] to the model.

Additive models containing single variables and then their combination as predictor variables were employed to model the changes of the scores of the first two PCA axes. The optimal degree of smoothing for the model terms was determined by including the smoothing parameter (k) in the likelihood function optimised by the model-fitting process. P-values based on likelihood ratio tests were used to evaluate the significance of each additional factor. Akaike's Information Criterion (AIC) and an adjusted coefficient of determination (R^2_{adjust}) were used to select the best model (with minimum AIC and highest R^2_{adjust}).

Further details of the models used can be found in Simpson & Anderson (2009). Both the PCA and AMs were performed with the R statistical software (R Development Core Team, 2009) using the vegan package (Oksanen et al., 2008) and mgcv package (Wood, 2006) for R, respectively.

4.3 Results

4.3.1 Monitoring records of climate and nutrients

Changes in the major water chemical and climatic variables over the 60-year time series are illustrated in Figure 4.1a–f. Both AirT and the annual NAO index exhibited high variability, with decreasing trends prior to 1987 and higher values after 1987. Average temperatures for the two periods were 8.65 and 9.27 °C, respectively, indicating an overall warming trend over the monitoring period. Average annual rainfall did not show high variability over the monitoring period, but a high amount of rainfall was observed in both 1954 and 2000. There was no relationship between annual rainfall and the NAO index ($P > 0.05$, $r^2 = 0.006$).

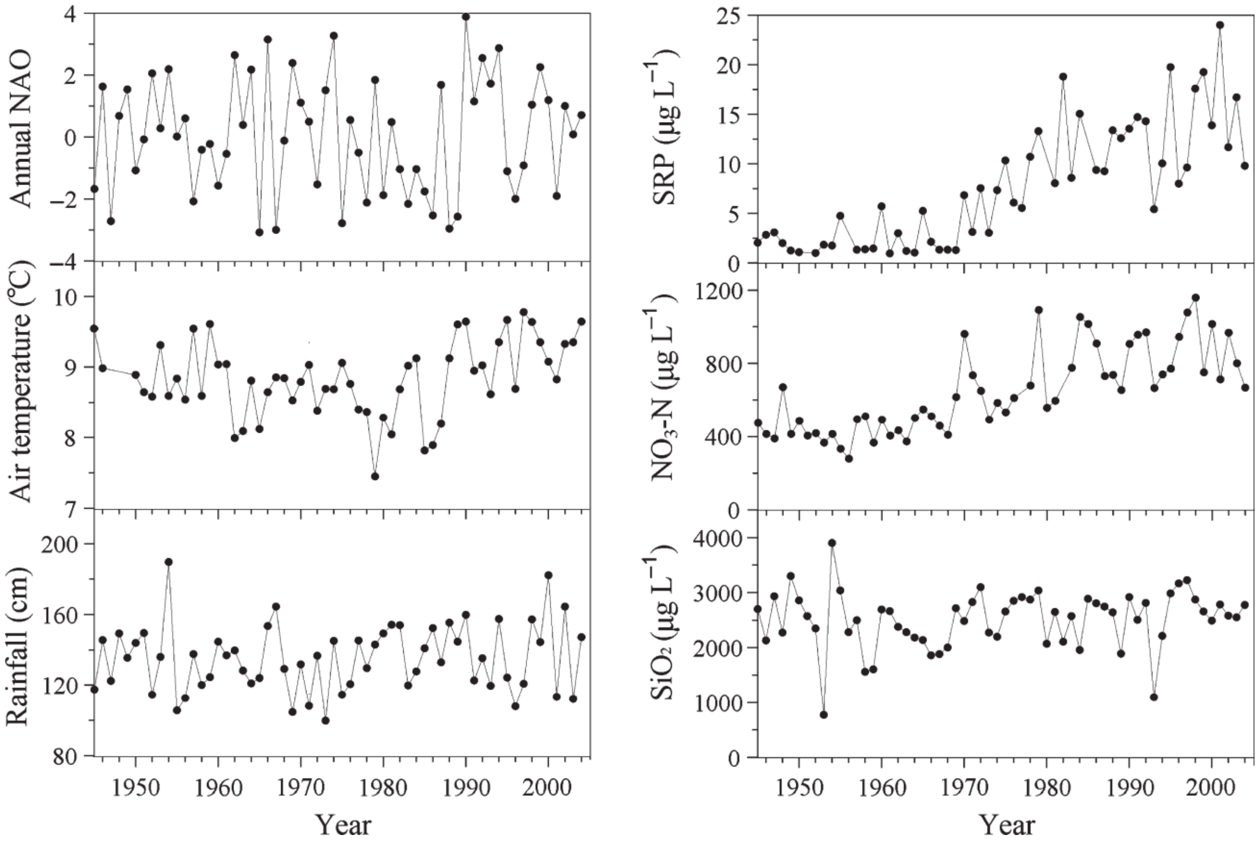

Figure 4.1 Annual averages for climatic (a–c) and January nutrient (d–f) variables over the monitoring period in Esthwaite Water, respectively.

Winter maxima for SRP and NO_3–N remained low before 1970, with average values of 2 and 467 μg L^{-1}, respectively. After 1970, particularly after 1975, increasing trends were observed in both nutrients, with average winter values of 12 and 797 μg L^{-1}, respectively, for the period 1970–2004. Concentrations of SiO_2 changed little over the monitoring period, with the exception of two low winter concentrations (in 1953 and 1993) and one high winter concentration of 3900 μg L^{-1} in 1954.

4.3.2 Sedimentary diatom records

The ^{210}Pb chronology for ESTH7 using the CRS approach indicated a relatively stable sediment accumulation rate (average 5 mm year^{-1}) in the upper 9 cm. Calibrated dates for samples from depths (mean of top and bottom values) of 1.88, 3.88, 7.13, 8.13, 9.13 and 10.13 cm were 2004 ± 2, 2001 ± 2, 1995 ± 2, 1993 ± 2, 1991 ± 2 and 1989 ± 2, respectively.

Overall, 116 diatom taxa were identified in the sediment core ESTH9 (only the main species are shown in Figure 4.2). Diatom assemblages were dominated by planktonic taxa and showed a typical succession found in many eutrophic lakes. The diatom stratigraphy was divided into two zones. In zone I (prior to 1975), *Asterionella formosa* Hassall and *Aulacoseira subarctica* (O. Mull.) were the dominant species, with average relative abundances of 28% in both cases. Other species typically found in relatively nutrient-poor waters, *Tabellaria flocculosa* (Roth) Kutz. and *Achnanthidium* *minutissimum* (Kutzing) Czarnecki, were present with abundances around 10%. *Fragilaria crotonensis* Kitton, *Cyclotella comensis* Grunow and *Cyclotella radiosa* (Grun.) Lemmerman were also present but with low abundances of around 5%. A major shift occurred around 1975 (zone II), with an expansion of taxa associated with more productive waters, such as *A. formosa, F. crotonensis* and *Stephanodiscus binatus* Hakansson and Kling. Correspondingly, formerly abundant species such as *T. flocculosa* and *A. minutissimum* gradually declined. Zone II was subdivided into two subzones, IIa (1975–1996) and IIb (1996–2004), caused by the substantial expansion of *Aulacoseira granulata* (Ehrenberg) and its subspecies *A. granulata* var. *angustissima* (O. Muller) Simonsen from c. 1996.

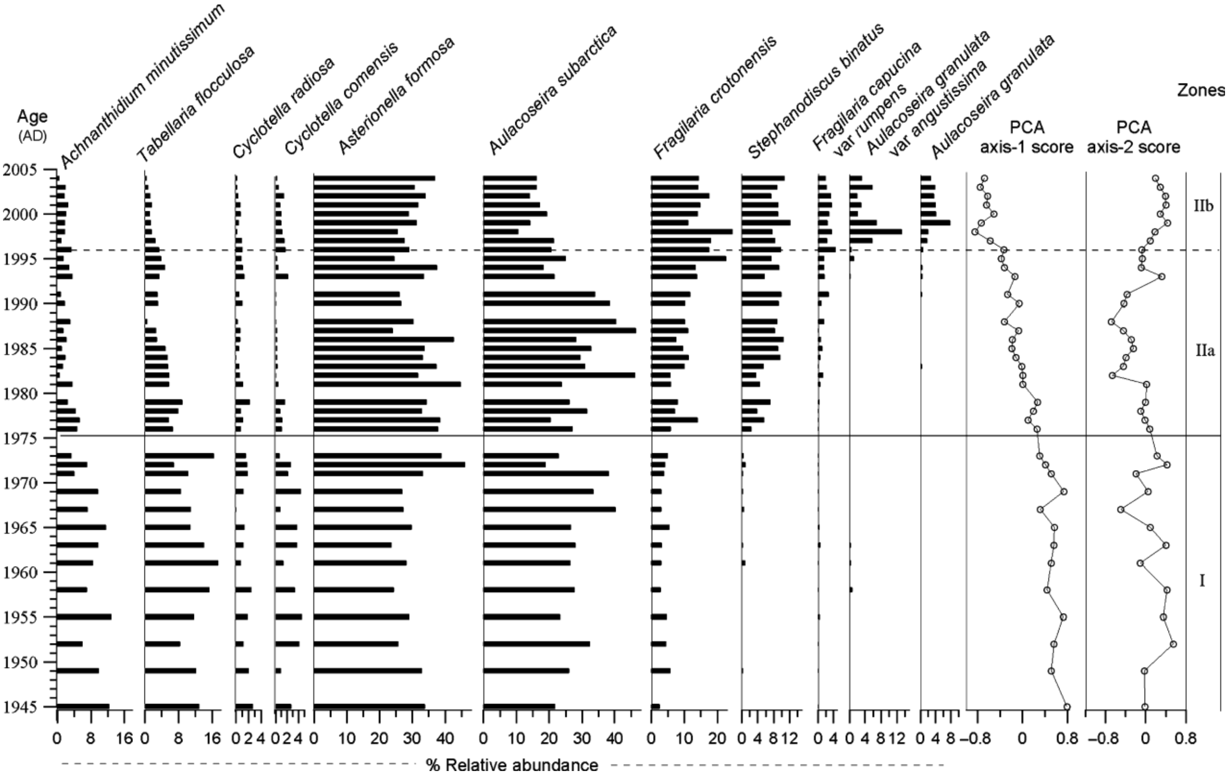

Figure 4.2 Diatom assemblage changes over the past 60 years in core ESTH9 from Esthwaite Water. Diatom data are expressed as % relative abundance, and principal component analysis axes 1 and 2 sample scores are shown. Zones of major compositional change are indicated by horizontal lines, with dashed lines for subzones.

Comparison with a broken-stick distribution revealed that the first two axes of PCA summarised well the major diatom community changes (Figure 4.2). Axis 1, with a distinct shift in sample scores at around 1975, accounted for 41% of the diatom variance. The scores of axis 1 were relatively stable prior to 1975 but increased gradually up the core, reflecting the progressive turnover in the assemblages. Axis 2 accounted for 16% of the diatom variance and exhibited higher variability than axis 1 and an obvious decrease after 1985. Only these two PCA axes were included in the AM analysis, since subsequent axes explained no more variance than expected under the null distribution.

4.3.3 Redundancy analysis

The RDA ordination biplot of samples and environmental variables (VIFs < 20) shows that several variables exhibit considerable collinearity (Figure 4.3 a). Three groups of closely related environmental variables were detected. Nutrient factors SRP, NO_3–N and SiO_2 were correlated with each other and were highly correlated with axis 1. The paired climate factors, AirT with annual NAO and rainfall with winter NAO, were the other two groups, explaining a considerable amount of diatom variance. Samples from the two zones defined in Figure 4.2 were separated along the environmental gradients, with zone I samples negatively correlated with the nutrient variables. In contrast, zone II samples were generally positively correlated with nutrients across the whole range of climate conditions. The sample representing the year 1972 fell into zone II owing to its high abundance of *A. formosa*.

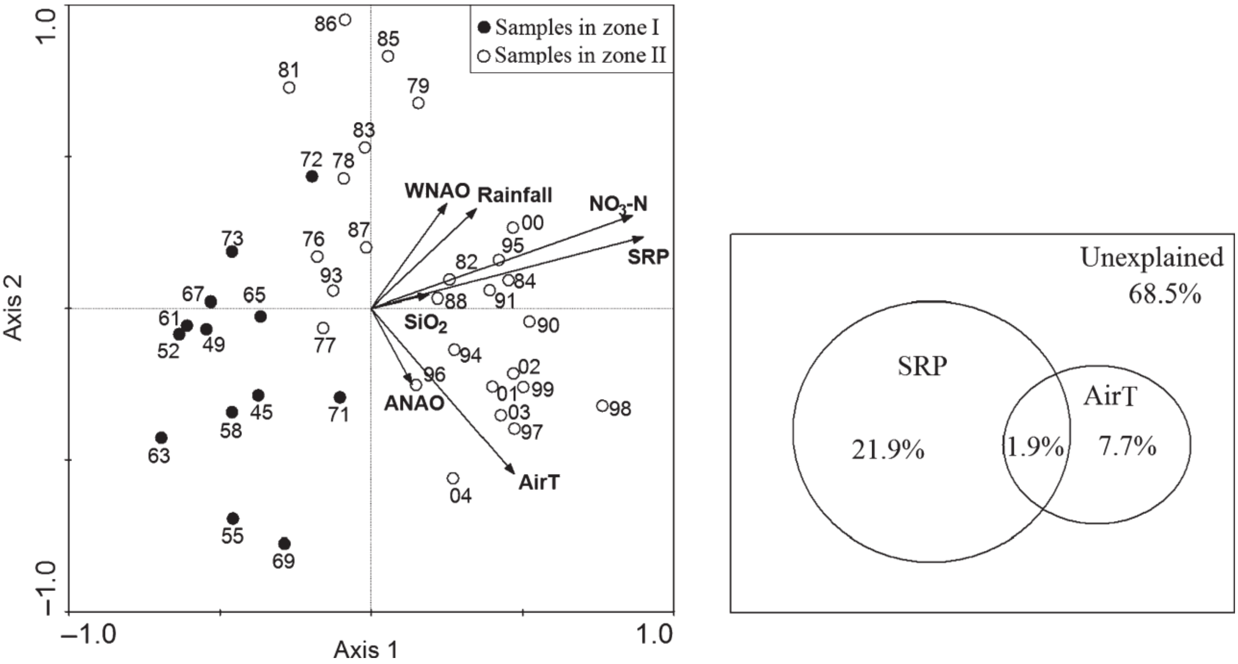

Figure 4.3 a) Ordination biplot showing environmental variables and samples plotted against redundancy analysis axes 1 and 2 for the 60-year sedimentary diatom record. Samples are labelled with the last two numbers of their dates.
(b) Variance partitioning of diatom composition, explained by soluble reactive phosphorus and air temperature. See methods for the abbreviations of environmental variables

Given the collinearity among variables illustrated in Figure 4.3 a, a forward manual selection RDA, with Monte Carlo permutation tests, showed that SRP and AirT jointly explained 32% of the diatom variance, compared with 41% for all variables. Partial RDA undertaken using SRP and AirT illustrated the amount of variation explained independently by each component (Figure 4.3 b). SRP was the most important variable and significantly explained 22% of diatom variance, while AirT explained 8%. The interaction between SRP and AirT, however, was weak, explaining only 2% of the diatom data.

4.3.4 Additive models

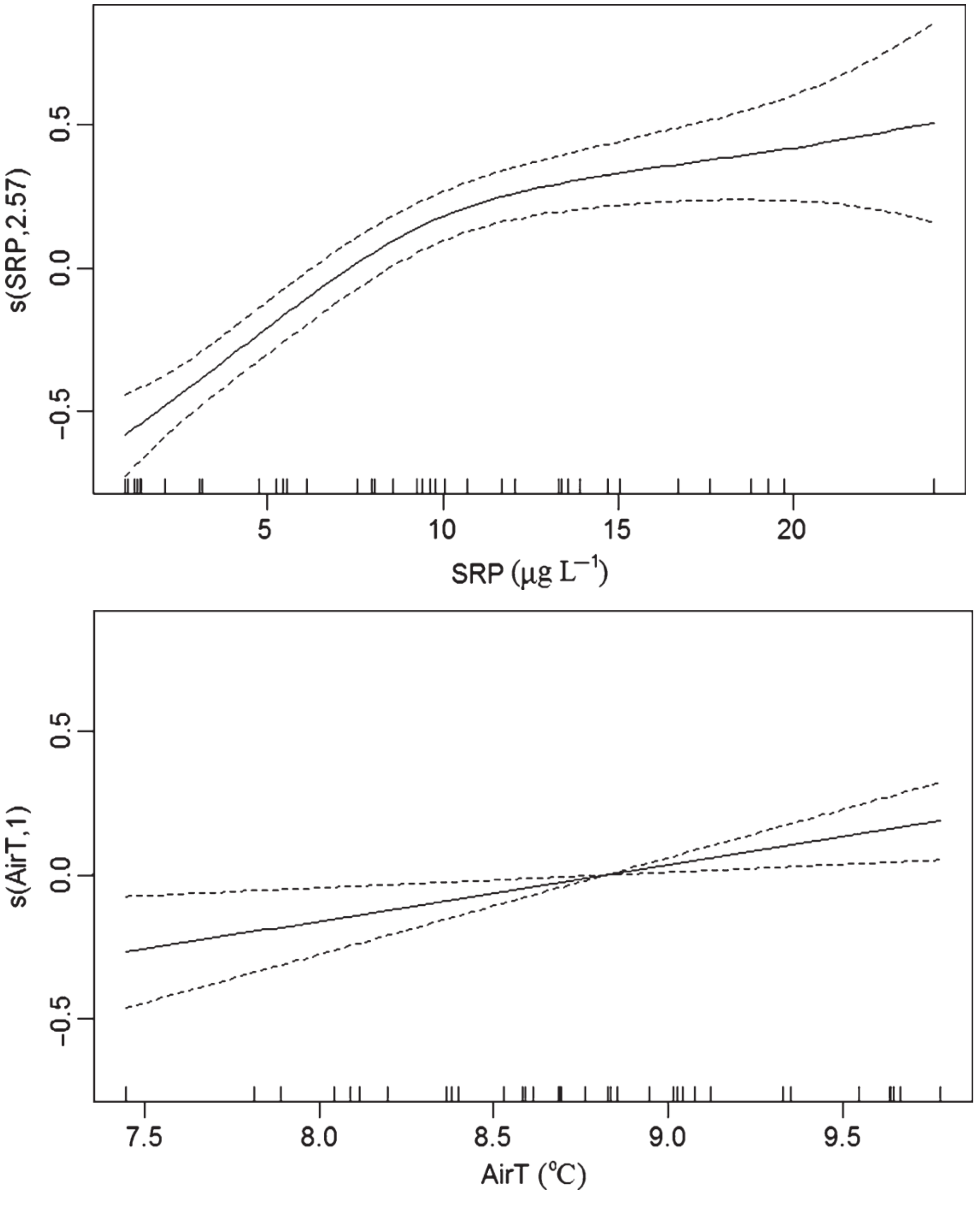

Figure 4.4 The fitted smooth functions for soluble reactive phosphorus (SRP) (a) and air temperature (b) from the final additive model for the PCAS1. The dashed lines are approximate 95% confidence intervals on the fitted functions. The tick marks inside the panels on the **x**-axis show the distribution of observed values for the two covariates. The numbers in brackets on the **y**-axis (2.57 and 1 for SRP and air temperature, respectively) are the effective degrees of freedom for each smoother.

A series of AMs including smooth functions of SRP and AirT as the single covariate were fitted to both sets of axis scores, with and without a CAR(1) correlation structure. The AIC and $R^2{}_{\text{adjust}}$ values for modelling the PCA axis 1 scores (denoted as PCAS1) with SRP and AirT together (with values of 18.074 and 0.704, respectively) exhibited significant improvement over those models with only the single variable SRP (21.510

and 0.623) and AirT (51.277 and 0.158). Consequently, the final model selected both SRP and AirT as predictors. SRP and AirT did not significantly ($P > 0.05$) model the PCA axis 2 scores (denoted as PCAS2) when modelled either solely or together (Table 4.1). Given the limited diatom variance explained by PCA axis 2, modelling was focused on PCAS1 only. The final AM fitted to PCAS1 (Figure 4.4) includes a significant smooth term for SRP ($P < 0.0001$) and AirT ($P < 0.01$). The fitted relationship between PCAS1 and SRP is nonlinear (effective degrees of freedom: edf = 2.57), while a linear smooth function was used for AirT (edf = 1). As SRP increases, the PCA scores increase, although the rate of increase is much reduced above 10 μg L^{-1}. The values of the link function for SRP increase with increasing SRP and have larger uncertainties at SRP >20 μg L^{-1} (Figure 4.4). In contrast, the smooth for AirT is much simpler with PCA scores increasing linearly with AirT (Figure 4.4b). The smooth functions clearly exhibit a weak response of diatoms to changing climate and a stronger more complex response to nutrients (Figure 4.4). When SRP values were low (e.g. <6 μg L^{-1} in 1975), diatom communities changed steeply (nearly linearly) with increasing SRP, while the response was weaker when SRP values were higher. The CAR(1) error structure was not required, as assessed by a likelihood ratio test comparing AMs with and without the structure ($P > 0.1$).

Vairable	PCA Axis 1			PCA Axis 2		
	edf	*F*	*P*	edf	*F*	*P*
SRP	2.57	31.7	1.92×10^{-9}	1	0.29	0.58
AirT	1	7.68	0.008	1	0.00	0.97

edf, effective degrees of freedom

Table 4.1Summary for the additive model fitted to diatom principal component analysis (PCA) axis 1 and 2 scores

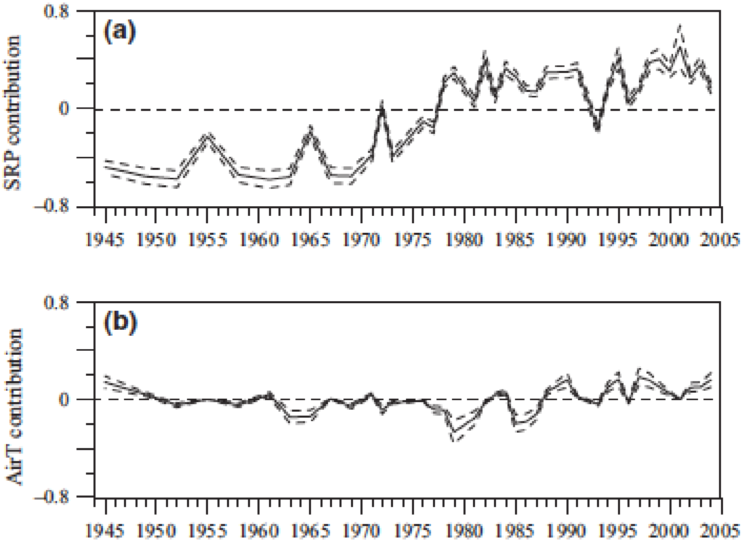

Figure 4.5 The contribution of (a) soluble reactive phosphorus and (b) air temperature to the fitted diatom principal component analysis axis 1 scores. The dashed lines are approximate 95% confidence interval on the contribution.

Contributions to the fitted values of the two covariates (SRP and AirT) are shown in Figure 4.5. The contribution of SRP to fitted PCAS1 is much larger than that of AirT, which is clearly illustrated by the same y-scale in the two panels (Figure 4.5). A significant change occurred at around 1975 for the contribution of both SRP and AirT. Prior to 1975, SRP made a major ‘negative’ contribution to PCAS1 (c. -0.5). After this time, the effect of SRP was slightly reduced but it still made a considerable ‘positive’ contribution from 1980 to 2004 (0.3–0.5). AirT exhibited almost zero effect on PCAS1 prior to 1975, but afterwards there was a small contribution of around ±0.2.

4.4 Discussion

Aquatic environmental change over the past 60 years Common to many lowland lakes in Europe and North America (see reviews in Smith, Tilman & Nekola, 1999; Schindler, 2006), monitoring records of water chemistry from Esthwaite Water indicate substantial nutrient enrichment of the lake over the past 60 years (Talling & Heaney, 1988). While improvements in wastewater treatment after 1986 reduced point source nutrient inputs, nutrients derived from catchment run-off, a fish farm installed in 1981 and sediment-P release have negated any potential reduction in lake nutrient concentrations (May, Place & George, 1997; Bennion et al., 2000). In addition, phosphorus and nitrogen accumulation from atmospheric deposition are currently important. Atmospheric input of P and N during 1986–1988 was 56 kg N km^{-2} year^{-1} at a site in the nearby Windermere catchment, and 3500 kg N km^{-2} year^{-1} averaged for the whole Lake District (Talling & Heaney, 1988). Current levels of nutrient deposition are expected to be higher still (Tipping et al., 2008).

Esthwaite Water has also experienced considerable climate change over the past 60 years. Regionally, the winter NAO is one of the most important factors affecting Esthwaite Water’s physical characteristics (George et al., 2004), and factors such as lake level, ice-out time and importantly stratification are all strongly influenced by weather patterns. When the NAO is positive, the lake catchment has experienced milder and wetter conditions over the past 60 years. The long-term records also show the influence of climate change: the winter (the first 10 weeks of each year) AirT variations at Ambleside show that the average temperature recorded during 1940–1970 was 3.0 °C and that recorded during 1970–2000 was 3.6 °C, while the average winter rainfall recorded for these periods was 5.7 and 7.1 mm day^{-1}, respectively (George et al., 2007). Several biological components of the lake ecosystem, particularly phytoplankton and zooplankton, have responded to changes in weather conditions in Esthwaite Water over intra- and inter-annual timescales (George, 2000; Talling, 2003; George et al., 2004; Jones & Elliott, 2007).

Diatoms in the core from Esthwaite Water clearly document environmental changes over the past 60 years, particularly in lake nutrient status. Oligotrophic species, such as *A. minutissimum, T. flocculosa, C. comensis* and *C. radiosa*, were present during

1945– 1970 when nutrient concentrations were low (average winter SRP 2 µg L^{-1}, Figure 4.1). With the slight increase in SRP during 1970–1975, the abundance of the mesotrophic species A. formosa increased significantly. However, the main change in the diatom community occurred after c. 1977, when eutrophication accelerated (average SRP 12 µg L^{-1} during 1977–2004, Figure 4.1). Species preferring eutrophic conditions, such as *S. binatus* (Findlay et al., 1998) and *F. crotonensis*, started to dominate and have remained abundant in the sediment ever since. The first appearance of *A. granulata* and *A. granulata var angustissima* (shift from zone IIa to IIb) occurred from c. 1996. The latter taxon had been first recorded in the region in the South Basin of Windermere (into which Esthwaite Water flows) in October 1991 (Canter & Haworth, 1992). These taxa commonly have high optima for silica and nitrate concentrations (Interlandi, Kilham & Theriot, 1999) and are also thermophilic species, generally associated with water temperatures in excess of 15 °C (Stoermer & Ladewski, 1976; Poulickova, 1992). Consequently, observed shifts were probably co-driven by seasonal nutrient (e.g. silica and nitrate) and climatic factors (e.g. summer temperature, wind) since annual values of these variables exhibited high variability over the period of *Aulacoseira* abundance (Figure 4.1). For example, monitoring records showed that the second highest average summer temperature (16.1 °C) over the period 1980–2000 occurred in 1995, with relatively higher values after 1996 compared with the earlier period (George et al., 2007). The increasing temperature under high nutrient conditions probably favoured the growth of *A. granulata*.

4.4.1 Redundancy analysis–based separation of nutrient and climate effects

Redundancy analysis revealed that SRP explained the largest amount of diatom variance of the measured environmental variables (22%), suggesting that this was the major driving factor of diatom community change over the 60-year data set. PCAS1 accounted for 41% of diatom variance and was highly correlated with SRP ($r = -0.753$, $P < 0.01$, $n = 39$). NO_3–N was also highly correlated with SRP ($r = 0.69$, $P < 0.01$, $n = 39$) and likely played an important subsidiary role in controlling diatom dynamics, whereas SiO2 explained only a limited amount of diatom variance (Figure 4.3a). Undoubtedly, all three nutrients are important to diatom growth in Esthwaite Water and elsewhere (Interlandi et al., 1999; Reynolds, 2006). However, their relative importance depends on supply rates and on the order in which they are consumed. In Esthwaite Water, the long-term data show that SRP is typically reduced to limiting concentration first, followed by SiO_2 and then nitrate (Maberly et al., 2011). Thus, our inter-annual data support this finding, suggesting that SRP is of considerable importance at seasonal to decadal scales in Esthwaite Water. AirT explained just 8% of diatom variance, suggesting that climate conditions imposed a weaker effect on diatom change than nutrients.

4.4.2 Additive model–based separation of nutrient and climate effects

The smoothing functions (Figure 4.4) and relative contributions (Figure 4.5) derived from AM describe diatom responses to changes in SRP and AirT. SRP availability was clearly more important than AirT in regulating diatom communities when SRP concentrations were low prior to 1975. In contrast, AirT showed almost no effect on diatom communities prior to 1975 but became stronger after 1975 even though the influence of nutrients remained dominant (Figure 4.5). The prevailing nutrient effect over the whole period (1945–2004) reflects the various stages of nutrient enrichment, all of which led to diatom community shifts. Furthermore, diatoms show little variation in their ability to compete for nutrients across temperature gradients from 5 to 20 °C (Van Donk & Kilham, 1990), and any change in one of the other factors (e.g. pH, nutrients) may change the diatom composition while temperature remains constant (Anderson, 2000). In Esthwaite Water, relatively moderate temperature variations were observed, for example the monthly maximum and minimum air temperature ranges were 5.4–18.7 and 0–10.2 °C for the period 1960–1990, respectively (data from http://www.metoffice.gov. uk/climate/uk/averages/19611990/sites/newton_rigg. html). Thus, when nutrients (particularly SRP) are in a range where they are potentially limiting the growth of diatoms, competition for nutrients, rather than climatic factors, drive the community-level shifts. A similar conclusion about the importance of nutrients and physical factors linked to climate change was drawn from a modelling study on Bassenthwaite Lake, also in the English Lake District (Elliott, Jones & Thackeray, 2006).

4.4.3 Synthesis: nutrient and climate effects on diatom communities

In general, climate (including temperature, rainfall, wind, solar irradiation) and nutrients have complex and interacting effects on aquatic ecosystems. For example, increasing temperatures not only lengthen the period of thermal stratification but also bring more nitrate into lakes as higher temperatures increase soil mineralisation (Whitehead et al., 2009). However, against a background of higher temperatures in Southern Europe, the predicted decrease in precipitation and higher evaporation will result in less run-off and, as a result, possibly lower nutrient loading to fresh waters (Jeppesen et al., 2009). Thus, the interaction between climate change and a change in nutrient loading may vary between lake types (e.g. deep versus shallow lakes) and different trophic states (Huber, Adrian & Gerten, 2008). In small and relatively shallow lakes, climate can obscure or exaggerate the nutrient enrichment process, since the heat and energy are more easily transferred within the lake than in larger, deeper systems. Nevertheless, in Esthwaite Water, it is interesting that the interaction between nutrient and climate factors was rather weak (just 2% in the partial RDA) in terms of its influence on diatom community changes over the 60-year period (Figure 4.3).

The effects of climate and nutrients on diatom communities vary depending on the timescale of the limnological records. In this study, both the RDA and AM based on the annual average data showed that climatic factors (including AirT, rainfall, ANAO and WNAO) imposed limited effects on diatom dynamics in Esthwaite Water. However, it is undeniable that weather is one of the most important factors controlling diatom dynamics on a seasonal basis (Van Donk & Kilham, 1990; Talling, 2003), a timescale normally not accessible to palaeolimnologists since most sediment records have coarser resolution. Indeed, Anderson (1995) showed that seasonal inter-annual oscillations in diatom plankton may be smoothed out in cores that better reflect longer-term changes (e.g. decades to millennia). This is perhaps one key reason for the limited effect of climate on diatom communities in this study. In fact, temperature, with distinct seasonal cycles but relatively stable interannual change, controls many fundamental properties of phytoplankton and is a key factor regulating primary production in most lakes (Reynolds, 2006). This is particularly true as nutrients become less limiting for phytoplankton. Some studies have shown climate warming to have induced forward shifts in the timing of the phytoplankton spring maximum in lakes across the Northern Hemisphere (Gerten & Adrian, 2000; Straile et al., 2003). Indeed, in Esthwaite Water, long-term monitoring records from 1945 to 2004 show that the timing of the spring bloom of *A. formosa* has been appearing progressively earlier (Patrick et al., 2004). However, these phenological changes are not resolvable in the sediment record of Esthwaite Water.

4.4.4 Combination of RDA and AM methods

Redundancy analysis extracted the minimum variable combination (SRP and AirT) for further AM procedures. Given the great flexibility of AM, it can provide an excellent fit in the presence of nonlinear relationships and significant noise in predictor variables (Hastie & Tibshirani, 1990; Wood, 2006). However, caution should be exercised to avoid over-fitting of the data, i.e. application of an overly complex model (e.g. with many degrees of freedom) to data so as to produce a good fit. Unexpected results may derive from an AM based on a group of predictors with collinearity (Zuur et al., 2009). The RDA including all the predictors illustrated the multi-collinearity of the environmental data set (Figure 4.3a). Consequently, a predictor selection process for complicated AMs is generally required (Wood, 2006). This study illustrates that the forward selection RDA method offers a good solution for effective predictor selection.

4.4.5 Combination of monitoring and palaeolimnological records

Monitoring and palaeolimnological data are highly complementary, and their combination in this study makes a valuable contribution to understanding how nutrients and climate have affected Esthwaite Water. In general, observational time-series data are very limited both in space and time (Battarbee et al., 2005), although they provide a precious and high-resolution description of past environmental change. Palaeolimnological data not only can complement monitoring data but can also extend well beyond it, affording an important means of validating ecological hypotheses and long-term model behaviour (Anderson et al., 2006; Sayer et al., 2010).

One possible disadvantage of using palaeolimnological records to extend monitoring data is that they may suffer from taphonomic biases and occasionally from uncertain chronology (Battarbee et al., 2005). Fortunately, increasing research has demonstrated that shifts in many biological components of aquatic ecosystems can be reliably recorded in the lake sediments (e.g. Cameron, 1995). In Esthwaite Water, there was also good agreement between the 60-year monitoring diatom data and corresponding fossil diatom assemblages, indicating that sediment records for this site are reliable (X. H. Dong, H. Bennion & S. C. Maberly, unpublished data). Furthermore, sediment records provide more comprehensive diatom habitats (including epiphytic and benthic species) than phytoplankton data, and, importantly, the analysis based on the 60-year data set can be used ‘experimentally’ to test the practicability of using the sediment record for interpreting longer-term changes.

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5. The role of cladocerans in tracking long-term change in shallow lake trophic status

Responsible: Thomas A Davidson[1*,2] Contributors, Helen Bennion[2], Erik Jeppesen[1,3,4], Gina H. Clarke[2], Carl D. Sayer[2], David Morley[2], Bent V. Odgaard[1], Peter Rasmussen[5], Ruth Rawcliffe[2], Jorge Salgado[2], Gavin L. Simpson[2] & Susanne L. Amsinck[1]

[1]Department of Bioscience, Aarhus University, Vejlsøvej 25, DK-8600 Silkeborg, Denmark

[2]Environmental Change Research Centre, Department of Geography, University College London, Pearson Building, Gower Street, London WC1E 6BT, UK

[3]Greenland Climate Research Centre (GCRC), Greenland Institute of Natural Resources, Kivioq 2, P.O. Box 570 3900, Nuuk, Greenland

[4]Sino-Danish Centre for Education and Research (SDC), Beijing, China

[5]Department of Quaternary Geology, Geological Survey of Denmark and Greenland (GEUS), Copenhagen K, Denmark

5.1 Introduction

Globally, freshwater ecosystems have been subject to a wide range of uses and abuses, particularly over the past two centuries, with generally deleterious impacts. Assessing the nature and extent of anthropogenically induced change and separating out the variation that is ‘natural’ is a key challenge to scientists. This need has been brought into sharp focus by the demands of the Water Framework Directive (WFD)(European Union, 2000) which requires the definition of reference condition of freshwater ecosystems (i.e. that expected in the absence of anthropogenic disturbance) and also an assessment of the ecological status measured against the divergence from reference condition. The WFD places emphasis on the ecological structure and function of aquatic ecosystems with biological elements (fish, invertebrates, macrophytes, phytobenthos and phytoplankton) at the centre of the status assessments. This important piece of legislation is set to drive the management of surface waters throughout Europe for the next few decades.

The sediment record in lakes is a valuable resource as it enables ecosystem change to be tracked over a range of timescales. A variety of techniques to reconstruct past physical, chemical and, more recently, the ecological condition of lakes have been developed (e.g., Smol et al., 2001). A number of indicators have been employed from palynological approaches looking at landscape change, to diatom records focusing on within lake change and how that relates to broader environmental problems such as acid deposition (Battarbee et al., 2010) or nutrient enrichment (Hall & Smol, 2010). Recent developments in palaeoecology, particularly the combination of contemporary and palaeoecological techniques in shallow lakes, have made it possible to reconstruct, more directly, ecological change (e.g., Brodersen et al., 2001; Davidson et al., 2005; McGowan et al., 2005; Sayer et al., 2010c). Submerged and floating leaved plants play key roles in physical, chemical and biological processes in lake ecosystems (Timms & Moss, 1984; Carpenter & Lodge, 1986; Moss, 1990; Jeppesen et al., 1997). Furthermore, the macrophyte flora has both inherent conservation value and is a key indicator of ecosystem health and as such has become one of the principal tools used to establish lake ecological status in the WFD (Søndergaard et al., 2005; Penning et al., 2008; Søndergaard et al., 2010). Establishing the ecological condition of a given lake benefits immensely from placing the current condition in the context of its past condition and change through time. In the absence of long-term monitoring, the use of macrophyte remains to reconstruct past aquatic vegetation has received increasing interest. The approach does have a number of methodological weaknesses, linked to the differential preservation of the remains of submerged taxa (Davis, 1985; Davidson et al., 2005; Zhao et al., 2006). Notwithstanding problems such as differential preservation, the plant macrofossil record has been shown to reliably infer the dominant component of the macrophyte flora in shallow lakes (Davidson et al., 2005; Salgado et al., 2010) and thus provides an extremely useful summary of ecosystem change.

The analysis of sub-fossil remains of cladocerans, carapaces, post-abdomens, claws, mandibles, sections of antennae and ephippia in both surface sediments and older core material has a long history (Frey, 1958). Cladocera remains have been employed in a wide range of studies investigating *inter alia*: lake ontogeny (Frey, 1958); trophic state (Hofmann, 1996); lake-level changes (Sarmaja-Korjonen & Alhonen, 1999; Sarmaja-Korjonen & Hyvarinen, 2002); saline transgressions (Amsinck et al., 2005), and changes in predation pressure (Kitchell & Kitchell, 1980; Kerfoot, 1981; Leavitt et al., 1989). Furthermore, the sub-fossils of cladocerans, in particular the chydoridae, have been used to investigate change in macrophyte abundance (Thoms et al., 1999; Johansson et al., 2005). This wide variety of applications reflects the fact that cladoceran assemblages are shaped by many factors (Jeppesen et al., 2001; Davidson et al., 2010b). This results from their position at the centre of the food web combined with the presence of both benthic and pelagic taxa which makes them sensitive to both bottom up and top- down structuring forces and shifts in the balance of benthic and pelagic productivity (Davidson et al. 2010a; Jeppesen et al., 2011).

The sensitivity of zooplankton to environmental variation makes their exclusion from the WFD appear a major oversight (Jeppesen et al., 2011). In contrast, macrophytes are recognised and utilised as one of the principal tools in the WFD to classify lake ecological status (Penning et al., 2008). Here we use the sediment record from multiple shallow lakes with both cladoceran and macrofossil records to compare (and contrast) the way in which macrofossil and cladoceran fossil remains reflect variation over time in shallow lake ecosystem structure and function. We employ plant macrofossils to provide an indication of how a particular lake has changed, and then ask the key questions: how well do the cladocerans reflect that change and what information can they provide on possible causes of change?

5.2 Materials and methods

5.2.1 Study sites

The data presented here are generally from lowland, nutrient enriched shallow lakes in the UK and Denmark (Table 5.1). The study consists of 19 sites and 20 cores, as two cores come from Ormesby Great Broad, in the Trinity Broad system. Apart from the Norfolk Broads, the other sites are located in Northern Ireland covering the lowlands of the Lough Erne catchment to the Garron plateau in the North-East of Northern Ireland. There are also two sites from Wales, Kenfig Pool in the south and Llyn Cadarn in Anglesey. Three sites come from Denmark and details of these sites have been published in a number of previous studies (Jeppesen et al., 1998; Brodersen et al., 2001; McGowan et al., 2005).

5.2.2 *Field methods*

Sediment cores in the UK were collected using either large diameter mini-Mackereth corer (diameter 52 mm; Mackereth, 1969), a Livingstone type piston corer (diameter 74 mm; Livingstone, 1955) or a, specially designed and built, wide diameter “Big-Ben” piston corer (i.d. 140 mm; Patmore et al., unpublished), between 1999 and 2010. These cores were collected, not from the centre of the lakes but from more the littoral zone, as plant macrofossil remains are generally more abundant in this area (Davidson et al., 2005). In Denmark, cores were sampled with a Kajak (upper sediments) and a Russian corer (deeper sediments) from the centre of the lake. For further details of coring methods are given in Odgaard (1993) and McGowan et al. (2005). Core details, including method, length and coring date can be found in Table 5.1.

5.2.3 *Dating*

The methods employed for sediment dating were either radiometric, employing ^{210}Pb and ^{137}CS (Appleby & Oldfield, 1983) or spheroidal carbonaceous particle (SCP) techniques (Renberg & Wik, 1984; Rose et al., 1995) and recent refinements of the technique (e.g., Rose & Appleby, 2005). In some cases the dating of the sediment cores did not unambiguously ascribe a full set of dates from coring date to 1850, and thus ecological change cannot always be ascribed to a particular point in time. The lack of a tightly constrained age-depth model is less important for the purposes of our study, as the comparison of the plant macrofossils and cladoceran records, with the exception of Lake Lading, was from the same core (see McGowan et al., 2005). Furthermore, it was not necessary to identify the specific time of change, but the aim was rather to compare the timing and extent of alteration in the macrofossil and cladoceran records.

Table 5.1Summary details of sites and sediment cores –coring methods BB (Big Ben), Liv (Livingtone piston corer), Mac (Mini-Mackereth corer), Rus (Russian corer). Dating methods – SCP is spheroidal carbonaceous particle technique.

Region	Site	Core	Location	Core method	Core site water depth (m)	Core length (cm)	Dating method	*Date*
Norfolk	Rockland Broad	ROCK1	N52°35.6', E 1°26.5'	BB	1.0	85	^{210}Pb/SCP	*11/11/2002*
	Ormesby Great Broad	ORMG1	N 52°40.6', E 1°38.3'	Liv	1.2	141	SCP	*07/03/2007*
		ORMG2		Liv	1.1	150	SCP	*07/03/2007*
	Ormesby Little Broad	ORMGL1	N 52°40.6', E 1°38.3'	Liv	2.0	150	SCP	*08/03/2007*
	Filby Broad	FILB1	N 52°40.6', E 1°38.3'	Liv	2.0	142	SCP	*08/03/2007*
	Rollesby Broad	ROLL1	N 52°40.6', E 1°38.3'	Liv	1.9	141	SCP	*08/03/2007*
	Felbrigg Lake	FELB1	N 52°54.1', E 1°15.3'	Mac	1.3	85	^{210}Pb	*15/03/1998*
Wales	Llyn Cadarn	CADA3	N 56°35.2', W 3°32.0'	BB	2.5	78	SCP	*22/09/2007*
	Kenfig Pool	KENF2	N 53°54.3', W 3°11.3'	Liv	2.6	78	^{210}Pb	*10/07/2002*
Northern Ireland	Lough na Trosk	TROS1	N 55°29.4', W 5°39.1'	Liv	1.2	92	^{210}Pb	*19/06/2007*
	Lough Garve	LGAR1	N 54°59.5', W 6°6.5'	Liv	0.7	85	^{210}Pb	*7/06/2007*
	Mill Lough	LMIL1	N 54°8.4', W 7°29'.0	Liv	2.6	149	^{210}Pb	*24/06/2007*
	Killymackan Lough	KILL1	N 54°8.0',W 7°29.7'	Liv	1.2	147	^{210}Pb	*24/06/2007*
	Kilroosky Lough	KILR1	N 54°11.5', W 7°14.6'	Liv	3.1	152	^{210}Pb	*25/06/2007*
	Knocballymore C	KNOC1	N 54°11.4', W 7°15.8'	Liv	2.05	157	^{210}Pb	*25/06/2007*
	Meenantully	MEEN1	N 54°32.1', W 8°0.1'	Liv	2.2	100	^{210}Pb	*21/06/2007*
	Lough Rushen	RUSH1	N 54°32.6', W 7°58.2'	Liv	2.1	107	^{210}Pb	*21/06/2007*
Denmark	Lake Ladding	LADD1	N 56º 13.0' E 9º 57.8'	K-Rus		115	^{210}Pb	*1993 &1995*
	Lake Søbygaard	BP2	N 56º 15.3', E 9º 48.4'	K-Rus	1.5	110	^{210}Pb	*1993*
	Lake Stigsholm	STIG1	N 55º 58.7', E 9º 29.4'	K-Rus		85	^{210}Pb	*1993*

5.2.4 Palaeoecological analysis of biological remains

Plant macrofossil remains, consisting of seeds, fruiting bodies, oospores, turions, leaves, spines and trichosclereids (star cells from Lily leaves) were enumerated from sub-samples of the sediment cores. The exact volume of sediment was determined by water displacement (Birks, 2001). Samples were washed through 350 and 150 µm sieves. The entire retent of the 350 µm was examined using a stereo-microscope at 10-20× magnification and identifiable plant remains were enumerated. A sub-sample, approximately one quarter of the total sample retained by the 150 µm sieve was analysed at a higher, 20-40× magnification also using a stereo-microscope, for vegetative fossils of 10-50 µm in diameter. Volumes between 25 cm^3 and 50 cm^3 were analysed. The data are presented as numbers of remains per 100 cm^3 of wet sediment. Macrofossils were identified by comparison with reference material held at the Environmental Change Research Centre, University College London. Reference material has been gathered over a series of years from a variety of sources, including collection directly from the field and extensive contributions from the Geological Survey of Denmark and Greenland (GEUS) and the Botanical Institute, Bergen University, Norway. The taxonomic resolution of the identification varies according to remain type as it is not always possible to describe remains to species level. Thus, in some cases an aggregate group of species corresponding to the highest possible taxonomic resolution was used. For example, *Potamogeton* leaf remains were grouped as *Potamogeton pusillus* agg. which will include *P pusillus* L., *Potamogeton berchtoldii* L. and perhaps *Potamogeton trichoides* L. *Potamogeton freisii* agg. consisted of both *Potamogeton freisii* L. and *Potamogeton compressus* L. Distinct morphotypes of *Chara* oospores were also identified, these likely reflect different species and the rudimentary nomenclature of A, B and C was kept constant across the different cores for the Trinity Broads cores. *Nymphaeaceae* trichosclereids are star cells which promote the buoyancy of lily leaves and may come from either *Nymphaea alba* L. or *Nuphar lutea* L.

In the UK, analysis of cladoceran sub-fossils was carried out as outlined in Davidson (2007). This is an adaptation of more standard methods (Korhola & Rautio, 2001) to include the enumeration of ephippia of those taxa which leave few chitinous remains (Jeppesen et al., 2001). For the cores analysed here ephippia were enumerated from the much larger volume of sediments used in the macrofossil analysis. For cladoceran analysis samples of at least 1 g were heated in a deflocculating agent (KOH) and sieved at 150 µm and 50 µm. Sub-samples of each fraction were identified using a compound microscope at 40-100×, the chitinous Cladocera remains were identified with reference to Flössner (1972), Frey (1958) and Alonso (1996). In Denmark, the method differs slightly; here approximately 5 g (wet weight) sediment was heated in 10% KOH for 20 minutes. To ensure reliability, total counts of rare subfossils were performed on the 140 µm fraction and the rest on subsamples (1-40% of total sample) from the 80-140 µm fractions. Sub-fossils were taxonomically identified in accordance with Frey (1959) and Flössner (2000) using a binocular microscope (100×) and an inverted light microscope (320×), and the most numerous subfossil of each taxon was used for the data analysis.

5.2.5 *Numerical methods*

Principal components analysis (PCA) was used to characterise variation the macrofossil assemblages, and the broken stick test was applied to assess the significance of the main axes of variation extracted by PCA. PCA was conducted on square root transformed data, which was also centred and standardised by taxa to allow the abundance data of plant remains to be used in the analysis. The differential production of remains makes use of absolute abundance data problematic as the various types of remains may be produced in very different quantities. Co-Correspondence Analysis (Co-CA), a relatively new ordination method described in detail by ter Braak & Schaffers (2004), was then employed to directly relate the variation in the macrofossil and cladoceran assemblages through time in the 20 cores. The macrofossil and cladoceran data were again centred and standardised for the Co-CA analysis, but as this analysis cannot work with negative values the data mean was shifted to exclude the possibility of negative values. Co-CA belongs to the suite of techniques using weighted averaging, such as correspondence analysis and canonical correspondence analysis (ter Braak & Prentice, 1988). Its principal quality, making it appropriate here, stems from the fact that Co-CA maximises the covariance between the weighted averages species scores of one species data matrix with those of another, and thus it identifies the ecological gradients common to both communities sampled in space or time (ter Braak & Schaffers, 2004). Co-CA has both a descriptive symmetric form, which relates the two species matrices without assigning either matrix to the response or predictor role, and an asymmetric predictive form, in which one of the species matrices is used to predict the other matrix. Predictive Co-CA uses a leave-one-out cross-validation procedure to estimate the number of significant Co-CA axes and determine the degree of variance in the response community (in this case macrofossils) explained by the predictor community (in this case the cladoceran assemblages). Here we used both the symmetric Co-CA to determine the axis 1 site scores for the macrofossil and cladoceran assemblages, and also the predictive Co-CA with the aim of inferring community responses in the macrophyte composition from the sub-fossil cladoceran data. A low percentage explained from the predictive Co-CA is not necessarily a sign of weak relationships; the cross-validatory is a different way of measuring the strength of relationships compared to other forms of constrained ordination such as partial CCA(ter Braak & Schaffers, 2004). In Co-CA, any fit above zero indicates that prediction is better than could have been expected by chance, implicitly validating the model (in contrast to explanatory methods where additional statistical tests are needed to establish model validity; Schaffers et al., 2008).

PCA was also used to characterise the change in community composition in the diatom data from Felbrigg Lake (for details, see Sayer et al., 2010a). Constrained clustering analysis CONISS (Grimm, 1987) conducted on the macrofossil data is presented for the three cores where change is shown in detail (ORMG2, BP2 and FELB1) as it identifies key points of change in the macrofossil assemblage. Analysis was conducted using the vegan (version 1.17-4, Oksanen et al., 2008) and cocorresp (version 0.1-9, Simpson, 2009) package in R (version 2.11.1, R, 2007); stratigraphic plots were produced in C2 (Juggins, 2003).

5.3 Results

5.3.1 Core Chronologies

Dating results for a number of the sites have been described in detail elsewhere (Brodersen et al., 2001; Jeppesen et al., 2002; McGowan et al., 2005; Davidson, 2006; Sayer et al., 2010a). For several sites, particularly those from Northern Ireland and the Trinity Broads, the core chronologies have not been published outside of reports to the funding bodies (Davidson et al., 2008a-b). It was possible to ascribe dates with varying levels of confidence to all the sediment cores presented here but resolution and confidence of the dating varied between sites. Given that the fossils analysed were from the same core (with one exception) and usually the same sample (17 of 20 cores) there are few assumptions even where the age model cannot be applied to the entire core with complete confidence.

5.3.2 *Comparing macrofossils and cladoceran sub-fossils*

The results of the PCA analysis on the macrofossil data demonstrate that large and, with one exception (ORML1), significant amounts of the variance were explained by the first axis, and often second and third axes; indeed, between 40 and 70 % of the variance in species data were explained by the first two axes (Table 5.2). The correlation coefficients of the Co-CA axis 1 and 2 scores for cladocerans and plant macrofossils for 20 cores (Table 5.2) and the plots (Figure 5.1) demonstrate a high degree of similarity in change through time between the plant macrofossil and cladoceran assemblages. There was uniformly high correlation between the axis 1 sample scores for the macrofossil (the response assemblage) and cladoceran (the predictor assemblage) community (Table 5.2). The plots of Co-CA axis 1 scores through time also identify points of significant ecological change in both the macrofossils and the cladocerans (e.g. 55 cm in ROCK1, 40 cm in KENF2, 35 cm in RUSH1, 25 cm in BP2; Figure 5.1 and Figure 5.3). Co-CA seeks to maximise the covariance between two assemblages and thus the highly similar changes in the axis 1 scores of macrofossil and cladoceran through time are to be expected. The percentage covariance explained by either 1 or 2 dimension in the Co-CA of the plant macrofossil and cladoceran assemblages provide further evidence (Table 5.2) of the linked nature of these two assemblages in shallow lake ecology. There were substantial proportions of variance (20.3 – 54.2 %) explained in the first axis. There were a number of sites where two axes of variation were significant (KENF2, ORMG2, ORML1 and FELB) and a large proportion of the variance in the macrophyte data was explained by the cladoceran assemblage in those two dimensions (e.g. 67.9% in Felbrigg Lake). There were, however, three sites where none of the axes in the Co-CA were significant (ROLL, CADA and RUSH). There is no obvious single reason why this would be the case: ROLL has a rather small sample number (n=7) whereas CADA and RUSH the variation in the macrofossil assemblage was spread over a number of PCA axes, perhaps making the covariance with the cladoceran assemblage more difficult to detect.

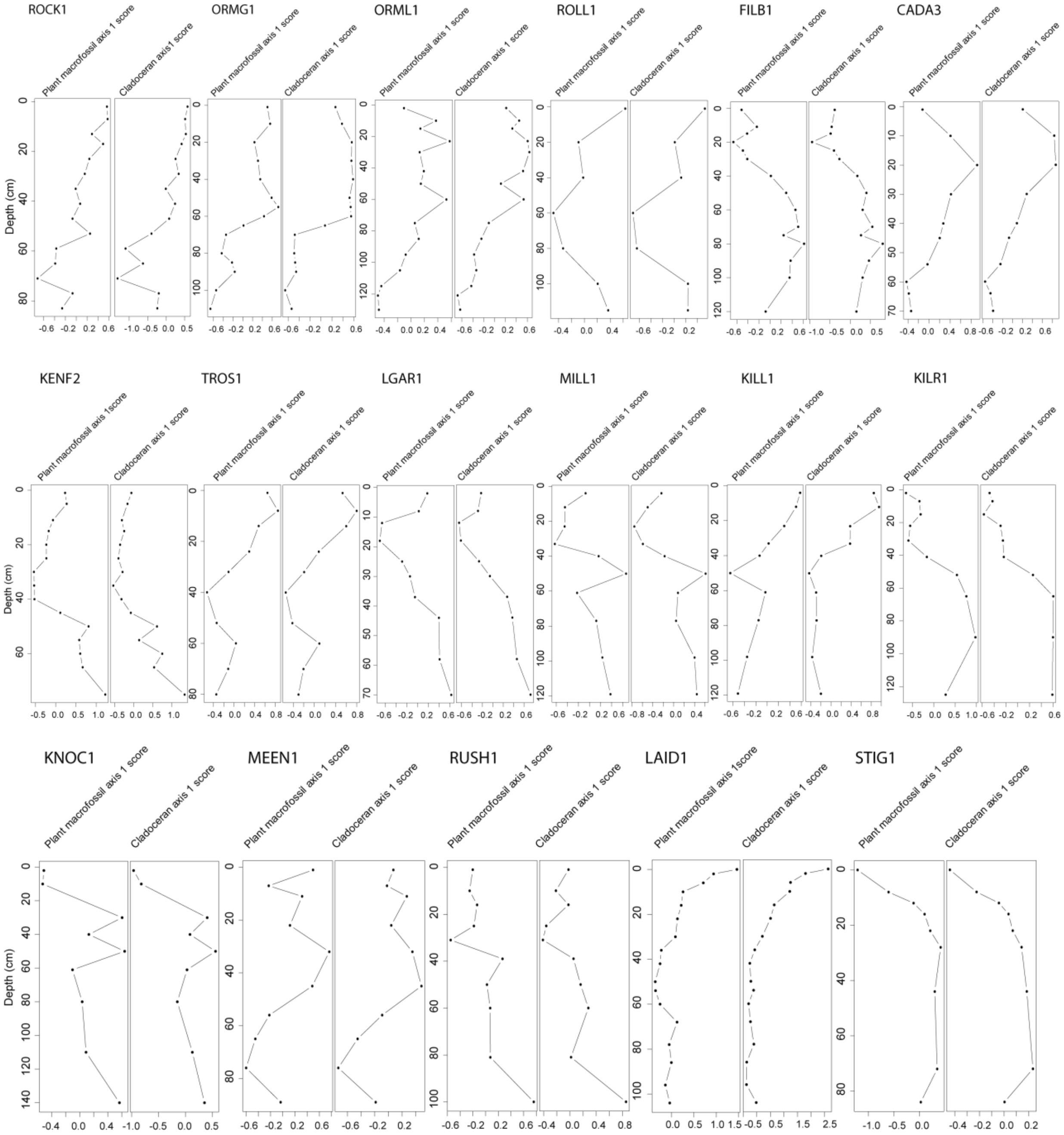

Figure 5.1 Comparison of Co-CA axis 1 scores for plant macros and cladocerans

		Macrofossil PCA			Macrofossil– Cladoceran Co -Correspondence			
		sig axes	Cumulative %variance		Correlation		Cumulative % co-variance	
Core	N		axis 1	axis 2	axis 1	axis 2	axis 1	axis1+2
ROCK1	15	1	39.1	56.6	**0.88**	0.95	**35.0**	50.7
ORMG1	15	2	34.6	55.9	**0.92**	0.92	**28.6**	44.6
ORMG2	15	2	31.5	51.2	**0.92**	**0.91**	**26.6**	**45.5**
ORML1	15	0	22.4	40.7	**0.86**	**0.92**	**26.1**	**40.4**
ROLL1	7	1	44	66.2	0.94	0.84	34.2	57.4
FILB1	15	3	28	50	**0.95**	**0.84**	**28.3**	**44.5**
FELB1	10	2	35.9	63.4	**0.93**	**0.91**	**42.3**	**67.9**
CADA3	10	3	36.5	60.3	0.88	0.89	28.5	43.5
KENF1	15	1	50	67.7	**0.92**	**0.95**	**30.4**	**43.1**
TROS1	10	4	32.5	56.8	**0.98**	0.93	**34.2**	51.8
LGAR1	9	3	36.1	65.9	**0.90**	0.89	**28.3**	48.1
LMIL1	10	4	38.3	61.2	**0.90**	0.88	**29.2**	47.1
KILL1	10	4	32.9	59.2	**0.90**	0.95	**44.5**	65.4
KILR1	10	1	38.8	65.3	**0.90**	0.88	**24.7**	41.2
KNOC1	9	1	42.6	61.6	**0.95**	0.94	**39.5**	56.3
MEEN1	10	3	34.2	61.1	**0.89**	0.89	**20.3**	62.6
RUSH1	10	3	38.2	70.6	0.91	0.88	23.1	41.2
LADD1	17	2	43.3	62.1	**0.94**	0.79	**54.2**	75.5
BP2	18	2	40.1	65.2	**0.84**	**0.61**	**38.3**	**69.3**
STIG1	9	4	37.4	61	**0.98**	0.88	**39.2**	55.2

Table 5.2 Results of PCA on macrofossil data only showing the number of significant axes and the cumulative percentage variance explained by those axes. Given also are the results of Co-Correspondence analysis – namely pearson product moment correlations between CoCA axis 1 and axis 2 scores for plant macrofossils and cladocerans and the cumulative percentage variance in the macrofossil assemblages explained by the variation in the cladoceran community. Bold lettering indicates Co-CA axes that explain significant amounts of compositional covariance under leave-one-out cross-validation.

Three sites are examined in more detail to illustrate the nature of change that has occurred over the last 250 years. These sites were selected because of: (1) relatively good chronological control, (2) the fact that all sites seem to have gone through a series of quite profound changes in macrophyte flora, and (3) the fact that the change in cladoceran fauna in these lakes generally mirrored the changes at the other sites.

Ormesby Great Broad – ORMG2

ORMG2 was collected from the Eastern arm of the Broad in an area of higher accumulation rates than the core from collected in the main body of the Broad (ORMG1, Rose unpublished data; Davidson et al., 2008a). The macrofossil assemblage of the core clustered into three zones: pre 1860 (below 70 cm), 1860 - 1980 (70 – 20 cm) and then from 1980 to the 2007 (above 20 cm) (Figure 5.2). Zone 1, the early period of the lake, 138-70 cm (pre 1860), dating from its formation as a medieval peat digging to the mid 19th Century contained the highest diversity of submerged plant remains with several *Potamogeton* taxa including *P. friesii* agg., *P. pusillus* agg., *Potamogeton obtusifolius* Mert. & Koch, *Potamogeton crispus* L. and *P. compressus*; the latter is currently extremely rare in the UK and the Norfolk Broads. The remains of these taxa declined towards the top of this zone. *Chara* oospores type 1 and 2 were very abundant in Zone 1 and *Chara* 3 and *Nitella* oospores were present throughout this section. Remains of *Ranunculus* sect *Batrachium* seed fragments and *Nymphaeaceae* trichoschlereids increased to a maximum abundance at 98 cm and then decreased towards the top of the zone (*ca.* 1860). Remains of *Z. palustris, Typha* spp., *Alisma plantago-aquatica* L., *N. lutea* and *Callitriche* spp. seeds also occurred at low abundance within this section of the core. In Zone 2, covering the period from 1860 to around 1980, there was a decline in the number of oospores of all the *Chara* morphotypes. *Nitella* also declined, and where it was present, it occurred in very low numbers after 1860, disappearing completely from the record at the top of this zone. Similarly, the diversity of *Potamogeton* remains declined after 1860 and the abundance of *Ranunculus* sect *Batrachium* seed fragments and *Nymphaeaceae* trichoschlereids declined towards the top of the zone. In the uppermost zone 20–0 cm (1980 AD to 2007), *P. pusillus* agg. and unidentified *Potamogeton* leaf tips (most likely *P. pusillus* agg. occurred but the leaves were too small to allow a definitive identification). *Z. palustris* seed remains increased to a maximum abundance of 176 per 100 cm^3 seeds at 6 cm. The uppermost sample also contained numerous remains of an unidentified filamentous algal species.

The change in the cladoceran remains corresponded with the changes in macrophyte remains. Zone 1, pre 1860, contained a number of plant-associated or benthic species, including *Alonella nana* (Baird), *Graptoleberis testudinaria* (Fischer) and *Camptocercus rectirostris* Schoedler (not shown in the Figure), alongside the ephippia of *Ceriodaphnia* spp., *Leydigia* and *Chydorid* spp. and the sporadic occurrence in low numbers of *D. hyalina* agg. In Zone 2, post 1860 (80 to 20 cm), there was an increase in the abundance of *Daphnia hyalina* Leydig and *Daphnia magna* Strauss appeared, and was present consistently in the record thereafter. This increase in the *Daphnia* taxa was coincident with a substantial change in the plant community. Furthermore, the plant-associated chydorid taxa disappeared in Zone 2 and *Bosmina longirostris* (Müller) increased slightly in proportion to around 60%. There was a slight decline in the

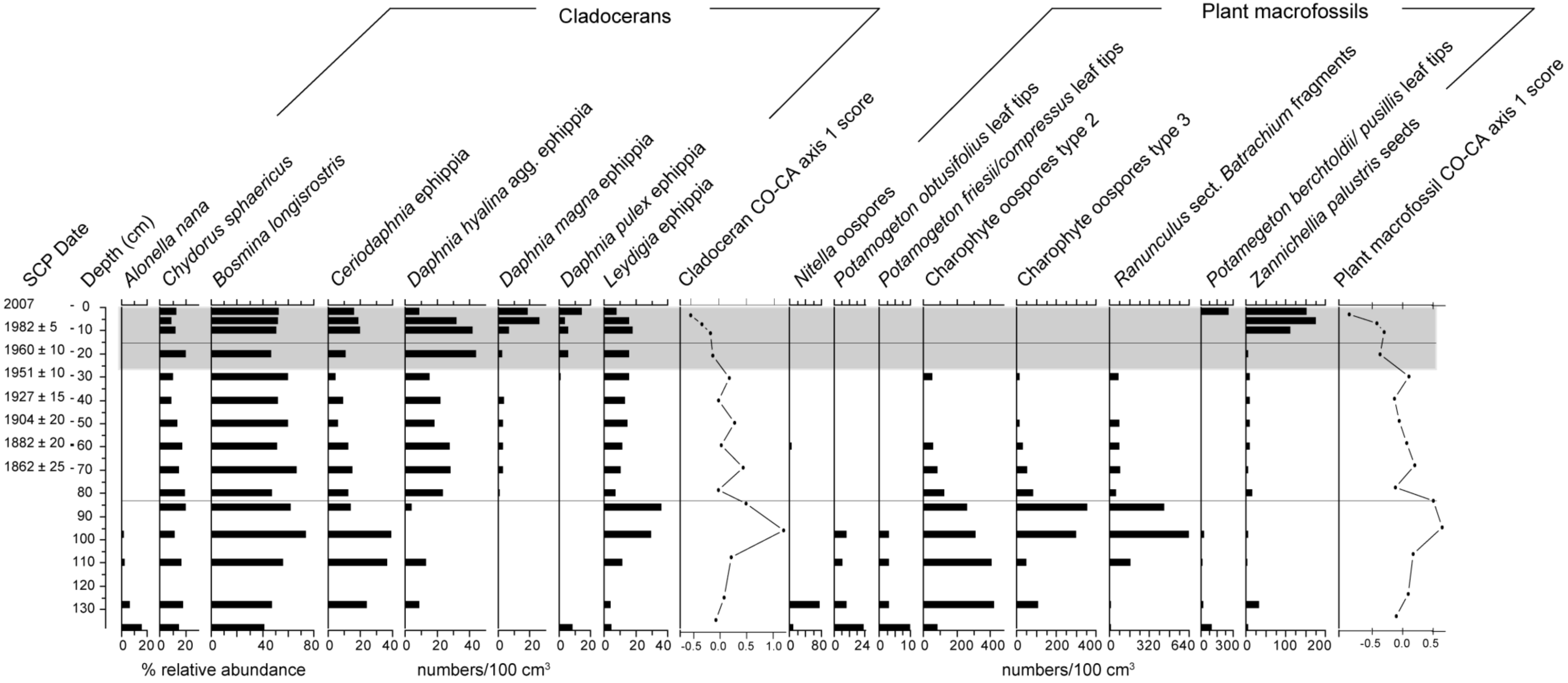

Figure 5.2 Macrofossil and cladoceran stratigraphy and Co-CA axis scores for Ormesby Great Broad – ORMG2 – The grey zone represents the period where the macrophyte flora is dominated by the PPZ community (*Potamogeton pusillus, Potamogeton pectinatus, Zanichellia palustris*) dominated.

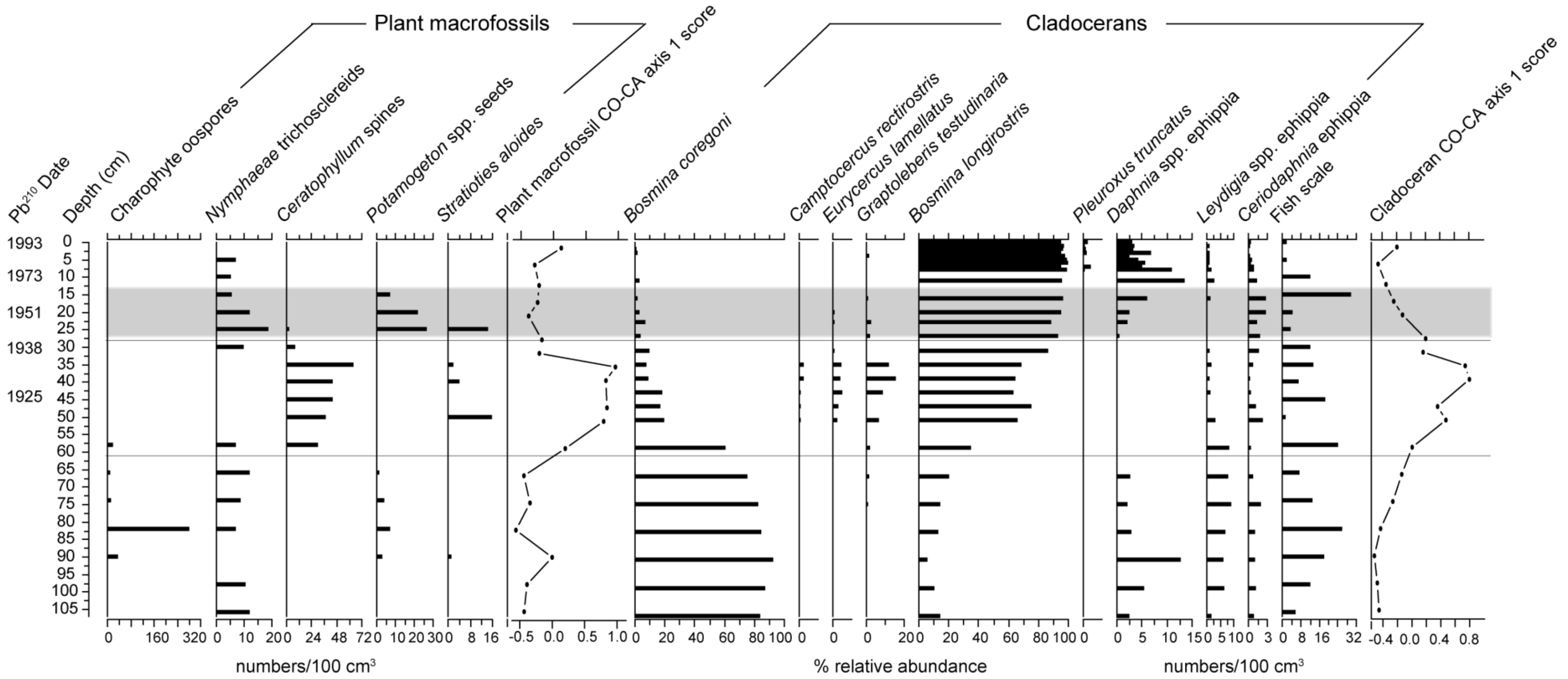

Figure 5.3 Macrofossil and cladoceran stratigraphy and Co-CA axis scores for Lake Søbygaard - The grey zone represents the period where the macrophyte flora is dominated by the PPZ community (*Potamogeton pusillus, Potamogeton pectinatus, Zanichellia palustris*) dominated.

abundance of *Ceriodaphnia* spp. and *Leydigia* spp. ephippia. In Zone 3, above 20 cm, there was a further change in assemblage with large bodied pelagic species (i.e. all the *Daphnia* groups), becoming more numerous. In addition, the large-bodied plant associated chydorid *Eurycercus lamellatus* (Müller) increased in proportion in the upper-most samples as did the smaller *Pleuroxus* taxa. Biomanipulation of the site took place in 1990 (Tomlinson et al., 2002) and some recovery in macrophyte abundance has been observed. The appearance of plant associated taxa, particularly the large bodied *E. lamellatus*, which is more abundant where fish predation is low (Davidson et al., 2010b), suggests both an increase in plant cover and a reduction in fish abundance in recent years.

Lake Søbygaard – BP2

Lake Søbygaard has undergone well-documented changes in macrophyte flora due to progressive eutrophication over more than a century (Jeppesen et al., 1998; Brodersen et al., 2001; McGowan et al., 2005). The macrofossil record indicates a shift in the dominant component of the macrophyte flora characterised by a progressive change, starting in the 19th century, from *Chara* to *Ceratophyllum* and then in the 1940/50s to *Potamogeton* taxa and eventually by the late 1960s and early 1970s submerged plants were absent (Figure 5.3).

The changes in the cladoceran record showed good accord with the changes in the macrophyte flora which were divided into three zones. In Zone 1 (below 55 cm), the pelagic *Bosmina coregoni* (Baird) was the most abundant taxa, *Daphnia* ephippia were present and ephippia of the benthic taxa *Leydigia* were abundant. The change from *Chara* to *Ceratophyllum* towards the end of the 19th century (Zone 1/2 transition at around 55 cm) in the macrofossil record coincided with a shift from *B. coregoni* to *B. longirsotris,* the disappearance of *Daphnia* ephippia and a decline of *Leydigia* ephippia abundance. In Zone 2, from around 1900 AD to the 1940s, several plant associated taxa, *E. lamellatus, C. rectirostris* and *G. testudinaria,* made a brief showing coinciding with the abundant *Ceratophyllum* remains. Zone 3, after 1940, was the last period in which submerged plants were present in the lake and coincided with a number of changes in the cladocerans: *Daphnia* ephippia reappeared, there was a slight increase in *Ceriodaphnia* ephippia, and *B. longirostris* increased its numerical dominance. As a result of inputs from the local sewage treatment works, submerged plants have largely been absent since the mid 1960s, being replaced by dense phytoplankton crops (Jeppesen et al., 1998). In the 1970s, there were a number of fish kills due to high loading of organic matter and the lake was periodically in a clear state with low phytoplankton crop (Jeppesen et al., 1996). This is perhaps recorded by the increase in fish scale numbers, but is also reflected by the increase in the *Daphnia* ephippia numbers resulting from their release from predation pressure (Figure 5.3)(Brooks & Dodson, 1965). Later, the lake became very turbid with extremely high phytoplankton biomasses and periodically high pH exceeding 10.5-11, this prevented fish spawning in a number of years leading to periodically high densities of *Daphnia* (Jeppesen et al., 1990).

Felbrigg Lake – FELB1

The historical changes in the macrophyte flora at Felbrigg Lake have been described in detail by Sayer (2010a), and they can be divided into three zones. The changes were similar to Søbygaard with two main shifts in the macrophyte flora. The first, *circa* 1850, was from a *Chara - Myriophyllum spicatum* L. - *Ceratophyllum* (zone 1) assemblage to a *Ranunculus-Ceratophyllum-Potamogeton* community (zone 2). The second alteration, in the mid-1960s, was to a flora dominated by fine leaved *Potamogeton* taxa and *Zanichellia palustris* L. (zone 3). There is, perhaps, some suggestion of a recovery in *Chara* in the 1970s (Figure 5.4). The Co-CA axis 1 scores demonstrate that the change in the cladoceran assemblage, in contrast to the diatom flora (Sayer et al., 2010a), was coincident with these main changes in the macrofossil assemblage (Figure 5.4) (Davidson et al., 2010a). The change in the cladoceran community composition was characterised by a gradual, long-term change from dominance by benthic, plant-associated taxa, such as *Acroperus harpae* Baird, *G. testudinaria* and *Chydorus sphaericus* to pelagic species, chiefly *B. longirostris* and *Daphnia* taxa (Figure 5.4). At around 1850, the change from zone 1 to zone 2, the cladoceran community shifted away from a relatively taxon rich and even assemblage (though dominated by *C. sphaericus*) and the relative abundance of *B. longirostris* and absolute abundance of *Daphnia* started to increase. There is documentary evidence of a fish kill in the 1970s and this is reflected in the higher abundances of *Daphnia* ephippia, *Chydorus sphaericus* and *Chara* oospores. The sedimentary record here show the effect of the loss of the dominant zooplanktivore in the 1970s and 80s when water clarity increased as fish predation pressure cascaded down the trophic levels, reducing the phytoplankton crop via intense grazing by *Daphnia* taxa, including *Daphnia magna* (Davidson et al., 2010a). The aquatic flora of Felbrigg Lake is currently dominated by fine-leaved *Potamogeton* taxa which are abundant until mid-summer and then suffer a precipitous crash in abundance after which the lake becomes turbid (Sayer et al., 2010b). The lake, therefore, inhabits both alternative stable states (*sensu* Scheffer et al., 1993) in a single growing season.

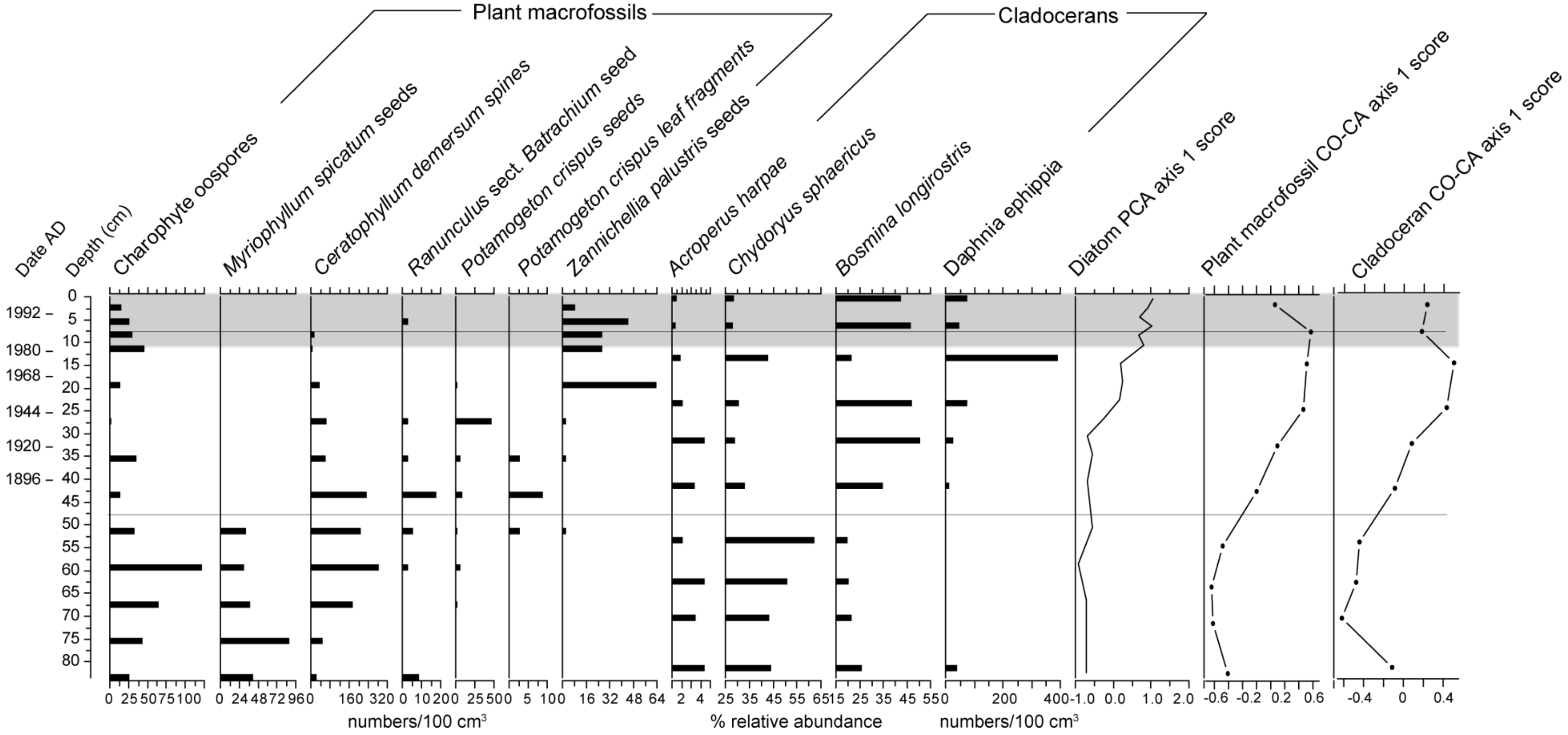

Figure 5.4 Macrofossil and cladoceran stratigraphy and Co-CA axis scores and diatom PCA axis 1 score for Felbrigg Lake - The grey zone represents the period where the macrophyte flora is dominated by the PPZ community (*Potamogeton pusillus, Potamogeton pectinatus, Zanichellia palustris*) dominated.

5.4 Discussion

The PCA axis scores from the analysis from the unconstrained analysis of the macrofossil assemblages showed that there was a large amount of variation captured in the first axis and often the other axes as well. The PCA results provide a framework with which to assess whether the main patterns in the covariance between the cladocerans and macrofossils is related to the main patterns of variance in the macrofossils. The data strongly suggest that the covariance between cladocerans and macrofossils is closely related to the main patterns of change in macrophytes through time. As stated by Schaffers et al. (2008), any fit above zero resulting from the leave-one-out cross validation in Co-CA indicates that prediction is better than could have been expected by chance. The Co-CA percentage cumulative variance explained values presented here (Table 5.2), therefore, demonstrate a profound and highly significant link between change in macrophyte and cladoceran communities in shallow lakes. This may be in part due to the fact that many cladocerans are macrophyte-associated (Whiteside, 1970), however, the close link between change in macrofossils and cladocerans was not solely the result of change in macrophyte associated taxa. The more detailed examples given, which were chosen in part as they are represent a typical sequence of eutrophication related change over time in the cladoceran fauna, illustrate that the change resulted, to a large degree, from the pelagic taxa. The data and analyses presented here clearly demonstrate that there is a very good agreement, at the centennial to decadal scale, between change in plant macrofossil and cladoceran sub-fossil assemblages, reflecting eutrophication induced change in shallow lake ecological structure.

The macrophyte flora at Ormesby Great Broad, Lake Søbygaard and Felbrigg Lake showed very similar compositional changes, albeit with different timing. These changes were from a mesotrophic flora with charophytes (both *Chara* and *Nitella*)*, M. spicatum, Ranunculus* sect. *Batrachium* and *Potamogeton* taxa (including broad-leaved taxa) followed by a decline or loss of *Chara* and ultimately ending in a community either dominated by fine-leaved *Potamogeton* taxa (Felbrigg/Ormesby Great Broad) or the complete absence of plants for several decades (Søbygaard). In the case of Ormesby Great Broad, the absence of submerged macrophytes has been countered by a post-biomanipulation recovery of fine-leaved *Potamogeton* taxa. The shift in the macrophyte flora, the loss of charophytes and the increasing dominance of taller-growing angiosperms, is a well established eutrophication-associated change demonstrated by both contemporary observation (Blindow, 1992; Duigan et al., 2007; Penning et al., 2008; Sand-Jensen et al., 2008) and by palaeolimnological techniques (Davidson et al., 2005; Salgado et al., 2010). Macrophytes are a principal tool utilised to inform the assessment of ecological condition within the WFD. Whilst the plant macrofossil record does not record all the species that were present (Rasmussen & Anderson, 2005), it does provide good information on the changes in the dominant components of the submerged flora (Davidson et al., 2005). Thus, the macrofossil records here provide a template against which change in the cladoceran record can be assessed.

While the alterations in the macrophyte flora are associated with increasing levels of nutrients (Søndergaard et al., 2010), they do not explicitly inform how ecological processes alter with the degradation of lake ecological status. The position of cladocerans at the centre of the food-web makes them sensitive to both bottom-up changes in resources and top-down shifts in predation or alteration of the food-wed (Brooks & Dodson, 1965; Vanni, 1987; Schriver et al., 1995; Jeppesen et al., 2003a). It is the combination of their central position in the food-web along with the presence of both benthic and pelagic taxa which ascribes cladocerans with such rich potential as indicators of environmental change.

The nature of the change in community composition over time in the 20 cores presented here showed some variation between sites. There were, however, some similarities with the main alteration in cladoceran community structure over the last 150 years being an increase in the proportion of pelagic taxa. In particular in the last 50 years, there has been an increase in the number of *Daphnia* ephippia in the sediments. In shallow lakes, the shift in cladoceran community composition from an assemblage with significant numbers of benthic taxa to one where pelagic taxa dominate may reflect the long-term shift from benthic to pelagic primary production (Vadeboncoeur et al., 2003; Davidson et al., 2010a).

At Felbrigg Lake the change in the cladoceran profile was coincident with the initial shift in the macrofossil record in the early 19th century, whereas a response in the diatom community was not evident until around 1940 (Figure 5.4). The chironomid assemblages of both Lake Søbygaard and Felbrigg Lakes were sensitive to the initial alteration in the ecology, in the early 19th century, shifting in concert with the macrofossil and cladoceran record (Brodersen et al., 2001; Brodersen & Quinlan, 2006; Davidson et al., 2010a). The cladoceran assemblage, however, may be better placed to elucidate the nature of change in ecosystem process associated with the decline in ecological quality of the sites. At Felbrigg Lake, the increase in the relative and absolute abundance of pelagic taxa (*Daphnia* and *B. longirostris*) in the early 19th Century very likely reflects an increase in the proportion of pelagic relative to benthic production, shown to be a broad-scale response of shallow lakes to eutrophication (Liboriussen & Jeppesen, 2003; Vadeboncoeur et al., 2003). At Felbrigg Lake, the gradual increase in the proportion of the pelagic cladoceran relative to benthic taxa continued to the mid- 20th century with a concomitant shift in the macrophyte flora until the point where there was a sharp reverse in the 1970s caused by the extirpation of the dominant zooplanktivorous fish (Davidson et al., 2010a). At this point, a shift from small-bodied pelagic taxa, (*B. longirostris*) to large-bodied *Daphnia* may have cascaded down to a recovery in the macrophyte flora as *Chara* oospores increased in number (Figure 5.4). The PCA axis scores of both the diatoms and the chironomids (Davidson et al., 2010a) did not respond to this top-down change to the system; it was uniquely the cladoceran record which recorded the top-down change in the lake.

At Ormesby Broad (ORMG2), the general patterns in the cladoceran assemblage were similar to those at Felbrigg Lake. The shift in macrophyte flora and the decline in ecological condition of the lake, in the middle of the 19th century were associated with the appearance of *Daphnia* ephippia.. The increase in *B. longirostris* was less marked than in Felbrigg Lake, perhaps as the Trinity Broads are deeper than Felbrigg Lake and would have been deeper in the 1800s AD, and so the pelagic habitat may have been substantial. *D. hyalina* and *D. magna* were present from their first appearance until the 1970s, a period associated with a decline in richness, diversity and abundance of plant macrofossils. The same changes were recorded in the second core from Ormesby Great Broad (ORMG1) as the initial shift suggested by the macrofossil record occurred with the appearance of *Daphnia* and an increase in *B. longirostris*. The temporal resolution of the samples makes the interpretation of change over the last 40 years difficult. However, the biomanipulation and restoration of the Broad that occurred in 1990 (Tomlinson et al., 2002) are reflected in the replacement of the smaller bodied *D. hyalina* with the larger *D. magna* and *Daphnia pulex* (De Geer) from the 1990s onwards. Furthermore, the recovery in macrophyte abundance (Hoare et al., unpublished data) is reflected by a small increase in the relative abundance of plant-associated taxa including *E. lamellatus* and *Pleuroxus* spp. This pattern was repeated in ORMG1 and also the cores from the other sites in the Trinity Broads, though the timing of the change appeared to vary. The uppermost lake in the chain was affected first, but the lowermost Broad in the chain (Filby Broad), whilst being the last to lose its high ecological quality flora of *Chara, Nitella, Ranunculus* sect *Batrachium* and *P. compressus*, was ultimately the most profoundly impacted by eutrophication.

In Lake Søbygaard the centennial scale benthic to pelagic shift in the cladoceran assemblage is not as clear as at Felbrigg or Ormesby Broad, at least for the beginning of the record. There was a substantial pelagic fauna historically in the form of the relatively large *B. coregoni* and *Daphnia* ephippia. The initial shift in the macrophyte flora in the late 19th century (around 60 cm) was associated with a shift from *B. coregoni* to *B. longirostris* and a reduction of *Daphnia* ephippia. The shifts in the proportion of pelagic taxa are more associated with top-down changes in predation pressure (Jeppesen et al., 1996; Davidson et al., 2010b) suggesting that the change here may have resulted from top-down, rather than bottom up pressures. The shifts observed here were more likely due to an increase in zooplanktivorous fish predation pressure as the body size of the dominant taxa reduced (Brooks & Dodson, 1965) or a reduction in the size of the pelagic habitat due to perhaps a gradual change in lake level. The change to a *Potamogeton* flora around 1940 is, however, clearly associated with a shift from benthic to pelagic taxa as *Daphnia* ephippia, in particular, increased in abundance.

In all three cores examined in detail, and in many of the others where only summary data were presented, the macrophyte community dominated by fine-leaved *Potamogeton* taxa (*P. pusillus*, *P. pectinatus* & *Z. palustris*) was consistently the last community present before the complete loss of plants. This community has been identified as susceptible to a mid-summer (in temperate regions) precipitous crash in abundance, meaning the lake has clear water and abundant macrophytes for half the growing season and few plants and turbid water for the second half of the growing season (Sayer et al., 2010b). This plant community is associated in all three cores with abundant *Daphnia* ephippia (see grey zone in Figure 5.2, 3 & 4). The existence of both stable states (*sensu* Scheffer et al. 1993) of clear water with abundant macrophyte cover and turbid water with macrophytes sparse or absent, within a single growing season has been observed at other sites (Bayley et al., 2007). This 'flipping' community is associated with relatively abundant *Daphnia* populations, purported to engender stability and buffer shallow lakes against a turbid, phytoplankton dominated state. An increase in *Daphnia* abundance at intermediate levels of nutrient enrichment has been observed in spatial studies covering a long trophic gradient (Jeppesen et al., 2003a), which fits well with the data presented here. Many restoration strategies in shallow lakes, such as biomanipulation (Søndergaard et al., 2007), aim, in part, to promote abundant grazing zooplankton. The data here suggest that abundant *Daphnia* grazing may not be a long-term solution to the restoration of shallow lake ecological quality. Whilst they can, via the trophic cascade (Carpenter et al., 1985), promote clearer water and encourage the growth of macrophytes, when viewed on a long-term, decadal scale, the data presented here suggests that they are associated with a macrophyte community which may be neither resistant nor resilient to phytoplankton becoming the dominant form of primary production. Indeed, this community of fine leaved *Potamogeton* taxa and abundant *Daphnia* may represent an intermediary between clear water and turbid conditions.

The cladoceran data, combined with the macrofossil data, demonstrate that on a centennial scale the control of phytoplankton biomass in shallow lakes has shifted from being predominantly bottom-up to top-down. Furthermore, the increasing proportion of pelagic production (Vadeboncoeur et al., 2003) appears to be reflected by a gradual shift from benthic to pelagic cladoceran taxa. Thus, pelagic cladocerans become increasingly important in the maintenance of the water clarity necessary to support a healthy macrophyte flora. The increased importance of grazing by zooplankton for the maintenance of water clarity may correlate with a decline in the resistance and resilience of a lake to stochastic forces, and could perhaps be a useful metric of ecological condition (Jeppesen et al., 2011). Our study demonstrates the power of sub-fossil Cladocera remains for tracking long-term change in lake ecological structure and function but the question of how effective they are at a finer resolution remains. There are, however, a number of investigations of laminated sediments (Nykänen et al., 2009; Nykänen et al., 2010) and on cores with higher temporal resolutions (Manca et al.,

2007) which suggest that the use of cladocerans as indicators of the ecological condition of a lake at a higher temporal resolution is possible.

A key methodological point to make here is that the close accord between macrofossils and cladocerans relies heavily on the analysis of ephippia of the pelagic taxa which are not represented by chitinous remains. The standard methods (Korhola & Rautio, 2001) do not always include analysis of ephippia, despite evidence that their inclusion provides information on the keystone taxa of *Daphnia* (Jeppesen et al., 2003b). The data presented here demonstrate that in the absence of ephippia analysis, the benthic to pelagic shift in cladoceran taxa would not be so unequivocally evident.

5.5 Conclusion

Cladocerans show good agreement with macrophytes in their response to ecological change and importantly provide additional information on alterations in ecological structure and function. Their position in the foodweb and the combination of benthic and pelagic taxa make this group particularly sensitive to ecosystem change. Indeed, our data suggest that Cladocera may be the most sensitive single indicator to detect eutrophication driven change in shallow lakes. This may be viewed as a double-edged sword as isolating the cause of change to such a sensitive group can be problematic, hence multi-indicator palaeolimnology is still recommended. Where comparison was possible between several fossil groups at Felbrigg Lake, cladocerans were the first to respond and the changes were the easiest to interpret. The change in the assemblage composition of the sediment cores studied here, both the summary data and those sites examined in more detail, was characterised by an increase in pelagic relative to benthic taxa associated with eutrophication. Analysis of sub-fossil Cladocera may have the potential to act as an early warning system for a significant decline in ecological condition. These properties combine to make the omission of zooplankton and cladocerans from the WFD assessment of ecological condition of lakes such a surprising and unwise decision.

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6. Climate change, restoration and ecological status in lakes: a Bayesian network modelling approach

***Responsible: S. Jannicke Moe*[1] *Contributors: Tuomo Saloranta*[2]*, Olli Malve*[3]*, Niina Kotamäki*[3]*, Anne Lyche Solheim*[1]**

[1] Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, NO-0349 Oslo, Norway

[2] Norwegian Water Resources and Energy Directorate (NVE), P.O. Box 5091 Majorstua, NO-0301 Oslo, Norway

[3] Finnish Environment Institute (SYKE), P.O. BOX 140, FI-00251 Helsinki, Finland

6.1 Introduction

The main objective of work package 5.2 was to address the impact of catchment management and climate change on pressures and ecological status in lakes. Climate change may impact ecological status directly and indirectly in multiple ways (Moe et al. 2010): e.g. by increasing physico-chemical pressures, by impacting the ecological baseline, by reinforcing the ecological response to a pressure gradient, or by reducing the ecological ability to recover. In this modelling study, we have focused on the combined impacts of restoration and climate change on ecological status based on phytoplankton (chlorophyll *a)*. We considered only climate impacts directly on lake processes and leave out potential climate impacts on river basin processes (such as water discharge and nutrient transport). In addition, we modelled the effect of lake restoration in terms of reduced P loading. Our study considered altogether 9 scenarios: 3 levels of restoration (no change; -20% P loading; -40% P loading) combined with 3 levels of climate change (no change; +2 °C air temperature; +4 °C air temperature). We explored the impacts of these scenarios on the lake status class according to a biological quality element (phytoplankton) as well as to supporting physico-chemical elements (total P and total N). Since ecological classification of lakes is dependent on the lake type, we have selected two common lake types of Northern Europe as an example (L-N2a - low altitude; L-N5 - high altitude).

6.2 Modelling approach

For this study we used a Bayesian network (BN) modelling approach. One of proposed the common approaches for all water categories (WPs 5.1-5.3) was development of conceptual models representing driver-pressure-impact-response-recovery chains. A Bayesian network can be developed as a conceptual model (Figure 6.1), but can also be parameterised and used as a simulation model. In brief, each variable (e.g. Total P, Chl-a) is illustrated by a node, which represents a discrete probability distribution (Figure 6.2). The cause-effect links are illustrated by arrows, which represent contingent probability tables (CPTs, Table 6.1). This modelling approach has many benefits, especially in relation to environmental risk assessment and management

(Moe 2010): it can easily combine data or other information from different sources; it can explicitly model uncertainties (as probability distributions); and it can predict the probability of different outcomes of interest (such as different status classes).

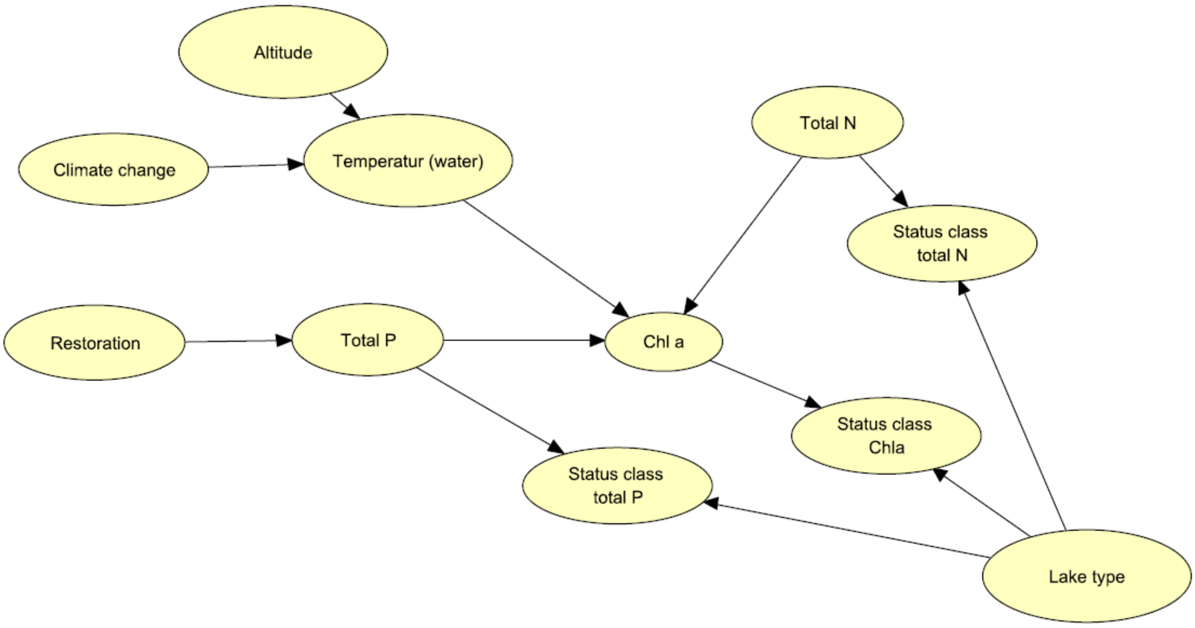
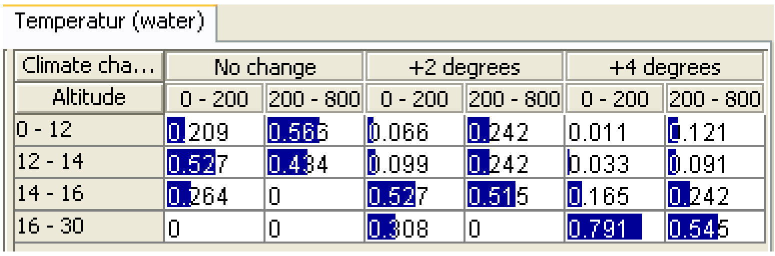


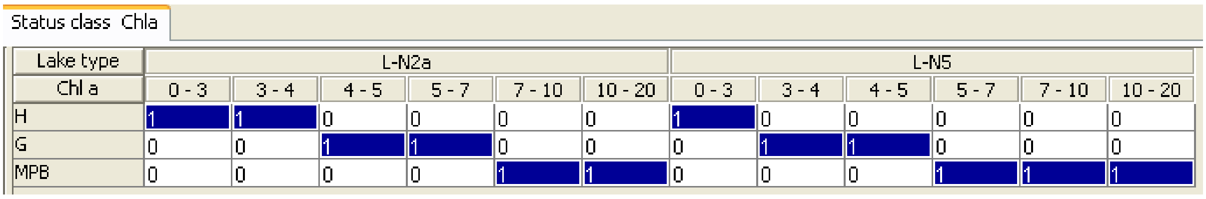
Figure 6.1 Schematic representation of the Baysian network for lakes

(A)


Temperatur (water)

Climate cha...	No change		+2 degrees		+4 degrees	
Altitude	0 - 200	200 - 800	0 - 200	200 - 800	0 - 200	200 - 800
0 - 12	0.209	0.566	0.066	0.242	0.011	0.121
12 - 14	0.527	0.434	0.099	0.242	0.033	0.091
14 - 16	0.264	0	0.527	0.515	0.165	0.242
16 - 30	0	0	0.308	0	0.791	0.545

(B)


Status class Chla

Lake type	L-N2a						L-N5					
Chl a	0 - 3	3 - 4	4 - 5	5 - 7	7 - 10	10 - 20	0 - 3	3 - 4	4 - 5	5 - 7	7 - 10	10 - 20
H	1	1	0	0	0	0	1	0	0	0	0	0
G	0	0	1	1	0	0	0	1	1	0	0	0
MPB	0	0	0	0	1	1	0	0	0	1	1	1

Table 6.1 Examples of conditional probability tables (CPT). (A) The conditional probability distribution of the node "Temperature (water)" (°C) depends the levels of both "Climate change" and "Altitude" (m). (B) The conditional probability distribution of "Status class Chla" (H=High; G=Good; MPB=moderate, poor or bad) depends on both Lake type and Chl a (µg/l).

6.3 Model construction and simulation

The construction of this Bayesian network model integrated two different lake models and data sources, from NIVA and SYKE respectively. The first part of the BN (effect of restoration and climate change on total P and temperature in lakes) was based on the "NIVA model", while the second part (effects of total P and temperature on Chl-a) was based on the "SYKE model". The NIVA model used the model code MyLake (Saloranta & Anderson 2007) to simulate climate and restoration impacts for a large number of Norwegian lakes, of which 124 lakes (types L-N2a and L-N5) were selected for this analysis.

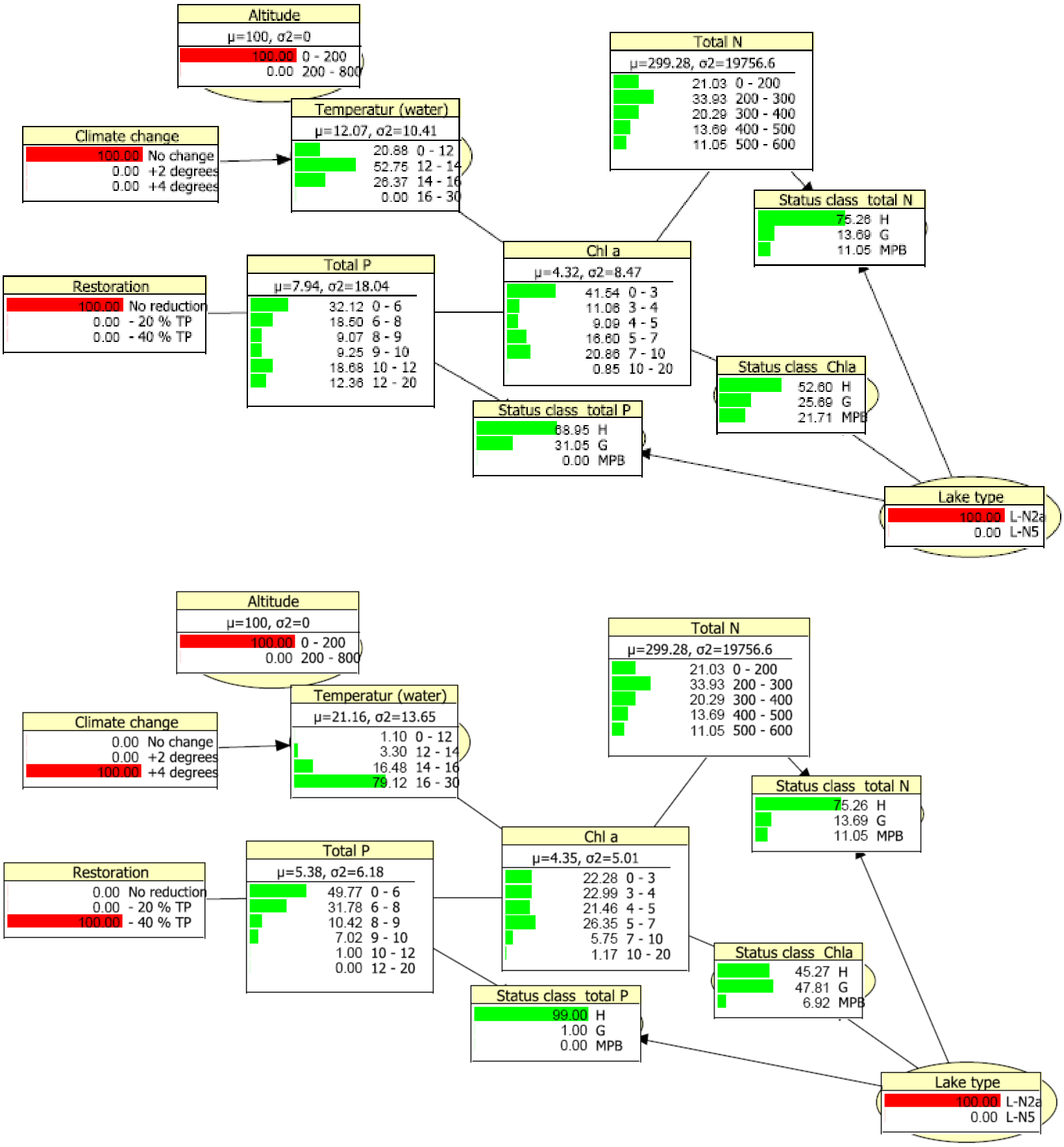


Figure 6.2 In the BN model each variable (e.g. Total P, Chl-a) is illustrated by a node, which represents a discrete probability distribution. The cause-effect links are illustrated by arrows, which represent contingent probability tables (see Table 6.1)

The SYKE model is a hierarchical model that simulates chlorophyll-a from nutrients and temperature observations, based on lake-type-specific estimations. This model has applied data from WISER WP3.1 (Lakes phytoplankton) from all of Europe, of which 337 lakes (types L-N2a and L-N5) were used for this analysis. Only lakes with complete set of observations were used, which means that the dataset is not representative for the region in general (high-status lakes are overrepresented). For both data sources, average values for summer months were used in this study. Discretisation of continuous variables was based on (1) official class boundaries for TN, TP and chl-a (Finland), and (2) regression tree analysis for identifying threshold responses in the variables. The entries of the conditional probability tables (Table 6.1) were calculated as the proportion of data points falling into each combination of the parent node levels.

The BN model simulations were run by selecting a scenario and a lake type (marked red in Figure 6.2), and recording the resulting status classes according to TN, TP and chl-a. The model also provides expected value (□) of e.g. chl-a, but with this modelling approach the probability distribution is more interesting than a point estimate.

6.4 Results

The predicted levels of nutrients and chl-a in this model exercise depends on many assumptions, of which not all can be justified. The most relevant result is therefore not the absolute probabilities, but the changes in probabilities (percentage points) across climate and restoration scenarios (Figure 6.3). TN was not affected by restoration or climate scenarios in this model, and remained as shown in Figure 6.2 across all scenarios. TP status class responded to restoration (reduction of P loading) by increased probability of High status. The highest restoration level resulted in 30 percentage point (pp) increase in probability of High status for lake types L-N2a, and 32 pp increase for L-N5. TP was not affected by the climate scenarios, in accordance with the model settings. Chl-a status class also responded to reduction of P loading by increase in probability of High status, although to a lesser degree than for TP (L-N2a: 10-12 pp increase; L-N5: 8-11 pp increase). At the same time, the risk of less-than-good status was reduced by 14-19 pp. Chl-a was also impacted by climate change: +4 degrees resulted in an 18-20 pp reduction of High status probability for L-N2a, and 22-23 pp reduction for L-N5. The increase in risk of less-than-good status, however, was only 1-7 pp in this model.

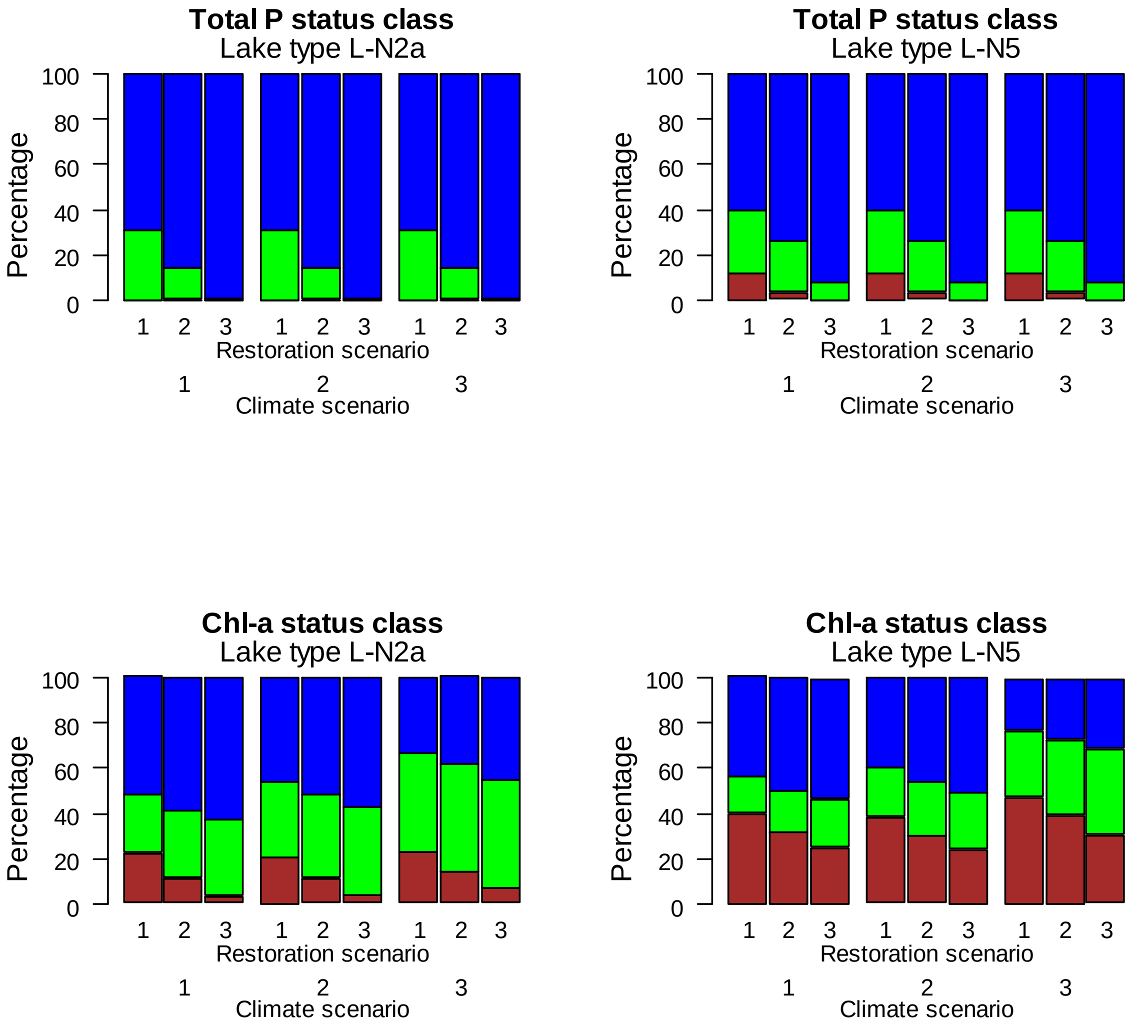


Figure 6.3 An illustration of the changes in probabilities (percentage points) across climate and restoration scenarios from the BN model

6.5 Concluding remarks

This study has focused on high status of lakes, because the source dataset was dominated by good- and high-status lakes. According to the BN model, a climate change of +2 °C would almost counteract the benefit from 20% P loading reduction, while +4 °C would more than outweigh the benefits from 40% P loading reduction. The risk of not meeting good ecological status was less affected in this study. Although "good ecological status" is the main WFD management goal, preservation of high status is also a WFD requirement.

As mentioned, this modelling exercise considers only climate change impacts on lake processes, notably phytoplankton growth rate. In reality one can expect additional impacts on river basins such as increased P loading. This study has therefore only explored one the many potential climate change impacts on ecological status of lakes.

The Bayesian network modelling approach presented here is very general, and can easily be extended to include more lake types and other biological quality elements, as well as different scenarios. Based on the work presented here, the BN methodology has also been adopted by the ongoing EU project REFRESH, as a common approach for linking ecological responses to physico-chemical pressures for all water categories and all biological groups.

6.6 References

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