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Deliverable D6.4-2: Analysis of cause-effect-recovery chains for lakes recovering from eutrophication

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Analysis of cause-effect-recovery chains for lakes recovering from eutrophication

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CEH-Report

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Content

Non-technical summary

In this review, we have combined a meta-analysis of over 743 lake-equivalent case studies from 364 peer reviewed publications. In addition, peer-reviewed multi-lake meta-analyses are combined with site-specific data from lake recovery case studies to examine the responses of freshwater lakes to eutrophication management in terms of their ecological structure and function. This analysis was conducted using the Driver, Pressure, State, Impact, Response (DPSIR) framework modified to include the recovery phase (Figure 1).

The main drivers of eutrophication identified in the literature included population growth, industrialisation, agricultural intensification, tourism and recreation. These drivers were associated with a wide range of primary and secondary pressures. The key primary eutrophication pressures were related to agricultural sources (e.g. animal waste, fertiliser applications, soil erosion), and discharges from industry (e.g. aquaculture, paper mills, food manufacturing) and the infrastructure associated with areas of high population density (e.g. waste water treatment works, housing, roads). Acidification and fishery management were the most commonly reported secondary pressures (29% and 20%, respectively), followed by industrial pollution (16%), climate change (13%), pesticide application (9%), salinisation (7%), ingress of invasive species (7%), alkalisation (4%), water level fluctuation (2%), boating (2%) and sediment dredging (2%). About 83% of the published case studies reported on the effects of eutrophication alone, whereas 15% documented responses to multiple pressures.

A range of approaches to eutrophication management were documented. That most commonly reported was a reduction of external nutrient loading (88% of returned publications). In contrast, in-lake management with or without external loading reduction, received relatively little attention (19% and 6% of returned publications, respectively). Of these, fish biomanipulation (41% of reported in-lake management cases) was the most commonly reported measure, followed by sediment phosphorus (P) capping (16%), drawdown (12%), sediment dredging (13%), flushing (6%), aeration/circulation (5%) and waterfowl/macrophyte biomanipulation (2%).

Responses to eutrophication management, in terms of changes in ecological structure, were assessed for phytoplankton (44% of case studies reporting ecological recovery), macrophytes (15%), zooplankton (14%), macroinvertebrates (13%), fish (12%), waterfowl (2%) and bacterioplankton (<1%). None of the studies included in the literature review reported specifically on the ecological responses of a lake in terms of progress towards Water Framework Directive (WFD) Biological Quality Element (BQE) targets.

The response of in-lake P concentration (the main state change indicator) following catchment nutrient loading reductions was seasonal. Summer concentrations were usually maintained at levels close to pre-management concentrations by P cycling between the sediments and the water column (especially in shallow lakes). In contrast, winter, spring and autumn concentrations tended to fall. There was strong evidence that ecological recovery was being delayed by sediment P processes, especially during summer months. Interactions between seasonally distinct P recovery trajectories and organism growth/colonisation traits (e.g. macrophyte production/colonisation strongest in spring compared to summer during transient period; phytoplankton response weakest in summer compared to winter/spring) were apparent and should be taken into consideration when assessing ecological recovery against WFD targets. The time span of the transient phase for total P (TP) ranged from about 5 years to more than 25 years, whereas that for total nitrogen (TN) ranged from less than 5 years to greater than 10 years. Whole-lake manipulation studies have been used to assess the effectiveness of in-lake management techniques (e.g. biomanipulation, sediment dredging, sediment P capping *etc*.) in reducing the time span of the transient period by controlling sediment P processes. These have met with mixed levels of success.

A range of biological management practices (especially fishery management) and extreme weather events were identified as key factors that were responsible for slowing down the recovery process. In contrast, the loss of nitrate nitrogen through denitrification and biological uptake, leading to a switch from P- to N-limitation of primary production in summer/autumn, was identified as a potential recovery enhancing process. Alterations in nutrient concentrations and biogeochemical cycling at the sediment-water interface, following nutrient management, can influence the magnitude and timing of nutrient delivery to downstream ecosystems. This phenomenon is likely to be highly sensitive to changes in local weather conditions associated with climate change. The North Atlantic Oscillation (NAO) was identified as an important driver of weather conditions that are important for maintaining ecological structure in lakes (i.e. precipitation, wind, temperature). Some case studies showed that the NAO could confound lake recovery when external loads were reduced by generating increased run-off and, consequently, higher nutrient inputs from external sources. Enhanced wind-induced mixing, which leads to habitat disturbance, may also be an important factor.

Our meta-analysis identified “impacted” and “recovered” biological communities following eutrophication management. The responses of WFD BQEs (i.e. phytoplankton, fish, benthic macroinvertebrates, macrophytes) were combined with other important groups of organism (i.e. bacterioplankton, zooplankton, waterfowl) to assess the effects of reductions in external pressures on the ecological recovery of lake ecosystems. It was found that alterations in the biological structure of these systems could, potentially, affect ecosystem function and the provision of ecosystem services.

Responses of the bacterioplankton community to eutrophication management are unclear as they have received little attention in the literature. However, the few studies that are available indicated a decrease in bacterial abundance and an increase in their relative contribution to energy transfer. In one particular case study, these changes were found to be associated, mainly, with an increase in *Daphnia* abundance and associated grazing pressure. It should be noted, however, that this apparently lake-specific response may not be useful for characterising lake responses more generally. No changes in production were reported, although it is hypothesised that changes in the quality and quantity of dissolved organic carbon (DOC) associated with eutrophication management may affect community composition and function.

The responses in the phytoplankton community were characterised by strong seasonal changes in community composition and biomass. In general, relative biomass of cyanobacteria decreased, whereas that of diatoms, cryptophytes and chrysophytes increased. The decrease in phytoplankton biomass was typically strongest in spring, winter and autumn in comparison with summer, probably as a result of sediment P processes maintaining TP concentrations at or near to pre-management levels in summer. The responses of heterocystous and non-heterocystous cyanobacteria varied, with non-heterocystous cyanobacteria decreasing in summer and autumn, and heterocystous cyanobacteria increasing in summer and decreasing in spring. A general reduction in diatom biomass was reported throughout the year, although the reduction was often strongest in spring. This spring reduction was associated with both silica (Si) and P limitation. Although an increase in the chlorophyll *a*:TP concentration ratio can occur as a result of responses to changes in the structure and function of higher trophic levels within a system, this ratio was also found to increase following eutrophication management. Phytoplankton responses were generally associated with reductions in the availability and seasonality of nutrients, resulting in shifts in the competitive advantages of specific phytoplankton taxa. For example, a reported increase in dinophytes in deeper lakes may have been the result of these organisms being capable of migrating vertically through the water column to access water with high TP concentrations in the hypolimnion. Factors confounding the phytoplankton responses included sediment P, N and Si processes, climate change effects (e.g. temperature, precipitation, wind), and fishery management leading to trophic cascades. Recovery times were consistent with estimates of the transient period described above.

The responses of the macrophyte community following eutrophication management were difficult to determine due to a lack of comprehensive and long-term lake recovery data. However, the most commonly recorded responses have been summarised using long-term data from oligotrophication case studies. These include an increase in colonisation depth, species richness (including relative characean abundance), number of nutrient intolerant species and species distribution. Full recovery of species composition was rarely recorded, potentially as a result of physical barriers to distribution and/or the loss of nutrient intolerant seed banks in cases where eutrophic conditions had been prevalent for many years. Increased water clarity was the most commonly reported driver of macrophyte community responses, although reductions in TN concentrations were also shown to be an important driver in some cases. At a structural level, macrophyte colonisation responses were observed relatively quickly (less than 5 years) after reductions in TP concentrations. However, at a community composition level, recovery timescales for macrophytes were reported to be greater than the transient period estimates outlined above. Factors confounding the responses of macrophytes included grazing by benthivorous fish and birds, distribution barriers and habitat disturbance due to extreme weather events.

The responses of the zooplankton community to reductions in TP inputs were characterised by increases in the relative abundance of *Daphnia* and other cladocera. This was coupled with an increase in the biomass ratio of zooplankton to phytoplankton. A decrease in zooplankton biomass and an increase in zooplankton species diversity (especially cladocerans) were also reported. These changes were associated with reduced TP concentrations, more shelter from predation associated with increased macrophyte cover, and an improvement in the food quality of the phytoplankton community. The main pressures confounding zooplankton responses included sediment P processes and fishery management. Rapid recovery (1-3 years) was demonstrated in one case study where multiple management techniques (i.e. diversion of nutrient inputs, biomanipulation and sediment dredging) were applied simultaneously.

The responses of macroinvertebrate communities to eutrophication management were characterised by an overall reduction in abundance, an increase in species richness and diversity, colonisation of deeper water benthos, and an increase in the chironomid:oligochaeate ratio. These positive responses were associated with a decrease in TP concentrations, a reduction in the delivery of organic detritus to the sediment, an improvement in dissolved oxygen concentrations in the sediments and release from predation pressure. The main pressures confounding recovery of the macroinvertebrate communities were sediment P processes and biomanipulation leading to high organic load to the sediments. Spatially distinct recovery trajectories were reported where shallow, well aerated, zones responded more rapidly than deeper, less aerated, zones. Recovery times were consistent with estimates of the transient period described above.

The responses of fish communities to eutrophication management were generally characterised by a decrease in biomass and a relative increase in piscivorous and percid fish species (especially in shallow lakes). A unimodal response curve of fish species richness to TP concentrations was reported for Danish lakes, with peak richness occurring at 10-400 $\mu g\ l^{-1}$of TP. Long-term studies of eutrophication-oligotrophication have highlighted the following pressure-response pattern in relation to the relative abundance of fish species in response to decreasing TP concentrations: cyprinids→percids→coregonids→salmonids. Responses (typically less than 10 years) in the fish community were commonly observed following reduction of TP concentrations. These responses were mainly associated with the strengthening of the spring clear-water phase and the provision of better habitat for piscivorous fish. Responses in the fish community did not appear to be strongly confounded by sediment P processes. However, fish stocking and removal practices were reported to confound community responses, especially where these were operated at an industrial scale.

The responses of the waterfowl community to eutrophication management were confounded by interactions between macrophytes and macroinvertebrates, and between herbivorous and benthivorous waterfowl. Few studies were available within which these interactions could be clearly disentangled. An increase in macrophyte cover and community composition (e.g. to favour *Chara* sp., *Elodea* spp., *Myriophyllum* spp. and *Potamogeton* spp.) was associated with an increase in herbivorous waterfowl (e.g. goldeneye, pochard and coot). However, herbivorous waterfowl were also reported to negatively impact on macrophyte colonisation and community composition. An increase in benthivorous waterfowl was also found to occur as a result of increased macroinvertebrate abundance. Response times for waterfowl following changes in macrophyte extent were reported to range from rapid (i.e. <1 year) to non-existent. The main factor reported to confound waterfowl responses was competition for macrophytes associated with benthivorous fish species.

The results from over 40 years (1968-present) of ecological monitoring at Loch Leven (Scotland, UK) were used to identify feedbacks between the components of the DPSIR chain within this lake on the basis of those identified more generally within the literature (Figure 2). These feedback mechanisms demonstrate the complexity of lake eutrophication management and highlight the potential “knock-on” effects of controlling single pressures within a multi-pressure system.

Keywords: freshwater, lake, eutrophication, recovery, end-point, structure, function, services, resilience

Preface

The WFD aims to remove the traditional dichotomous approach to environmental management by combining catchment scale understanding across a range of aquatic ecosystems to improve ecological status within specific river basins. This requires an assessment of the ecological responses and interactions across lakes, rivers and estuaries related to eutrophication, hydromorphological change, and acidification. WP 6.4-2 '*Comparison of cause-effect and recovery chains between water bodies*' will produce a series of literature reviews designed to provide comparative assessments of recovery of the three ecosystem types following the management of these three pressures. This document forms part of this common analysis and focuses on the recovery of lakes from eutrophication.

1. Introduction

Global freshwater resources sustain human life through the provision of clean drinking water, irrigation for agriculture and food provision. In addition to these life sustaining services, freshwater lakes perform a wide range of other “ecosystem services” (ES) that are of importance across local, national and global scales. ES are the benefits that people obtain from the natural environment (MEA, 2005). They include provisioning services (e.g. delivery of food, water, pharmaceuticals, energy), regulating services (e.g. carbon sequestration, climate regulation, water purification, disease control), supporting services (e.g. nutrient cycling, seed dispersal, primary production) and cultural services (e.g. providing inspiration, facilitating recreation, enabling scientific discovery). These services are produced by complex processes and interactions that are intimately linked in such a way that the exploitation of one ecosystem service can cause knock-on effects on many others (Heal et al., 2001; Pereira et al., 2005; Reid et al., 2005). The ES provisioning capacity of lakes has been greatly reduced following industrial and agricultural development along with population growth and is expected to be further impacted by climate change and a wide range of other drivers (Figure 1).

Eutrophication is the breakdown of resilience mechanisms leading to structural and functional deterioration of aquatic ecosystems as a result of nutrient, mainly P and N, enrichment (Carpenter, 1999). Eutrophication is generally accepted to be one of the most important anthropogenic drivers of lake ecosystems across the EU (Withers & Haygarth, 2007) and the rest of the world (Bennett at al., 2001; Schindler, 2006) and research into lake management has received significant attention at the global scale (Jeppesen et al., 2003). Our understanding of pressure-state relationships that occur during environmental degradation (i.e. between nutrient enrichment and ecological structure) is advanced in comparison with our knowledge of pressure reduction-state relationships that develop during recovery. Research leading to our understanding of the degradation phase has been conducted mainly over an intensive period of research spanning about 45 years. This research has included multi-lake comparisons, whole lake experiments, paleolimnological reconstructions and controlled manipulations in the laboratory and has been benefitted greatly from the maintenance of funding for long-term environmental monitoring across a range of study sites.

Our understanding of the sources of nutrients in the catchment leading to eutrophication in lakes has been successfully used to underpin large scale management strategies. For example, P-stripping measures are now common in waste water treatment works across Europe leading to a marked reduction in catchment P loading to eutrophic lakes in developed countries (mainly through improvements in sewage treatment and agricultural practices), however, fertiliser applications and P loading in developing countries continues to rise (Withers & Haygarth, 2007). Ecological responses following external nutrient load reduction are less well understood with “end-point” recovery commonly reported to take decades post management (Søndergaard, 2007). There is, therefore, a need to review the literature to (1) describe the common structural and functional composition of lake ecosystems under impacted, recovering and end-point recovery conditions and (2) identify those processes responsible for regulating ecosystem resilience to recovery.

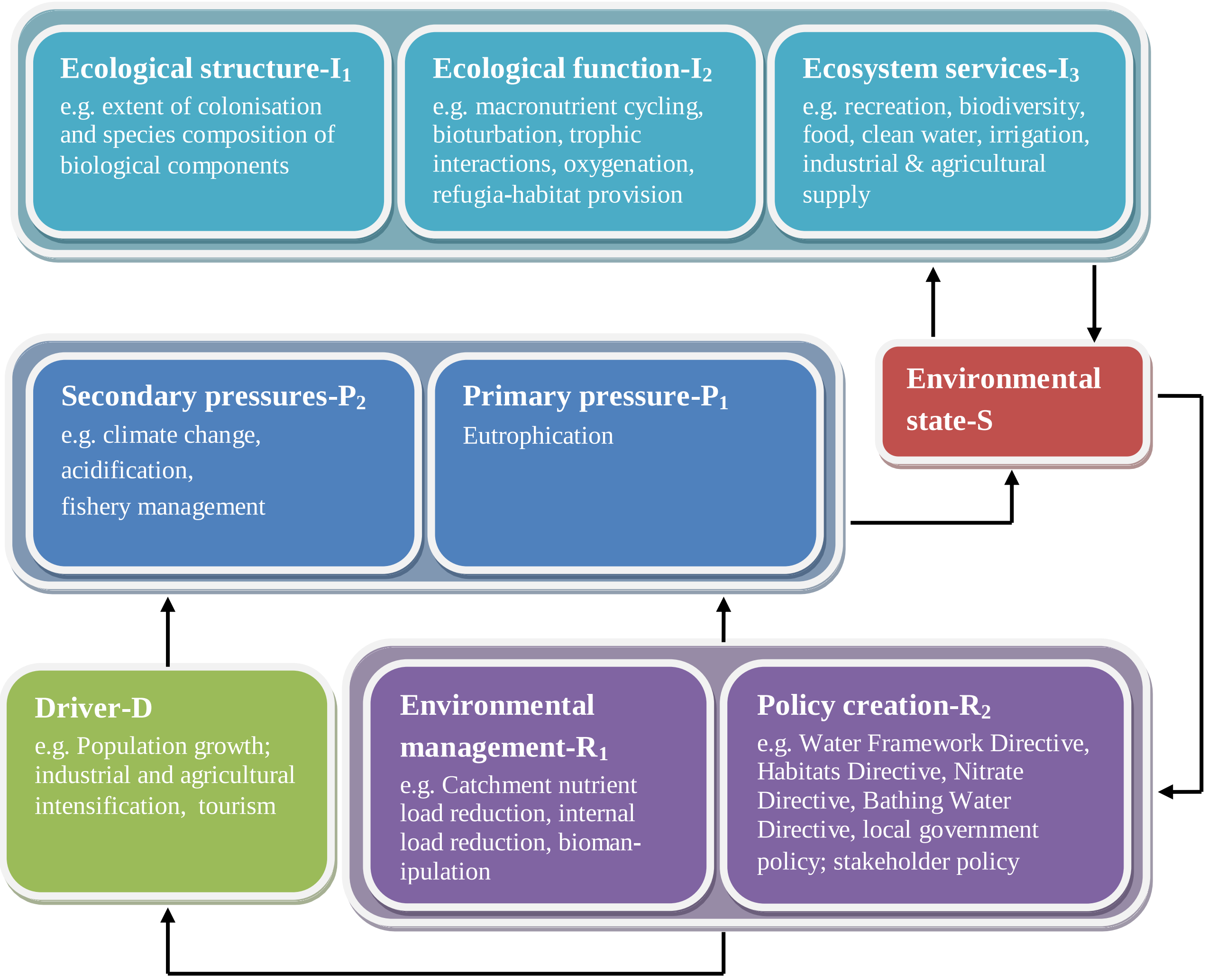


Figure 1. Conceptual diagram of the Driver, Pressure, State, Impact and Response (DPSIR) framework as it applies to the management of eutrophic lakes.

1.1. Lake eutrophication management and the DPSIR framework

The Water Framework Directive (WFD) has challenged EU member states to implement management measures to safeguard or improve the ecological quality of all water bodies and attain “good or better ecological status” by 2015. Water bodies within defined River Basin Districts must be partitioned into categories that include groundwater, inland surface waters, estuarine waters, coastal waters, artificial waters and heavily modified waters, and then subdivided into types based on geographical and morphological traits. Finally, the water bodies within each category must be classified in relation to pressures and associated impacts and compared to reference conditions associated with unimpacted waterbodies (e.g. Solheim, 2005). These guidelines are designed for the implementation of integrated management at the catchment scale, a process that requires a clear understanding of cause-effect-recovery chains and interactions across ecosystems, if it is to be successful.

A wide range of indicators have been developed, or are under development, with which the responses of WFD Biological Quality Elements (BQEs; i.e. phytoplankton, microphytobenthos, macrophytes, fish and macroinvertebrates) to environmental pressures, and the management of those pressures, may be quantified. These indicators are distributed unevenly across geographic region, water body category and type, and in some cases, habitat type (e.g. littoral and profundal macroinvertebrate communities in lakes). To standardise the assessment of indicators across key pressures, and across ecosystem categories and types, the European Environment Agency (EEA) has adopted an extended version of the Pressure, State and Response (PSR) framework developed by the OECD. This extended framework can be used to comparatively assess the complex feedback mechanisms that exist between societal development and its impact on the state of the environment through quantitative and qualitative description of the following:

- *Driving forces*: changes associated with socioeconomic development that result in pressure on the environment
- *Pressures*: measurable changes in environmental processes (e.g. fish stocking and fertilizer application) that may negatively impact on the state of the environment
- *States*: measurable changes in the environment (e.g. P concentration increase, temperature increase) that are expected to impact on the ecological state of a waterbody
- *Impacts*: measurable alterations to ecological structure (e.g. macrophyte community composition) leading to the degradation of functional capacity (e.g. *refugia* habitat-provision), indicating the necessity for a management response
- *Responses*: actions taken by stakeholders to mitigate the impact on the environment through the management of pressures leading to an improvement in the state of the environment.

The DPSIR framework has recently been developed for use in marine and estuarine systems to quantify pressure-impact chains in relation to the likelihood of failing WFD criteria at the regional scale (Borja et al., 2006). This work has helped to target management responses in line with WFD guidelines within the specific waterbody categories for which the relative influence of drivers and pressures on the state of the environment, and the associated environmental impact, was largely unknown.

Our understanding of the components of the DPSIR framework for eutrophication in lakes is relatively well advanced (e.g. drivers and pressures summarised in Table 1) in comparison to other waterbody categories and pressures. However, there is still a need to synthesise existing evidence in the peer reviewed literature using the DPSIR approach. Evidence is also available with which the impacts of management responses on pressures and states may be summarised using the DPSIR framework. This evidence base is composed of individual case studies, multi-lake analyses and comprehensive review articles, which describe the effects of specific management responses in terms of ecological impact. In addition, this work provides an opportunity for the DPSIR to be developed to include responses not only in ecological structure but also in the performance of ecosystem functions.

1.2. Meta-analysis methodology and the study objectives

The WFD aims to remove the traditional dichotomous approach to environmental management by combining catchment scale understanding across a range of aquatic ecosystems to improve ecological status within specific river basins. This requires an assessment of ecological responses and interactions across lakes, rivers and estuaries in relation to eutrophication, hydromorphological change and acidification. WISER Workpackage (WP) 6.4-2, i.e. '*Comparison of cause-effect and recovery chains within water bodies*', will produce a series of literature reviews designed to provide comparative assessments of recovery in these three types of ecosystem following management intervention to address the three pressures outlined above.

The WP 6.4 working group identified the following specific aims of this work:

- Analyse and compare cause-effect and recovery chains across water categories, based on processes, functional features, over-arching biological processes and global change.
- Detect the antagonistic, neutral, additive or synergistic nature of the impact of multiple stressors within one water body/category.
- Detect commonalities among different cause-effect and recovery chains and develop a method to combine recovery effects in a summary 'catchment' metric.

It was proposed that these aims would be achieved by conducting a series of common literature reviews and meta-analyses encompassing all three pressures across the three water body types. These analyses would then be combined to produce catchment scale assessments of cause-effect and recovery chains, with the results contributing towards the development of a catchment scale WFD metric. This report forms part of the common literature review and meta-analysis and focuses on the recovery of lakes from eutrophication.

A series of common questions were proposed with which the impacts of management responses on the state of the environment could be assessed. In order to standardise recovery analyses within and between water body categories, the indicators of environmental impact used included not only ecological structure but also processes and functional aspects associated with any structural change. Information on biological processes relevant to connectivity, metapopulation dynamics, biological interactions and global change were combined to describe processes that were found to be confounding recovery.

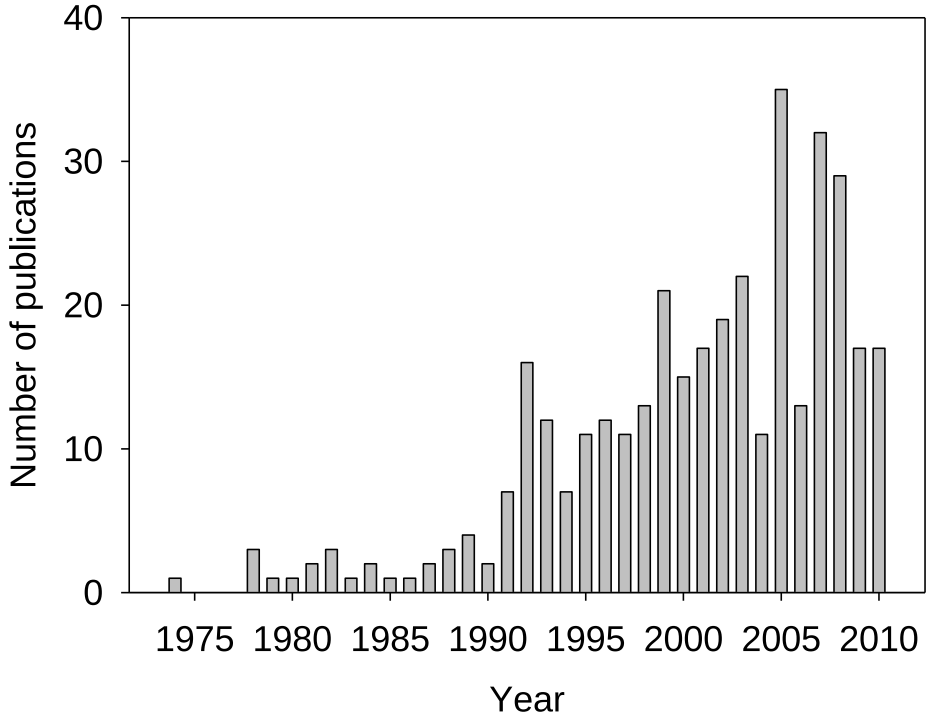


Figure 2. Number of publications per year returned from the ISI Web of Knowledge^{SM} *search undertaken in January 2011 using the search term "lake+eutrophication+recovery".*

The common questions included:

- What are the most common pressure scenarios?
- What are the most common management approaches?
- What WFD BQEs and other organism groups are most commonly reported?
- What are the structural and functional changes in end point biological communities when compared to impacted states?
- What confounding processes are important in determining response trajectories and end points?
- Will the recovery of lakes from eutrophication potentially impact downstream ecosystems?

We addressed these questions by conducting a search of the peer reviewed literature using ISI Web of Knowledge^{SM} in January 2011. The aim was to compile all available publications in which the term "lake + eutrophication + recovery" was contained within the topic of the article. This returned 364 publications. Each paper was catalogued and summary information manually extracted to produce a meta-database on which the analyses described in the following sections were conducted. The meta-database provided 743 lake-equivalent recovery case studies (LECs).

The majority of the papers were published between 1990 and 2010 (Figure 2). These publications covered around 274 named lakes from 41 countries, although the majority reported on lakes in Denmark, Finland and the Netherlands when multi-lake analyses are included (Figure 3). The lakes included in the meta-analysis were biased towards relatively small, shallow lakes (<10 km^2 in area and <5 m mean depth).

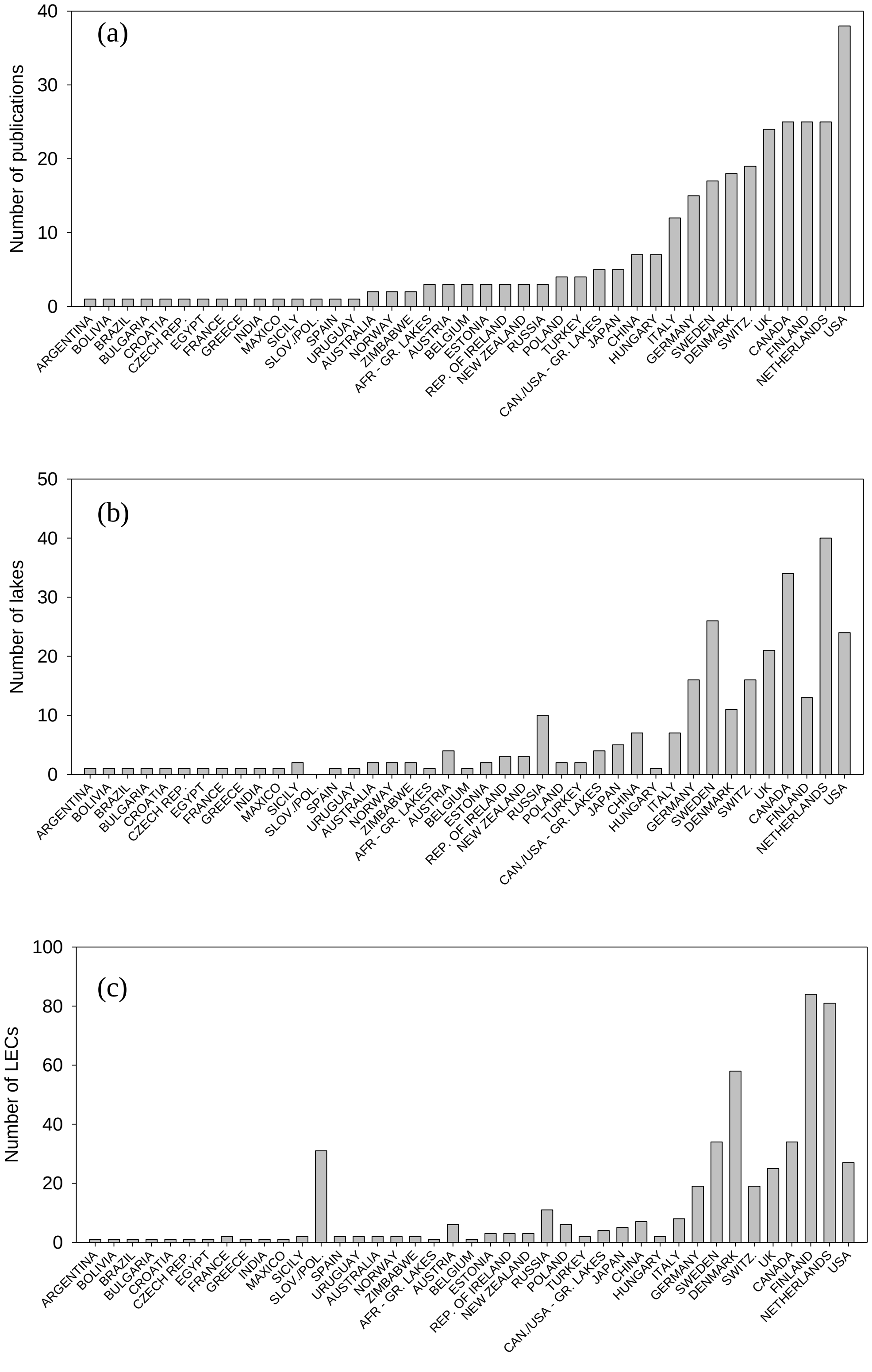


Figure 3. Distribution of (a) the number of publications, (b) the number of individual lake case studies and (c) the number of lake equivalent case studies (LECs) returned by the literature search, by country.

2. Analysis of single and multi-pressure scenarios

The capacity for a lake to recover to its original state is not only dependent upon a sufficient reduction in the primary pressure, but also on the occurrence of secondary pressures that may confound the recovery process. All primary and secondary drivers and pressures reported in the meta-dataset are summarised in Table 1.

Table 1. Drivers and pressures checklist for nutrient enriched freshwater lakes that were used in the analysis of pressure-impact relationships. Drivers are underlined and pressures are in italics.

Eutrophication drivers and pressures

Primary

- Agricultural intensification
  - *Fertiliser run-off*
  - *Animal waste run-off*
  - *Soil erosion and losses*
- Industrial intensification
  - *Textiles discharges*
  - *Food manufacturing dicharges*
  - *Paper mill discharges*
  - *Mining discharges*
  - *Distillery discharges*
  - *Aquaculture discharges*
- Tourism and recreation
  - *Food waste*
  - *Fish stocking*
  - *Sediment disturbance by boats*
  - *Garden waste*
  - *Fertiliser run-off from gardens*
  - *Inputs from feeding/roosting waterfowl*
- Population growth
  - *Sewage discharges*
  - *Waste disposal*
  - *Construction discharges*
  - *Transport/road run-off*
  - *Detergent and soap discharges*
- Other pressures
  - *Atmospheric deposition*
  - *Internal nutrient loading*
  - *Cyanobacterial* N_2*-fixation*

Secondary pressures

- *Sediment dredging*
- *Sediments disturbance by boats*
- *Metal pollution from mining*
- *Invasion by non-native species*
- *Pesticide discharges*
- *Climate change*
- *Fishery stocking*
- *Fish removal*
- *Acidification*
- *Macrophyte harvesting*
- *Water level management*
- *Waterfowl introduction*
- *Extreme weather events*
- *Industrial thermal-regulation inputs*

We screened the meta-data to assess the common pressure-scenarios for lakes in which eutrophication was the primary pressure. This screening returned 302 LECs for which eutrophication was the only reported pressure and 45 LECs for which there were also secondary pressures reported. The number of LECs that reported a range of secondary pressures is shown in Figure 4. Acidification, fisheries management, industrial pollution and climate change were the main secondary pressures impacting on nutrient enriched lakes and, with the exception of industrial pollution which covers a wide range of independent pollutants and practices, these are discussed below. Surprisingly, the role of invasive non-native species was rarely reported as a secondary pressure affecting ecological responses to eutrophication control in lakes, even though invasive species (especially macrophytes) were commonly reported to occur during the recovery process. It was concluded that multi-pressure scenarios may have been under represented in the literature for a number of reasons, including:

- secondary pressures were not considered to alter the impact of the target BQE and, therefore, were not reported,
- secondary pressures were not yet identified at the study site, and
- no data existed with which the secondary pressures could be quantified.

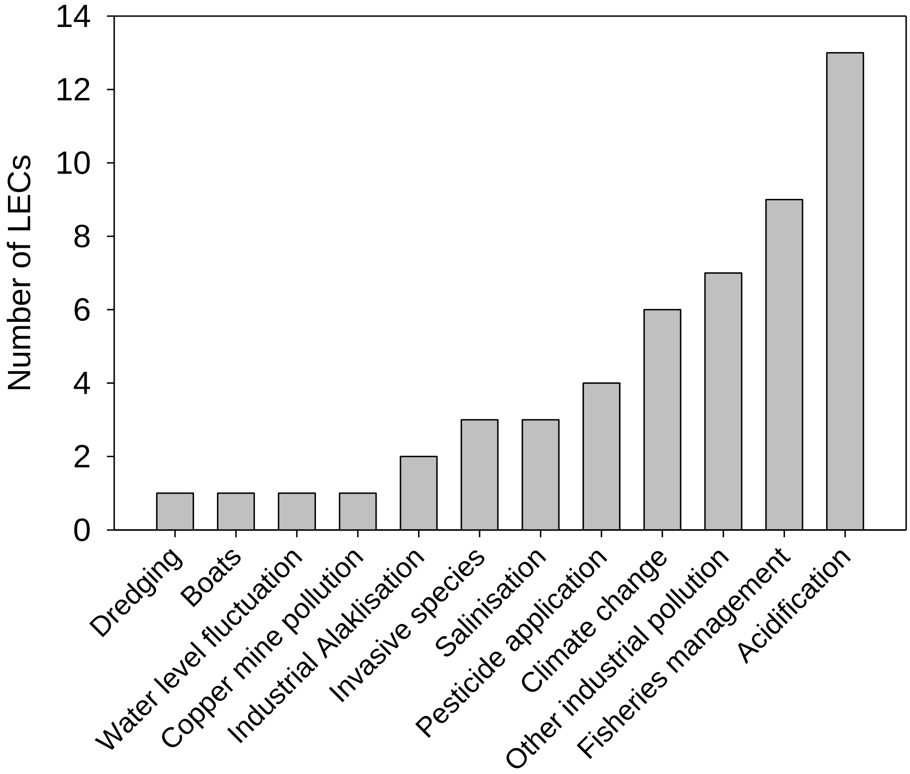


Figure 4. Number of LECs reporting each of the secondary pressures shown along the horizontal axis in combination with eutrophication.

In contrast, a wide range of secondary pressures have been reported at Loch Leven (Scotland), a shallow lake that is undergoing recovery from eutrophication following a significant (60%) reduction in external nutrient load (May and Carvalho, 2010). It is likely that each of the pressures shown in Figure 5 has an impact on every BQE at this site at some level, either directly or indirectly, through complex feedbacks within the system. Although current research aims to quantify the relationships between pressures and the BQEs in Loch Leven, no single article has reported on all of these pressures in the context of lake recovery from eutrophication.

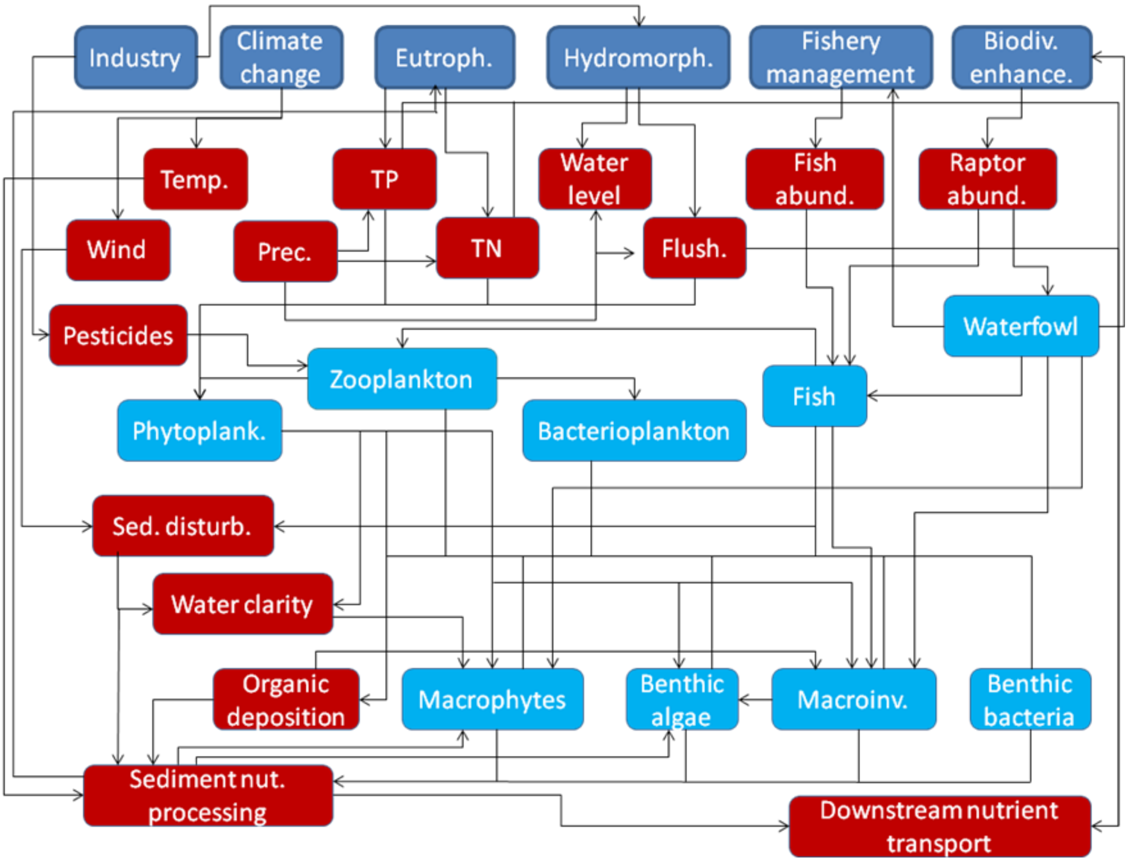


Figure 5. Inter-relationships reported/hypothesised in the literature between primary (eutrophication) and secondary pressures [dark blue], changes to environmental state [red] and impacts on biological quality elements (BQE) [light blue] in Loch Leven between 1968 and 2010.

Schindler (2006) reviewed a range of factors known to confound the recovery of lakes from eutrophication and stressed the need for better understanding of multiple pressures and identified the following secondary pressures as being of particular importance: (1) the aggravation of eutrophication by climate warming, (2) the overexploitation of piscivorous fishes and (3) changes in silica (Si) supply from the catchment as a result of climate change. Schindler (2006) hypothesised that the latter could lead to a reduction in Si concentrations in lakes leading to cyanobacteria outcompeting diatoms within the phytoplankton community.

2.1. Climate change

The North Atlantic Oscillation (NAO) index is used as a proxy for weather conditions, especially in north western Europe, and is calculated by comparing patterns of sea level atmospheric pressures near the “Icelandic low” and the “Azores high” of the North Atlantic Ocean (Jones et al. 1997; Jones et al., 2003). The main climatic variations associated with the NAO are warmer temperatures from late-autumn to early-spring and stronger, more westerly winds during years of strong positive NAO values (Slonosky et al., 2000). Past studies have identified NAO as a good (although variable; Gerten & Adrian, 2001) indicator of climatic forcing of ecological and physical processes in European lakes (reviewed by Straile et al., 2003). For example, coherent positive correlations have been observed between the indices of the NAO and surface and hypolimnetic lake water temperatures (Livingstone, 1999; Livingstone et al., 2000; Livingstone & Dokulil, 2001; Dokulil et al. 2006) as well as lake chemistry variables (Monteith, et al. 2000; Evans et al. 2001; Weyhenmeyer et al., 2004) across a range of European lake types. These drivers have, in turn, been linked to alterations in the ecological signatures of lakes, most strikingly affecting plankton dynamics and the onset of the clear-water phase (Gerten & Adrian, 2000; George, 2000; Straile, 2002).

In shallow lakes, the temperature effects of the NAO have been shown to drive ecosystem functioning through the regulation of steady state change (Scheffer et al., 2001; Rip, 2007). Regulation of wind intensity and direction may also have direct impacts on the depth of wind induced turbulence and, therefore, habitat disturbance in the littoral zones of lakes (Spears & Jones, 2010).

The occurrence of extreme weather events is expected to increase as a result of climate change. Shallow lakes appear to be particularly sensitive to such events, with changes in ecological state being triggered by hurricanes (Havens et al., 2001; Scheffer, 1998), high intensity rainfall (Rip, 2007; Nöges et al., 2010), drought leading to water level decrease (Coops et al., 2003), severe winter ice events leading to anoxia and winter fish kills (Scheffer, 1998), and heat waves (Schindler, 2006). The importance of climate change for the future of biodiversity and policy creation within the EU has been comprehensively reviewed by Moss et al. (2009). Other specific climate change effects documented as impacting on the recovery of specific environmental state indicators, and on ecological structure and function indicators, are discussed throughout this report.

2.2. Acidification

Although lake acidification is expected to alter the recovery process and end-point biological communities in lakes following eutrophication management, few studies report specifically on this type of potentially confounding impact at the whole lake scale. Clearly, soft water lakes are most sensitive to acidification pressures and inferences can be made with respect to the likely impacts based on available literature. In the Experimental Lakes Area (ELA) of Ontario, Canada, Vinebrooke et al. (2002) observed a decline in species compensation with increasing trophic level in relation to increasing acidification. Similar experimental studies have reported increases in phytoplankton biomass with additions of P at low pH levels (Blomqvist, 1993; Perez et al., 1994; Reynolds et al., 1998). The effects of acidification on the phytoplankton are generally considered to be a switch in community composition from chrysophytes, cryptophytes and diatoms to non-N_2 fixing cyanophytes or to dinoflagellates (Blomqvist, et al., 1993). However, the combined effects of acidification and eutrophication on phytoplankton community structure are still contested within the literature, with experimental studies showing either an increase, or no change, in community structure as eutrophication and acidification increases (Irfanullah & Moss, 2005; Reynolds et al., 1998). A series of mesocosm experiments conducted in Delamere Lake (UK; Irfanullah & Moss, 2005) reported the impacts of acidification (pH 4.5 – pH 8) on the structure and function of the plankton community under eutrophic conditions (mean chlorophyll *a* concentrations of 290 µg l^{-1}), as follows:

- low pH did not control the structure of the phytoplankton, rotifer or small cladoceran communities,
- low pH probably hampered reproduction of *Daphnia*, although *Daphnia* still controlled phytoplankton biomass through grazing, and
- no change in the level of predation of *Daphnia* by *Chaoborus* larvae at low pH was observed.

The impacts of acidification on macrophytes in soft water lakes with a conductivity 1-2 meq l^{-1} are well reported (Arts, 2002; Brouwer & Roelofs, 2001). In general, acidification causes a switch from an unimpacted community dominated by acid intolerant soft water macrophytes (e.g. *Myriophyllum alterniflorum, Isoetes echinospora, Pilularia globulifera, Elatine hexandra, Eleocharis acicularis, Echindodorus repens, Echinodorus ranunculoides, Lythrum portula, Nitella flexilis, Potamogeton gramineus, Potamogeton polygonifolius, Chara globularis, Apium inundatum, Callitriche hamulata, Rannunculua flammula, Rannunculus peltatus*), through an intermediate phase of very soft water acid tolerant species (e.g. *Lythrum dortmanna, Isoetes lacustris, Lythrum uniflora, Lythrum natans, Scirpus fluitans, Utricularia australis, Sparganium minimum, Hypercium elodes, and Rannunculus ololeucos*), to a deteriorated end point that was characterised by loss of all submerged macrophytes coupled with the development of *Sphagnum*, other bryophytes, *Juncus bulbosus* and filamentous epiphytic and benthic algae. The changes to the state of the environment that lead to macrophyte community succession during acidification are complex and mainly driven by resource supply and in-lake transformations. Soft water lakes are characterised by having poor N, P and dissolved inorganic carbon concentrations and, as a result, favour isoetid macrophytes capable of accessing limited carbon supplies through a range of traits (e.g. dark CO_2 fixation, photo-respired C recapture, extensive root system, sediment aeration leading to increased microbial CO_2 production; Brouwer & Roelofs, 2001). Through the aeration of the sediment surface, isoetids also reduce the likelihood of sediment P release. Acidification alters these transformation processes by removing isoetids. This results in an increase in CO_2 and ammonium-N concentrations in the water column, with little effect on P concentrations reported (Brouwer & Roelofs, 2001). The shift from isoetid to filamentous algae, sphagnum and *Juncus bulbosus* creates a feedback whereby the build up of organic matter on the sediment increases the likelihood of anaerobic conditions and an associated increase in sediment nutrient release rates, which maintains the unfavourable community. Shading of the isoetids by filamentous algae and sphagnum is also likely to be an important stabilising process.

Damage to the crustacean zooplankton community in thousands of lakes across Ontario and north eastern United States has also been attributed to acidification (Havens et al., 1993). The ranking order (from most to least sensitive) of acid sensitivity, quantified using acid toxicity tests, for the six zooplankton species included in the study was *Daphnia galeata mendotae*, *Daphnia retrocurua*, and *Skistodiaptomus oregonensis* > *Diaphanosoma birgei* > *Mesocyclops edax* > *Bosmina longirostris*. This order suggests that, in acidified lakes, the zooplankton community will become dominated by smaller zooplankton and, therefore, the shift from small to large bodied zooplankton observed during recovery from eutrophication may be unbalanced.

2.3. Fisheries management

Fisheries management practices vary in scale from fish stocking to support recreational fishing in small lakes to industrial fishing in large lakes. Any alteration to the fish community can result in top-down impacts on lower trophic levels through an increase or reduction in grazing pressures (Carpenter & Kitchell, 1996). Kane et al. (2004) reported an interaction between dissolved oxygen concentrations associated with eutrophication and the abundance of rainbow smelt in relation to the impact of industrial fishing effort and natural variability on the copepod *Limnocalanus macrurus* in Lake Erie. However, the community structure of fish in Lake Erie is known to be affected by many multiple drivers including P loading, industrial pollution, wetland management, invasive non-native species spread and commercial fishing activities. As a result, the recovery of the fish population following reductions in P loading to Lake Erie cannot be attributed to this activity alone. It has also been enhanced by the management of industrial fishing practices to target non-native species in favour of stressed native species over the same period.

An assessment of long-term trends in fish stocks in Lake Peipsi and Võrtsjärv (Estonia) indicated industrial fishing pressure as the main driver in changes in populations of pikeperch (Kangur et al., 2002). Changes in the pikeperch community were attributed to the use of trawls and fine meshed bottom seines (decline in population abundance), and to the management of fishing practices to restrict the use of trawls and bottom seines (increase in population abundance), which lead to variation in predation pressure on coarse fish and vendace. However, eutrophication of both lakes has reduced the resilience of the planktivorous vendace population.

Stocking of benthivorous fish species to support recreational sports fishing is common in small and shallow lakes. The impacts of bottom feeding fish on sediment P release have been well quantified, with catch *per* unit effort estimates for common carp (*Cyprinus carpio*) in excess of 2 kg *per* fyke night-catch expected to result in an increase in nutrient concentrations and a decrease in water clarity in 129 lakes in Iowa (Jackson et al., 2010). In the UK, the lake at Llandrindod Wells (Wales) provides an example of the role of common carp (~ 105 kg ha^{-1}) as a forward switch resulting in a state change from macrophyte dominated (clear water phase) to a turbid phytoplankton (i.e. cyanophyte) dominated state (Moss et al., 2002). These fish species may also be considered non-native invasive and are discussed in detail below.

Fish communities have been managed for fisheries purposes throughout Europe for hundreds of years. This has resulted in a huge scientific literature on the subject, the review of which is far beyond the remit of this report. However, a relatively recent coverage of the field of fish stocking and introduction may be found in the proceedings of a symposium on this subject edited by Cowx (1998).

With a more recent history from the 1980s to the present, and a more restricted scope in terms of the species involved, fish community management has also been undertaken for biomanipulation purposes in which fish numbers and species composition are manipulated to produce cascading changes in the zooplankton, phytoplankton and, ultimately, in the water quality of a standing water body. An authoritative review of this field on a global basis is provided by Hansson et al. (1998). Such studies have relevance to the present report because biomanipulation in Europe frequently involves the removal, or at least great reduction, of roach populations due to this species frequently being a major predator of zooplankton populations, particularly in eutrophic waters. Such biomanipulated fish populations have been removed or reduced by manual removal through forms of netting or electric fishing, by the addition of predatory fish, or by the use of chemicals such as rotenone. The U.K. experience with biomanipulation, where fish removal/reduction methods are tightly restricted, is reviewed by Moss et al. (1996), with Perrow et al. (1997) providing a more fish-focused account and Phillips et al. (1999) concentrating on its practical aspects. In the U.K., such work has been focused almost entirely on the Norfolk Broads of south-east England, with the manual removal of roach, and to some extent other species, by repeated electric fishing, some netting and some egg removal as reviewed by Perrow et al. (1997) and Phillips et al. (1999). One particularly clear conclusion which can be drawn from these and other studies is that the complete removal of roach and similar species from a standing water body is extremely difficult to achieve when it is attempted only by their physical capture using nets or electric fishing. Even if only a few individuals evade capture, the population biology of such small cyprinids is such that they will rapidly recover in population abundance within a few years.

2.4. Non-native invasive species

Non-native invasive species are defined by the GB non-native species secretariat as “any non-native animal or plant that has the ability to spread causing damage to the environment, the economy, our health and the way we live.” Many non-native invasive species are introduced by humans for a specific purpose (e.g. aquaculture; Figure 6). However, by definition, they also have the ability to spread *via* transport pathways throughout the environment and infest lakes. This spread may operate with and without human intervention. A summary of the types of non-native invasive species important in freshwater lakes and their vectors of infestation is outlined in Table 2.

Table 2. Summary of organism groups, mode of introduction, environmental impacts and examples for non-native invasive species considered to pose a high risk to the recovery of lakes from eutrophication (Manchester & Bullock, 2000).

Type of organism	Purpose	Impacts	Examples
Fish and shelfish	Angling, accidental introduction	Competition, predaition, habitat disturbance, disease vector, increased sediment P release, reduction of macrophyte cover	Grass carp, common carp, crayfish
Invertebrates	Accidental introduction	Competition with native species, grazing of phytoplankton	Zebra mussel, alien gammarids
Plants	Accidental introduction	Prolific vegetative growth, forms dense matts leading to deoxygenation, outcompetes native flora.	*Crassula helmsii, Egeria densa* and *E. Nutalii*

The results of the EU DAISIE project (DAISIE European Invasive Alien Species Gateway: http://www.europe-aliens.org) for inland aquatic ecosystems highlight the scale of the problem of non-native invasive species across EU member states (Figure 6). It should be noted that the problems of non-native invasive species are member state specific. This has been recognised through the publication of state-specific information on regulation, distribution and control measures at both EU (e.g. European Network on Invasive Alien Species: NOBANIS) and national scales (e.g. GB Non-native species secretariat). Here, we focus on the potential interactions between invasive species and recovery from eutrophication using examples of invasive species that are commonly reported in the literature for eutrophic lakes.

Although the spread of non-native invasive species is clearly an issue for environmental management across the EU in general, some studies have also reported on the potential importance of invasive species as a secondary pressure that confounds ecological recovery of native flora and fauna following eutrophication management. For example, Rosenthal et al. (2006) reported a decrease in the germination of macrophyte species (with the exception of *Najas flexilis* and *Chara spp*.) from seed banks of 9 lakes as a result of invasion by crayfish (*Orconectes rusticus, O. propinquus, O. virilis, and O. immunis*). A decrease in macroinvertebrate abundance has also been reported in the presence of common carp (Matsuzaki et al., 2009). The impacts of invasive carp species (e.g. common carp and grass carp) are well documented (e.g. Jackson et al., 2010). For example, impacts of non-native common carp (*Cyprinus carpio* L.) include resuspension of sediments leading to a decrease in transparency and an increase in TP and phytoplankton abundance, and a decrease in macrophyte and macroinvertebrate species composition and abundance (Miller & Crowl, 2006; Matsuzaki et al., 2009; Jackson et al., 2010). Large scale biomanipulation studies have been widely conducted to manage non-native invasive fish species and their impacts on water quality across Europe (Hosper, 1998), although successes are often short-lived due to re-invasion (Søndergaard et al., 2007).

Schlüter (2007) reported on a comprehensive study of competition between invasive ruffe (*Gymnocephalus cernuus L.*) and the native perch (*perca fluviatilis L.*) in Lake Constance, Germany, across an eutrophication-re-oligotrophication gradient. Competition between these species was concluded to be of low importance, with the following competition avoidance strategies identified (1) feeding behaviour, where ruffe are capable of using mechano-physiological adaptations to locate food under turbid or dark conditions whereas perch are visual predators; (2) seasonal and age-specific (for perch) interspecific consumption of food in mixed communities; (3) food availability where ruffe are specialist consumers (benthivorous) and perch are generalist consumers (benthivorous and planktivorous); and (4) habitat availability where ruffe favour deeper and darker habitats during the day (Box 1). In this case, Schlüter (2007) hypothesises that ruffe and roach will co-exist in the re-oligotrophic Lake Constance.

The impacts of invasive dreissenid mussels (e.g. Zebra mussel; *Dreissena polymorpha*) have been well documented in the literature. Likely impacts include (1) a reduction in phytoplankton biomass (up to 45% for more than 7-10 years post invasion; Higgins et al., 2011) and total P concentrations in the water column (Hecky et al., 2004); (2) maintenance of relatively high benthic-pelagic energy transfer (Hecky et al., 2004; Higgins & Vander Zanden, 2010); (3) alterations to the stoichiometry of N and P supply to the overlying water column to favour strong N limitation (Arnott & Vanni, 1996); and (4) alterations to the benthic macroinvertebrate community composition (Nalepa et al., 2003). Divergent recovery trajectories have been reported in the macroinvertebrate community of Lake Huron (Nalepa et al,. 2003) following P abatement, where *Gammarus* were favoured over sphaeriids and the oligocheate trophic index more strongly reflected oligotrophic conditions in invaded habitats than habitats that were not invaded by dreissenid mussels. In the case of Lake Veluwe, Ibelings et al. (2007) argue that *Dreissena polymorpha* populations should be protected due to their positive effects on water quality and the increased resilience of the clear-water regime that they generate.

Carpenter et al. (1999) document the importance of macrophyte control measures (uncontrolled clear cutting) and eutrophication as contributory factors in the replacement of the native macrophyte community (*Potamogeton* spp., *Ceratophyllum* spp., *Myriophyllum* spp.) by the invasive species, *Myriohyllum spicatum*, in Lake Mendota (USA). Reductions in external nutrient loading and a move towards targeted and controlled removal of *Myriohyllum spicatum* has resulted in a gradual return of the native macrophyte community, although extent and species richness remained checked almost 40 years after the onset of management.

There is a requirement for a coordinated European response to analyse species' functional traits within non-native invasive species lists so trait and functional replacement may be assessed against distribution maps and native species lists across the EU (Lambdon et al., 2008). A wide range of distribution maps have been produced across Europe (DAISIE European Invasive Alien Species Gateway: http://www.europe-aliens.org). However, these need to be supplemented with expert knowledge (e.g. Roman & Darling, 2007), laboratory experiments (e.g. Barrat-Segretain & Elder, 2004), field experiments (e.g. Ali & Soltan, 2006; Rosenthal et al., 2006) and meta-analyses (e.g. Matsuzaki et al., 2009; Higgins & Vander Zanden, 2010) to examine the ecological processes associated with invasions that may potentially confound ecological recovery of native populations following eutrophication management. This would complement the existing documentation that details European level responses to identification of the scale and distribution of non-native species (Pysek et al., 2010) and will allow the community to better develop control measures for inter- and intra-EU transport pathways (Shine et al., 2009).

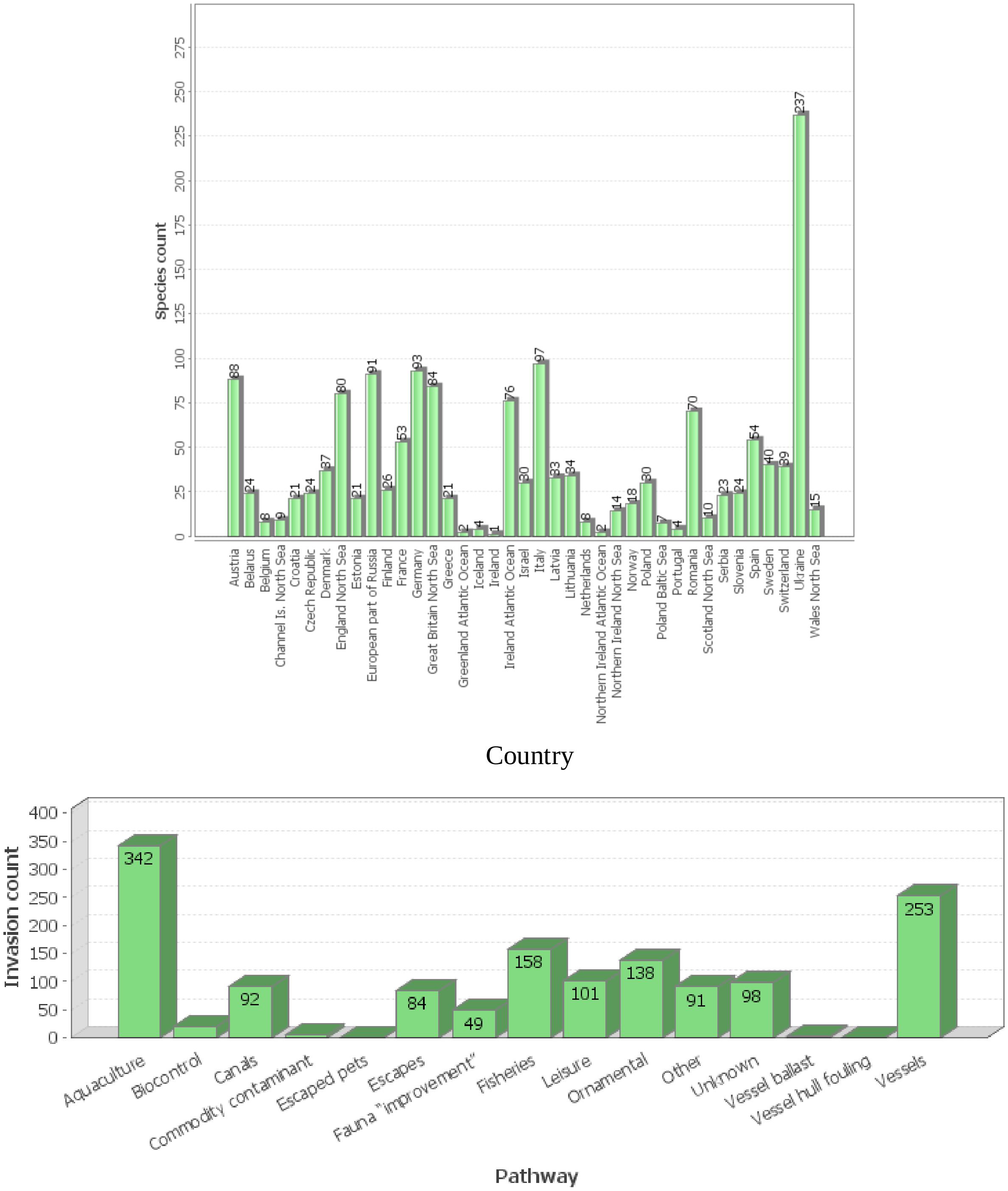


Figure 6 The number of non-native invasive species in each EU country (upper panel) and the pathways reported to be responsible for transporting non-native invasive species into inland aquatic systems reported (lower panel). After EU FP6 DAISIE European Invasive Alien Species Gateway: http://www.europe-aliens.org.

3. Management of eutrophication pressures

A range of eutrophication management approaches were documented in the literature meta-database (Figure 7). The most commonly reported approach was the reduction of external nutrient loading (88% of returned publications) with in lake management, only, and external load reduction in combination with in-lake management being less commonly reported (6% and 19% of returned publications, respectively). Fish biomanipulation (41% of reported in-lake management cases) was the most commonly reported in-lake management measure followed by sediment P capping (16%), drawdown (12%), sediment dredging (13%), flushing (6%), aeration/circulation (5%) and waterfowl/macrophyte biomanipulation (2%).

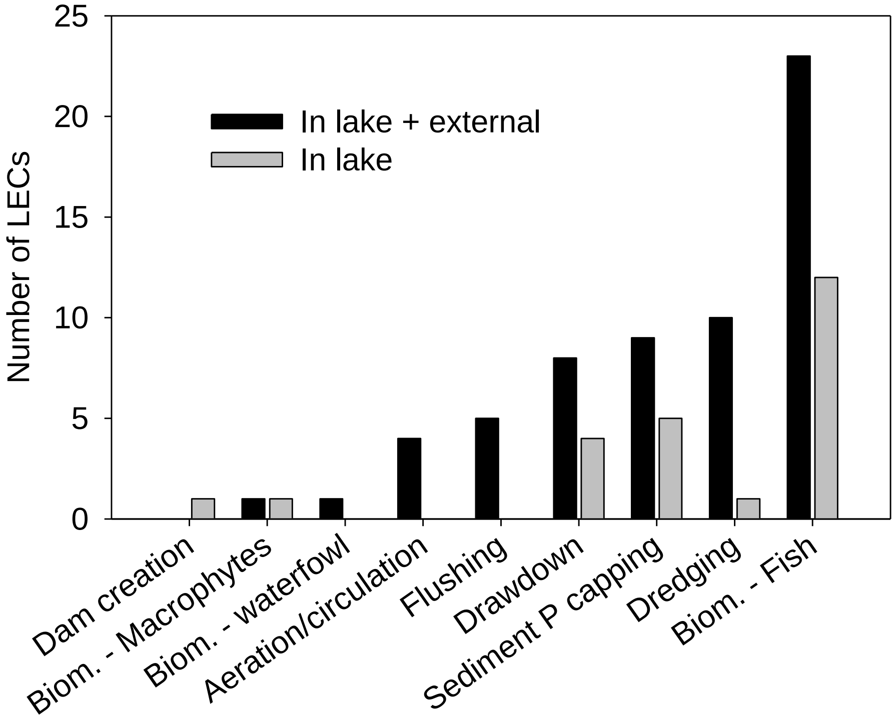


Figure 7. Number of LECs reporting in-lake management measures in combination with external nutrient load reduction and in lake management measures in isolation.

Comprehensive reviews have been published detailing lake restoration theory (Scheffer, 2004), specific management techniques (Cooke et al., 1993; Hupfer, 2008; Hickey & Gibbs, 2009), and successes and failures (Sas, 1989; Moss et al., 1996; Søndergaard et al., 2007). For this reason we will not attempt a comprehensive review of management practices. However, an emerging body of literature has clearly demonstrated the importance of managing multiple pressures, simultaneously, to improve the likelihood of structural and functional recovery following eutrophication management (for example, Lake Kraenepoel, Belgium (Van Wichelen et al., 2007; Box 2) and Tiefwarensee, Germany (Mehner et al., 2008). This approach requires comprehensive understanding of primary and secondary pressures (i.e. long-term pre-management monitoring) acting on a water body and has included combinations of external load reduction and biomanipulation, sediment dredging and/or sediment P capping. When correctly applied, the simultaneous management of multiple pressures can achieve rapid recovery (i.e. <5 years for the studies cited above) as demonstrated in the studies cited above.

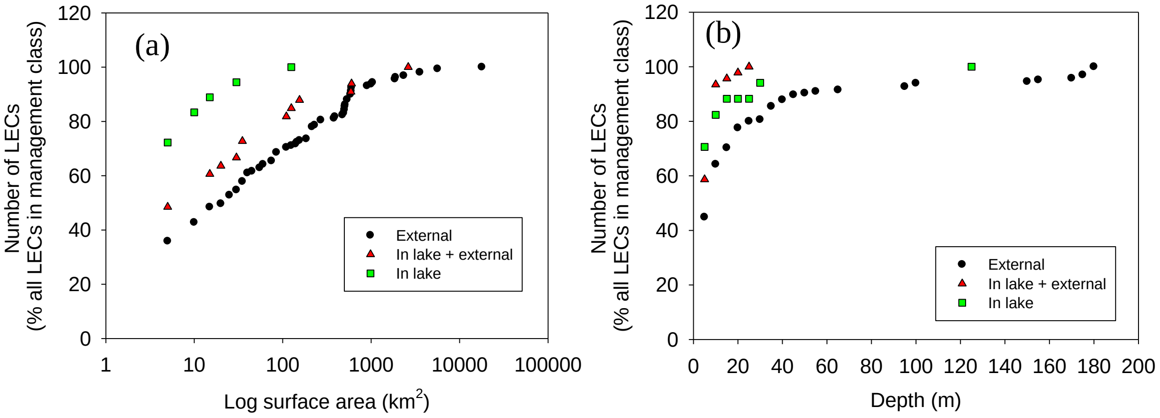


Figure 8. Number of LECs in (a) 5 km^2 surface area classes and (b) 5 m mean depth classes summarised by management scenarios, i.e. external nutrient load reduction only, in-lake management and external nutrient load reduction, and in-lake management only.

It is also apparent that the knowledge-base underpinning the use of various management techniques is biased towards small and shallow lakes (Figure 8). This is most probably due to the fact that more small and shallow lakes are eutrophic when compared to large and deep lakes and due to the relative ease of manipulating and monitoring smaller sites. Financial restraints may also be important, particularly where in-lake measures are considered. The number of publications reporting in-lake measures is strongly biased towards small (<10 km^2) and shallow (<5 m) lakes.

BOX 1: Lake Kraenepoel, Belgium

Lake type

Small (0.22 km^2), shallow (mean depth 1.0m; maximum depth 1.5m) lake composed of two basins separated by a dam.

Catchment characteristics

The lake is situated within the former heathlands of northwest Belgium

Driver

Increasing population density and agricultural intensification leading to elevated nutrient inputs and use of the lake for fish culture.

Pressure

Nutrient enrichment and sediment disturbance by benthivorous fish (mainly common carp).

State

Summer PO_4-P concentrations of *ca*. 1000 µg L^{-1} and 600 µg L^{-1} for the south and north basin, respectively. Evidence of strong internal P loading. NO_3-N concentrations of about 3000 µg L^{-1} and 2500 µg L^{-1} for the south and north basins, respectively.

Impact

Problem algal blooms, loss of submerged macrophytes, high turbidity, high biomass of exotic fish species.

Response

Diversion of nutrient rich rivulet, dewatering, removal of exotic fish species, stocking with pike, sediment removal (north basin only).

Recovery

Nitrate, phosphate and phytoplankton concentrations all decreased in the north basin after sediment removal within 1 year of restoration, mainly because in-lake nutrient cycling was shut down. The improved water quality in the north basin was associated with a shift from abundant *Potamogeton spp*. to more “benthic” *Littorelletea* vegetation. Of particular note was the emergence of *Hypercium elodes* and an increase in the number of pre- and post-restoration desmid species from 3 to 30, respectively.

In the southern basin (without sediment removal), reductions in nitrate, phosphate and phytoplankton concentrations were less pronounced despite the removal of external nutrient inputs. It is likely that the source of nutrients switched from external load to internal load in the south basin, given the high remineralisation rate that is expected to be associated with dewatered surface lake sediments. The south basin became acidified (to about pH 4) a few months after refilling, probably as a result of oxidation of sulphides during the drying period and subsequent release of sulphides to the water column on refilling; refilling with rainwater/groundwater probably reduced the buffering capacity of the lake to changes in pH. Acidification resulted in the immobilisation of phosphates at low pH and favoured nitrification; direct pH effects on the ecology of the lake were also expected and a shift from *Potamogeton* spp. to *Littorelletea* vegetation was not reported in the south basin.

Cladoceran zooplankton community species richness and conservation value increased in both basins within 1 year of restoration, although currently species richness is still lower than reference conditions. Potential reasons behind this low species richness include (1) the lack of a viable seed bank in the remaining sediments and (2) incomplete community succession. A clear water macrophyte-dominated state was achieved within 1 year of restoration in the lake and lasted for at least 5 years.

References

Louette et al. (2009); Van Wichelen et al. (2007).

4. Changes in state and effects on the structure and function of lakes

The literature review returned 333 LECs in which the recovery of at least one WFD BQEs was reported following external nutrient load reduction alone, 130 LECs in which only in-lake management was conducted and 51 LECs in which in lake and external nutrient load management measures were conducted (Figure 9). Reports on phytoplankton were most common (44% of case studies reporting ecological recovery) followed by macrophytes (15%), zooplankton (14%), macroinvertebrates (13%), fish (12%), waterfowl (2%) and bacterioplankton (<1%). In the following subsections we summarise the results from these LECs with particular focus on recovery responses in community structure and function. Any processes acting to confound recovery are also discussed.

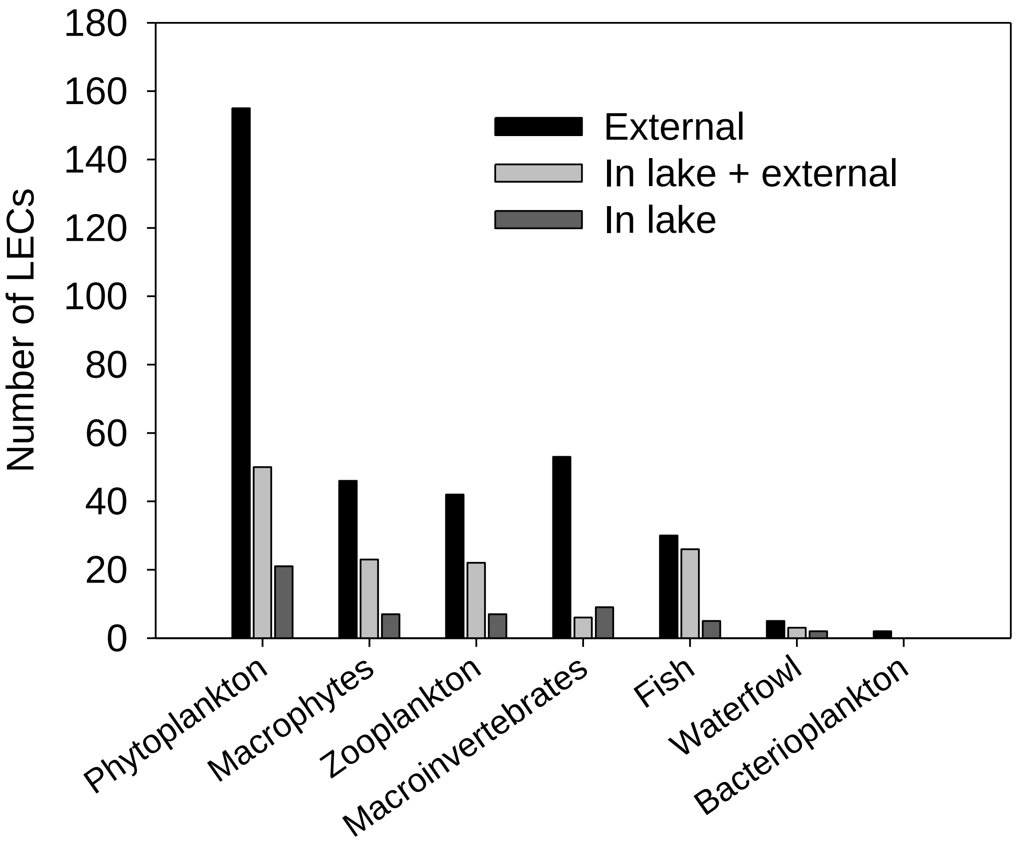


Figure 9. Number of LECs returned in the literature review for three management scenarios (external nutrient load reduction only, in lake management coupled with external nutrient load reduction, and in lake management only) for each of the 7 BQEs.

4.1. Recovery trajectories of phosphorus following management

The management of eutrophication through P-reduction is based on the general assumption that phytoplankton production is P-limited in all freshwater lakes. This assumption is based on the following research:

- Multi-lake studies that revealed a strong relationship between phytoplankton biomass (usually expressed as chlorophyll *a* concentration) and TP concentration across a range of sites and geographical regions (Dillon & Rigler, 1974; Schindler, 1978; Vollenweider & Kerekes, 1980; Phillips et al., 2008),

- site specific studies, including Loch Leven (Carvalho et al., submitted) and Windermere (Pickering, 2001), detailing the increase in phytoplankton biomass associated with increasing TP concentrations,
- whole lake experiments in the experimental lakes area of Ontario where increases in P rather than N were shown to result in increased phytoplankton biomass (Schindler, 1977), and
- catchment based studies demonstrating that reductions in P loading tend to be more easily achieved than reductions in N loading (Reckhow & Simpson, 1980).

Although compelling evidence exists to support the control of eutrophication through reductions in P loading alone, it should be noted that factors other than P limitation can control phytoplankton biomass in lakes, which can lead to unexpected recovery trajectories in lakes after eutrophication management. Within the UK, N-limitation has been found in a range of lake types, including shallow eutrophic and mesotrophic lakes (James et al., 2005; May et al., 2010) and upland lakes (Maberly et al., 2003). Also, the relationship between TP and chlorophyll *a* is known to “break down” at TP concentrations above about 100 µg P l^{-1} in lakes from the UK and Ireland (Phillips et al., 2008), and those from other temperate regions (Vollenweider & Kerekes, 1980). This phenomenon has been generally attributed to N-limitation under P-replete conditions (Chow-Fraser et al., 1994). In relation to the WFD lake water quality targets, a high proportion (about 30% on average across WFD lake types) of lakes in Scotland were found to have high TP (i.e. to fail WFD good/moderate boundary targets) but low chlorophyll *a* concentrations (i.e. to pass WFD good/moderate boundary targets) in 2008 (Figure 10; Spears et al., unpublished data). A summary of the factors responsible for retarding the chlorophyll *a*:TP relationship are summarised in Table 3.

There has been recent controversy about the role of N- and P-limitation in lakes and estuaries and the effectiveness of reducing only one of these nutrients to improve water quality (Pearl, 2009; Schindler & Hecky, 2008). In a Policy Forum Review in the journal *Science*, Conley et al. (2009) concluded that effective control of the negative impacts of nutrient enrichment ought to involve controlling and reducing the availability of both nutrients.

Table 3. Summary of factors responsible for altering the relationship between chlorophyll a (Chl) and total phosphorus (TP) in lakes. N/A indicates not applicable.

Pressure or gradient	***Threshold or indicator***	***Chl:TP effect***	***Reference***
Non-P limitation			
N-limitation	*>50-1000 µg TP* l^{-1}	*Decrease*	*Macaulay et al., 1989*
N-limitation	*>100 µg TP* l^{-1}	*Decrease*	*Chow-Fraser et al., 1994*
N-limitation	*N:P <12 by weight*	*Decrease*	*Dillon & Rigler, 1974*
N-limitation	*N:P <10 by weight*	*Decrease*	*Sakamoto, 1966*
N-limitation	*N:P <35 by weight*	*Decrease*	*Smith, 1982*
N-limitation	*N:P <22 atomic ratio*	*Decrease*	*Prairie et al., 1989*
N-limitation	*N:P <17 by weight; > 100 µg TP* l^{-1}	*Decrease*	*Canfield, 1983*
N-limitation	*N/A*	*Decrease*	*Nicholls & Dillon, 1978*
N-limitation	*N:P <10*	*Decrease*	*Phillips et al., 2008*
N-limitation	*>1000 µg TP* l^{-1}	*Decrease*	*Sterner, 2008*
N/P Co-limitation	*>10 and <1000 µg TP* l^{-1}	*Variable*	*Sterner, 2008*
Effects of light and shading			
Light limitation of primary production	*High sediment load*	*Decrease*	*Jones & Bachman, 1976*
Light limitation of primary production	*High sediment load*	*Decrease*	*Canfield & Bachman, 1981*
Light driven cellular chlorophyll content	*High irradiance*	*Decrease*	*Nicholls & Dillon, 1978*
High sediment shading during monsoon events	*>50 µg TP* L^{-1}	*Decrease*	*An & Park, 2002*
Shading by humic substances		*Decrease*	*Havens, 2003*
Grazing pressures			
Grazing by dreissenid mussels	*N/A*	*Decrease*	*Hall et al., 2003*
Zooplankton grazer control by fish	*Strongest at high TP*	*Increase*	*Jeppesen et al., 1998*
Reduced zooplankton grazing resulting from dominance of filamentous cyanobacteria	*>100 µg TP* L^{-1}	*Increase*	*Chow-Fraser et al., 1994*
Macrophyte refugia increases zooplankton grazing pressure in very shallow lakes	*N/A*	*Decrease*	*Scheffer, 2004*
Lake type			
Increasing depth	*N/A*	*Decrease*	*Phillips et al., 2008*
Increasing alkalinity in shallow/very shallow lakes	*N/A*	*Decrease*	*Phillips et al., 2008*
High alkalinity resulting in P loss in calcium precipitate	*N/A*	*Decrease*	*Håkanson et al., 2005*
Increasing chlorophyll a concentration	*N/A*	*Increase*	*Present study*

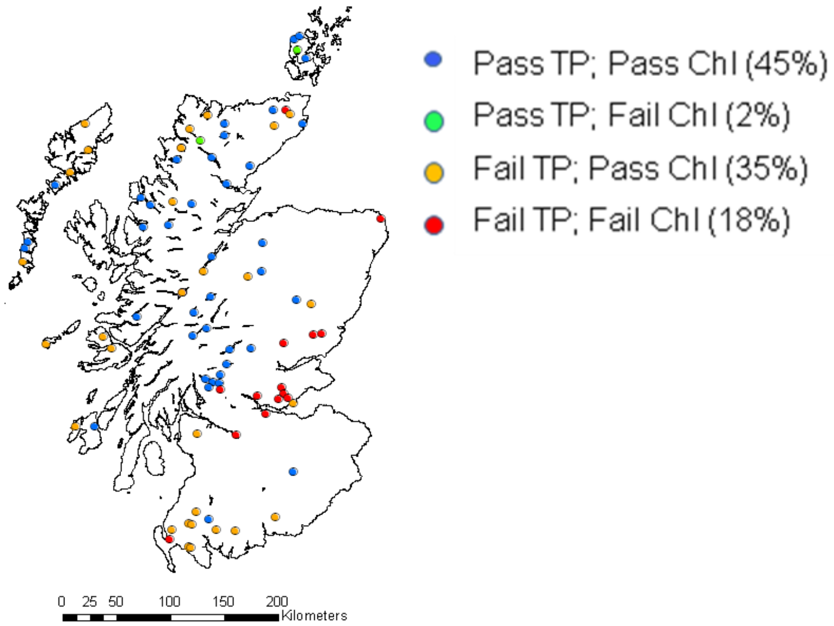


Figure 10. Geographic distribution of lakes in Scotland that fall into one of four EU Water Frameowrk Directive total phosphorus (TP) or chlorophyll a *(Chl) water quality classifications. Data were provided by the Scottish Environment Protection Agency for 2008.*

In shallow lakes, in-lake biogeochemical processes (Figure 11) can regulate reductions in TP concentrations leading to changes at the seasonal, annual and decadal scales. Jeppesen et al. (2005b) reviewed the recovery of 35 lakes following external nutrient load reduction and estimated that internal P loading delayed the recovery of lakes between about 10-15 years. However, examples are also available in the literature of lakes in which internal loading has delayed recovery for up to 20 years (e.g. Lake Søbygård, Denmark; Søndergaard, 2007) post external load reduction. The timing of this transient period is known to be driven by a range of factors including retention time, pollution history, sediment P composition and concentrations, and depth (Sas, 1989).

Responses in water column TP concentrations during the transient period often reflect a switch in the dominance of external and internal loading (Box 2; Søndergaard et al., 2005a & 2007). When the external loading is reduced, winter/spring and autumn in-lake TP concentrations are often reduced whilst sediment P release, which predominantly reaches its peak during summer months, acts to maintain or increase summer TP concentrations. As the magnitude of sediment P release in summer decreases over time, summer in-lake TP concentrations also decrease. So, the ecological responses of organisms with a high turnover rate (e.g. phytoplankton, zooplankton, macroinvertebrates and bacterioplankton) may be more pronounced in winter, spring and autumn than at an annual mean level. Additionally, the improvement in water clarity linked to reduced TP concentrations in spring has been shown to provide macrophytes with a “window of opportunity” for rapid colonisation of deeper water sediments (Scheffer, 2004).

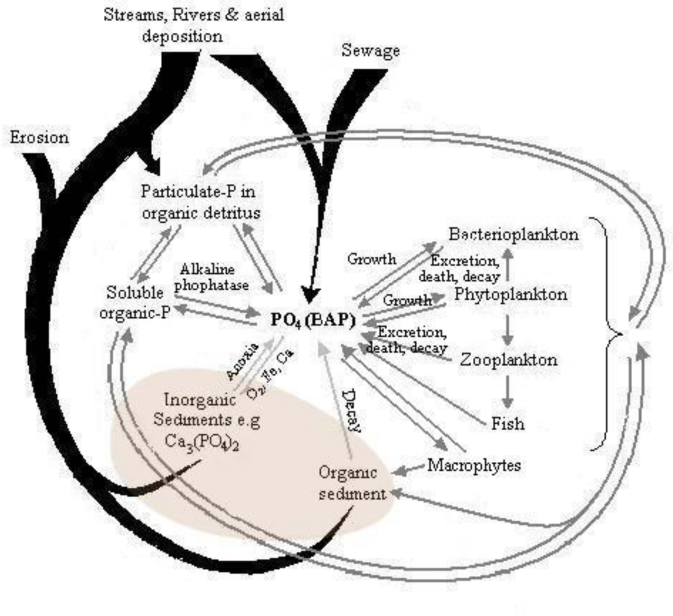


Figure 11. Simplified aquatic phosphorus cycle in lakes. Heavy black lines indicate external loading, dark grey lines are internal processes and light grey lines represent internal loading. Those stages contained within the beige area occur within the sediment. Modified from Horne & Goldman (1994). Biologically available phosphorus is labelled BAP within the diagram.

BOX 2: LOCH LEVEN, SCOTLAND

Lake type

Large (13.3km^2), shallow (mean depth 3.9m; maximum depth 25.5m), well mixed, alkaline lake with a water retention time of *ca*. 0.5 years; predominantly phosphorus (P) limited.

Catchment characteristics

Catchment area 145km^2; mainly lowland agriculture with some forestry in upland areas.

Driver

Increasing population density, agricultural intensification and industrial development increased the P input to the loch from *ca*. 5 t y^{-1} in the early 1900s to *ca*. 20 t y^{-1} by 1985.

Pressure

Nutrient enrichment.

State

Winter P concentrations of *ca*. 40 µg l^{-1}; P retention coefficient of 0.61; accumulated organic sediments with high nutrient content.

Impact

Problem algal blooms, high turbidity and loss of macrophytes.

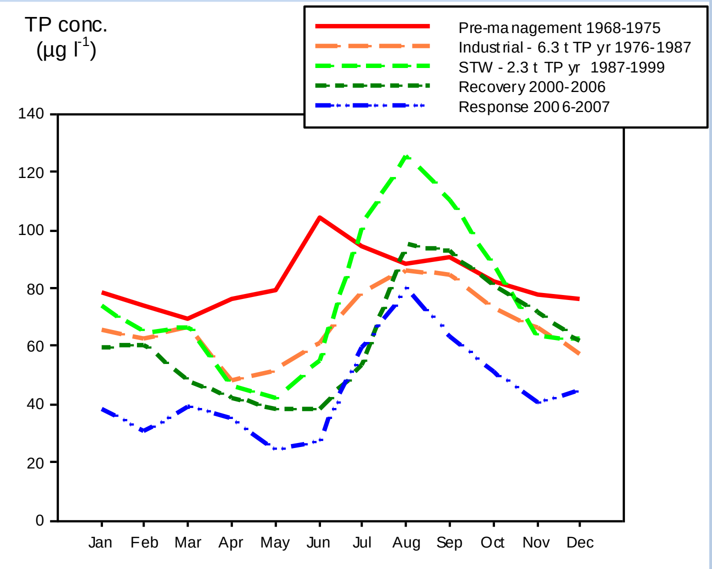
Response

Improved control of nutrient rich sewage effluent discharges, cessation of P inputs from industry, and better farm management reduced the P input.

TP recovery

External loading reduction occurred over a 24 year period. Industrial inputs from a woollen mill were reduced in 1976-1987 (Phase 1) and sewage works were upgraded in 1987-1999 (Phase 2). The response in in-lake winter and spring TP concentrations was rapid after

Phase 1, with concentrations being reduced by about 75% in winter and 60% in spring compared to pre-management levels. Further decreases in spring concentrations to about 50% of pre-management conditions were observed after Phase 2. Summer concentrations remained high, with summer concentrations increasing after Phase 2 and a pronounced summer peak developing. This switch from high baseline TP concentrations throughout the year to low winter, spring and autumn TP concentrations with a pronounced summer TP peak represents a switch in dominance from external to internal loading in the lake. The magnitude of the summer TP peak decreased in the 8 years after Phase 2, as did concentrations in general across all seasons. However, summer TP concentrations of around 80µg l^{-1}, and winter and spring baseline TP concentrations of around 30µg l^{-1}, were still common. Recovery of the lake is still incomplete.



References

May et al., submitted; Carvalho et al., submitted.; Spears et al., 2007

4.2. Recovery trajectory of nitrogen following management

The responses in N following external nutrient load reduction also follow seasonal trends that are driven by sediment processes and changes in the biological structure of the lake. In an analysis of 35 lakes to which external nutrient loading had been significantly reduced, Jeppesen et al. (2005b) found a delay of <5-10 years for steady state N concentrations to be achieved in lakes where reductions in N loading had been reported. Summer TN concentrations decreased and the ratio of dissolved inorganic nitrogen (DIN) to TN (DIN:TN) increased in the majority of lakes after recovery, probably due to a reduction in summer phytoplankton biomass and, therefore, organic N content of the water column. Similar reductions in TN have been reported by Søndergaard et al (2005) although, in this case, N load reductions were not expected to be the driver of the in-lake N concentration decrease. Instead, phytoplankton biomass decreased as a result of reductions in TP load coupled with denitrification and macrophyte uptake of dissolved N leading to reduced water column TN concentrations. These estimates of the transient period for N are in general agreement with the results of Jensen et al. (1992), where steady state TN conditions were reached within 1 year of a 30% reduction in external N loading (Lake Søbygaard, Denmark).

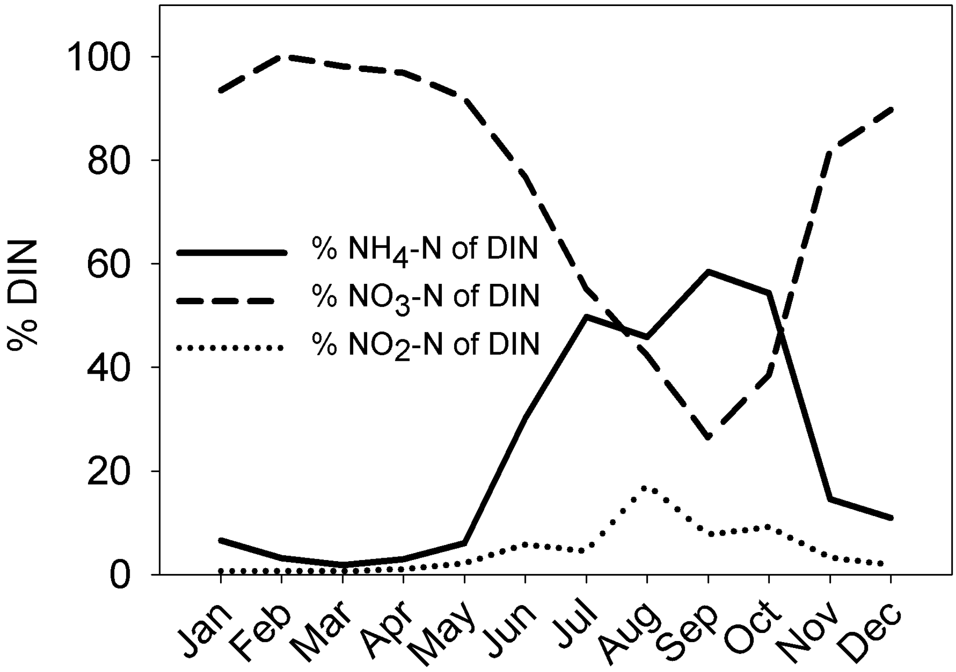


Figure 12. Average monthly NH_4-N, NO_3-N and NO_2-N concentrations expressed as a percentage of DIN (i.e. NH_4-N+NO_3-N+NO_2-N) concentration in Linlithgow Loch (mean depth – 2.3m; surface area – 40.6 ha; data span - 1994-2010). After Spears & May (2011).

The trends in monthly dissolved inorganic N (DIN: i.e. NH_4-N+NO_3-N+NO_2-N) concentration in many recovering lakes indicate a reduction in DIN from winter through to late summer-early autumn (Figure 12). This reduction has been attributed to a combination of denitrification and biological uptake, both of which are expected to increase with temperature (Jensen et al., 1992; van Donk et al., 1993). By comparing the seasonal trends of NO_3-N, NO_2-N and NH_4-N (collectively DIN), it is also apparent that the relative composition of DIN varies seasonally (Figures 12). The rapid response in N concentrations in the water column following external load reduction can be explained by the N removal processes outlined in Figure 13.

These processes have been quantified by Trolle et al. (2008) to produce a model with which changes in N loading to Lake Ravn (Denmark) could be assessed. Wehenmeyer et al. (2007) conducted a comprehensive meta-analysis of factors controlling the rate of NO_3-N loss between spring and summer in 100 north-mid-European lakes. They found that (1) the rate of NO_3-N loss increased with decreasing lake depth; (2) the NO_3-N loss rate was positively correlated with spring NO_3-N concentrations (at lake depths <12.5m); and (3) reductions in external N loading, including atmospheric loading, and an increase in water temperature associated with climate change have resulted in a decrease in the occurrence and duration of NO_3-N depleted conditions across a sub set of 16 European lakes that had long-term data sets. In a warming climate, it is likely that N removal processes will be enhanced, potentially leading to an increase in the resilience of cyanobacteria to oligotrophication measures (Schindler, 2006; Wehenmeyer, 2007;

Wehenmeyer et al., 2008). However, N loading may also be enhanced under future climate change scenarios with regional-scale uncertainty in climate predictions leading to uncertainty in the expectations of future N status in lakes (Jeppesen et al., 2011).

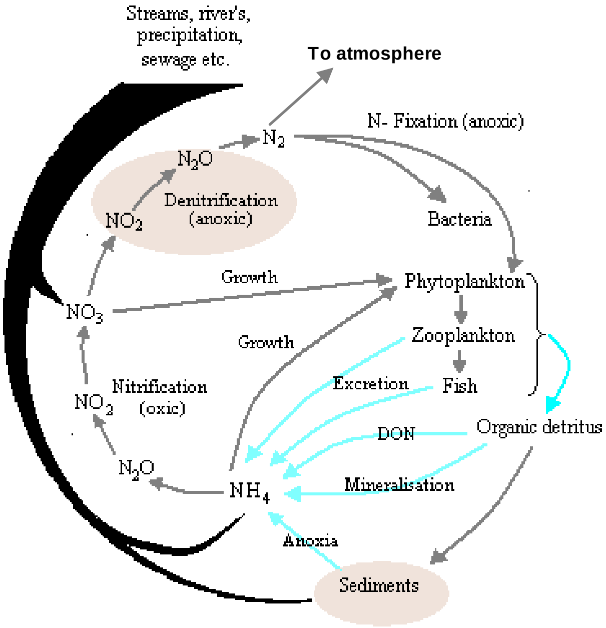


Figure 13. Simplified aquatic nitrogen cycle in lakes. Black arrows mark external loading, grey arrows represent internal lake processes and the blue arrows indicate internal loading events. The area marked in beige highlights those processes that occur in the sediment. Modified from Horne & Goldman (1994).

4.3. Colonisation trajectories of ecological indicators

Lake creation studies provide insight into colonisation trajectories without the significant alterations in environmental state associated with eutrophication management. The ecological responses documented in these studies will not reflect recolonisation of organisms exhibiting some level of dormancy in an impacted system but, instead, will reflect natural distribution and colonisation processes associated with ecological recovery.

An example of a well documented lake creation project is given by Yallop and O'Connell (2000), who followed the ecological development of three artificial lakes at the Wetlands Centre, London. The project was designed to enhance habitat for waterfowl by introducing macrophytes as a source of food and a *refugium* for macroinvertebrates and fish. The lakes were created in 1995 and inundated between 1996 and 1997. In this scheme, early planting of aquatic plants was abandoned due to extensive growths of filamentous macroalgae. For the first two years, all three lakes were characterised by such growths, phytoplankton blooms were frequent, and concentrations of TP and turbidity were high. TP concentrations decreased in all of the lakes in 1999, although they remained relatively high (>100 µg TP l^{-1}).

In 1999, one of the lakes, Sheltered Lagoon, underwent a switch from a phytoplankton dominated state to a clear water macrophyte dominated state. This coincided with the development of extensive beds of the macrophyte *Myriophyllum spicatum* (spiked water-milfoil) and a reduction in the cover of filamentous algae. This switch was not caused by the lowering of nutrient concentrations. Instead, it has been attributed to the shallow and sheltered nature of the lake and the fact that a drop in water level preceding the switch provided a "window of opportunity" for light levels at the sediment surface to be temporarily increased.

Between 1999 and 2001, two of the lakes, Sheltered Lagoon and Main Lake, oscillated between a turbid, phytoplankton dominated state, and a macrophyte dominated state, whereas Reservoir Lagoon, remained turbid and dominated by phytoplankton and benthic filamentous green algae (dominated by *Enteromorpha* sp.), throughout. The main driver of the undesirable phytoplankton dominated state in Reservoir Lagoon was identified as high grazing from waterfowl and the relatively high diversity of macrophytes in Main Lake was attributed to low grazing levels. Water level fluctuations (increasing competitive advantage) and elevated pH (pH>10 decreasing propagule survival) were both proposed as secondary pressures on the macrophyte community in Sheltered Reservoir (Yallop *et al*., 2004). The various state shifts reported in the Wetland Centre lakes are summarised in Table 4.

This case study highlights the importance of the stable states hypothesis when considering the climax ecological structure in newly created shallow lakes (Scheffer, 2004). In the early stages of lake succession, and where TP concentrations are high (i.e. summer TP concentrations of 200-5000 µg TP l^{-1}, in this case), the dominant autotrophic community will be rapidly growing phytoplankton and filamentous benthic algae. Once this community has established, it will shade out macrophytes, thereby reducing the likelihood of a switch from phytoplankton to macrophyte dominated state. The high biomass of phytoplankton will die back during the winter months, returning P to the sediment where it will be remineralised and released into the water column, thus sustaining the feedback loop and resistance to change. Further resilience was evident in the above case study in the form of high waterfowl grazing of macrophytes and high pH, which reduced propagule success. The steady state hypothesis suggests that shallow lakes can switch between phytoplankton and macrophyte dominated states, with no change in P load, as a result of a disturbance (Scheffer, 2004). In the case of Sheltered Lagoon, it was initially hypothesised that this switch took place as a result of a temporary increase in the euphotic depth associated with water level reduction (Yallop & O'Connell, 2000). The fact that this phenomenon was not observed in Main Lake or Reservoir Lagoon was attributed to this lake being particularly sheltered from wind induced sediment disturbance. Thus lakes should be expected to follow alternative colonisation trajectories based on lake specific pressures.

Table 4. Summary of state shifts in the Wetland Centre lakes, after Yallop et al. (2004). RL: Reservoir Lake; ML: Main Lake; SL: Sheltered Lagoon. Clear: clear water macrophyte dominated state (with dominant macrophyte species indicated in brackets); Turbid: phytoplankton or benthic filamentous algal dominated turbid water state; TP and phytoplankton crop measured as summer means (May - September). Macrophytes consumed expressed as percentage of macrophyte community estimated to be removed by calculated grazing rates for waterfowl community. Species key – Myriophyllum spicatum (M); Elodea nutalii (E^1)*; Zannichellia palustris (Z), Potamogeton pectinatus* (P^1)*; Potamogeton pusilis* (P^2)*; Elodea Canadensis* (E^2)*. ND = no data. Chl a = chlorophyll a.*

Lake name	Year	State	TP (mg l^{-1})	Macrophyte max. biomass (kg dw^{-1} ha^{-1})	Phytoplankton crop (µg Chl *a* l^{-1})	Macrophytes consumed by waterfowl (%)
SL	1998	Turbid	0.2 – 5.0	ND		
	1999	Clear (M)	0.38	2450	13	
	2000	Clear (E^1,M)	>0.10	1983	11	7.7
	2001	Turbid (E^1)		Low	150	7.3
RL	1998	Turbid	0.2-5.0	ND		
	1999	Turbid	0.39	620	45	
	2000	Turbid	>0.10	1650	45	22.0
	2001	Turbid			58	15.0
ML	1998	Turbid	0.2-5.0			
	1999	Turbid (Z)	0.19	230	105	
	2000	Clear (P^1,P^2,E^2)	>0.10	1717	8	32.9
	2001	Clear-Turbid ($P^{1,2}$)			46	8.5

The Olentangy River Wetland Research Park (ORWR) is a research site on which two wetlands (1 ha. in area; <1 m deep) were created to have similar hydrological signatures (Mitsch et al., 2005). These wetland systems included both large shallow areas to favour marginal macrophyte species and open water "deeper" (up to 100 cm) areas to support submerged macrophyte species. The project addressed a range of hypotheses designed to compare the effects of macrophyte introduction by planting with natural macrophyte colonisation. The tested hypothesis was that "planted and unplanted basins will be similar in function in the beginning, diverge in function during the middle years and ultimately converge in structure and function". This is conceptualised in Figure 14.

The theoretical recovery trajectories presented in Figure 14 were comprehensively tested in the two ORWR constructed wetlands using macrophyte community composition and productivity estimates over a 10 year period following wetland creation (Mitsch et al., 2005). The key results from this study included:

- survival of planted macrophytes was higher for the emergent community (~ 5 – 80% survival of individual plants) than the submerged community (<10 % survival; *Potamogeton pectinatus*) within 1 month of planting,
- macrophyte cover increased annually in each wetland for the first 5 years, with an apparent stable community being established at this time,
- macrophyte colonisation rate was higher in the planted wetland for the first 3 years.

- after 3 years, the unplanted wetland was dominated by a monoculture of *Typha* spp., whereas the planted wetland had a more diverse community (*Sparganium eurycarpum*, *S. tabernaemontania*, *Typha* spp. and *Scirpus fluviatilis*),
- herbivorous grazing by muskrats reduced macrophyte cover in both wetlands (to 27.6% and 17.4% cover in the planted and unplanted wetlands, respectively) in Year 6. This peak in muskrat grazing was attributed to an association between high macrophyte cover in Year 5 and an associated increase in muskrat productivity due to improved habitat. Muskrat numbers dropped in Year 7 apparently in response to low macrophyte cover in Year 6,
- an experimental drawdown was conducted in the spring of Year 7 in an attempt to “re-set” the seed bank. This resulted in the highest recorded macrophyte cover (73% and 74% cover for the “planted” and “non-planted” wetlands, respectively) and a decrease in the dominance of *Typha* spp. in both wetlands. The community structure of the wetlands had generally converged by this point,
- macrophyte productivity (expressed as dry weight) increased in both wetlands throughout the study. Productivity was consistently higher in the unplanted wetland, with the onset of an apparent plateau reported in the unplanted wetland, only, in Year 10, and
- macrophyte community diversity (expressed as community diversity index) was consistently higher in the planted wetland than in the unplanted wetland.

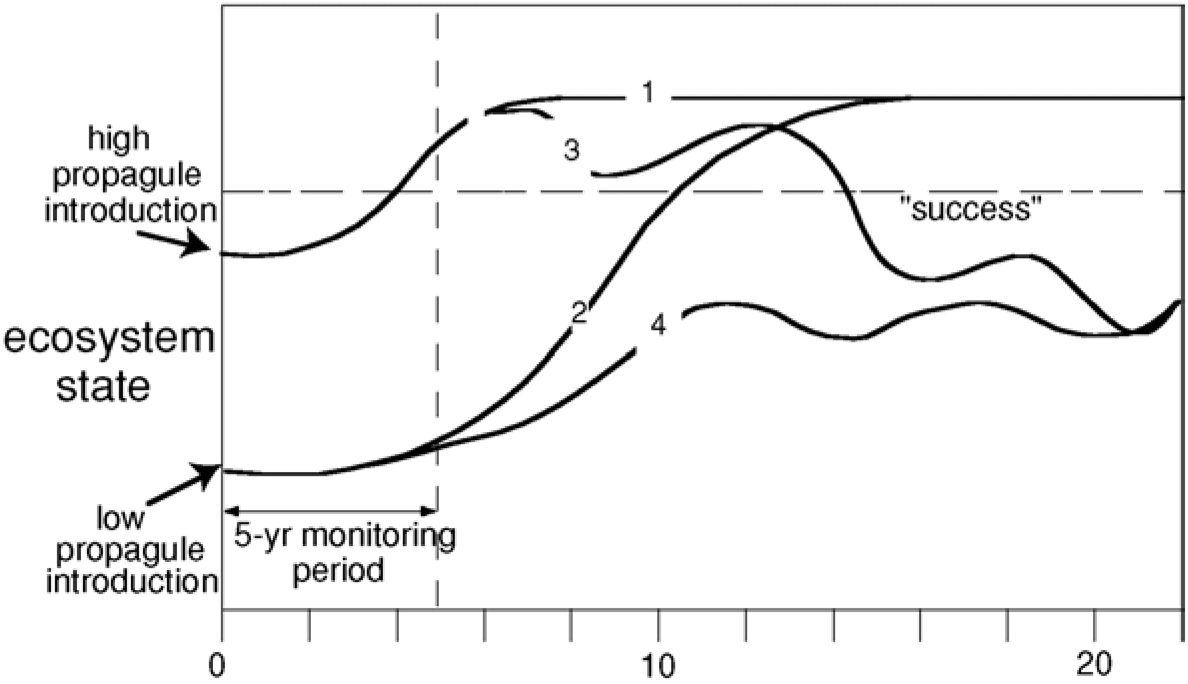


Figure 14. Hypothetical recovery scenarios based on macrophyte colonisation for created wetlands (after Mitsch et al., 2005). Scenarios 1 and 2 represent recovery trajectories with no secondary pressure; scenarios 3 and 4 represent recovery trajectories with secondary pressures leading to deterioration in the recovery end point in terms of ecosystem state.

Table 5. Summary of the findings of 364 peer reviewed publications in terms of the timescales and trajectories of structural and functional ecological recovery of lakes after eutrophication management. References were retrieved from Web of Science using the search term [Lake+Eutrophication+Recovery] in January 2011.

Organism group	Main changes in environmental state	Impacts on ecological structure	Impacts on ecological function	Factors confounding recovery
Bacterioplankton (<18 years)	Decrease in TP leading to change in zooplankton community	Unclear – potential increase due to DO increase but potential decrease due to higher grazing rates by *Daphnia*	Increase or decrease in contribution to energy transfer	Unknown
	Increase in DO			
	Decrease in labile DOC through reduction in planktonic production			
Phytoplankton (2-20 years)	Reduction in TP concentration	Overall reduction in phytoplankton biomass (especially in spring and summer). Reduction may be slower in summer due to internal loading	Decrease in quantity and increase in quality of food for zooplankton	Sustained P availability in metalimnion of stratified lakes leading to dominance of metalimnetic cyanobacteria
	Increase/decrease in TN concentration	Reduction in spring diatom biomass	Decreased organic matter deposition to the sediment	N limitation prior to restoration leading to no response in phytoplankton community
	Increase/decrease in Si concentration	Increase in importance of diatoms, cryptophytes and chrysophytes in shallow lakes	Lower mass of nutrients available for internal nutrient cycling	Increase in Si concentrations in summer caused by P limitation of diatoms in spring
		Reduction in relative contribution of cyanobacteria to total phytoplankton community at meso-oligotrophic end point TP concentrations	Increase in DO concentrations at the sediment surface	Increased external loading and persistent internal loading
		Replacement of non-heterocystous cyanobacteria with heterocystous cyanobacteria following strengthened N limitation at mesotrophic end point TP concentrations	Increased resilience to negative switches from clear water conditions	Natural and human induced changes in fish stock leading to trophic cascades through zooplankton

		Decrease in cyanobacteria and an increase in relative contribution of dinophytes and chrysophytes in deep lakes	Lower risk of cyanobacterial toxin production	Feedback mechanisms between buoyancy regulating cyanobacteria and sediment P cycling in poorly flushed lakes
		Species richness increase towards mesotrophic TP end point	Higher overall genetic diversity	
Zooplankton (1-17+years)	Reduction of TP concentration	Increase in *Daphnia* and large cladoceran relative abundances (e.g. *Daphnia hyalina* and *D. galeata*) in relation to smaller taxa (e.g. *D. galeata, D. ambigua, Ceriodaphnia pulchella*), and especially in relation to rotifer biomass, as nutrient conditions change from hypertrophic to mesotrophic	Increased relative grazing pressure on smaller "edible" phytoplankton and bacterioplankton	Presence of predatory zooplankton as a result of top down effects of fish
	Increased macrophyte cover as *refugia*	Increase in zooplanton:phytoplankton ratio	Higher intensity clear-water phase in spring	Fish stocking with zoplanktivorous fish
	Increase in edible phytoplankton relative to cyanobacteria	Increase in cladoceran species richness	Increased resilience of ecosystem to reverse switch through control of phytoplankton	Recovery of zooplanktivorous fish following biomanipulation
	Decreased zooplanktivorous fish abundance relative to piscivorous fish	Increase in cladoceran body size	Greater relative importance as a nutrient source at low nutrient concentrations	Inputs of pesticides
		Decrease in total zooplankton biomass.	Higher overall genetic diversity.	Inputs of other industrial pollution.
		Increase in oligotrophic indicator species including *Ceriodaphnia cornuta*, *Daphnia gessneri*, other small cladocerans like *Moina micrura*, *Bosminopsis deitersi*, *Notodiaptomus cearensis* and oligotrophic calanoid copepod species towards oligotrophic conditions	Decreased organic matter deposition to sediments	Occurrence of marine macroinvertebrate grazers following salinisation

Macroinvertebrates (10-20 years)	Reduction in organic matter to sediment	Reduced overall abundance.		High benthivorous fish abundance
	Increased DO concentrations in benthos	Increased species richness and diversity		Stratification leading to anoxia in benthos
	Change in grazing pressure related to fish community change	Plecoptera, Ephemeroptera, Coleopteran, Trichoptera all increased in relative abundance		Increase in external loading and/or persistent internal loading
	Expansion of macrophytes into deeper waters	Increase in relative abundance of indicator taxa, e.g. Cladocera, gastropods & Hydracarina - "oligotrophication". More extensive colonisation of deeper water linked to macrophyte recovery.		Persistent organic sediment loading
		Increase in chironomid to oligocheate ratio		Invasion by dreissenid mussels
Macrophytes (2-40+ years)	Reduction in TP and TN concentrations	General shift from macroalgae (e.g. *Cladophora* and *Enteromorpha* spp.) => tall angiosperms (e.g. *Potamogeton pectinatus*; *Myriophyllum spicatum* etc.) => short angiosperms (e.g. *Eleocharis acicularis and Littorella uniflora*), characean macrophytes (e.g. *Chara globularis* and *Nitellopsis obtuse*) and mosses (e.g. *Fontinalis antipyretica)* as nutrient concentrations are reduced from hypertrophic to oligotrophic conditions	Decrease in sediment P release at low-moderate biomass leading to aeration of sediments or an increase in sediment P release at high biomass; this results in hypoxia in benthos or reduction in sediment disturbance leading to decrease sediment P release	Increase in external loading and/or persistent internal loading
	Reduction in phytoplankton biomass	Increase species richness towards mesotrophic conditions.	Partitioning of P from phytoplankton to macrophyte biomass	Grazing by herbivorous waterfowl (e.g. coot) and fish (e.g. bream and roach)
	Increase in water clarity	Increase macrophyte colonisation depth towards meso-oligotrophic conditions	Increase in benthic primary production	Habitat disturbance due to wave action and water level fluctuations

	Improvement in substrate quality	Increased frequency of occurrence towards mesotrophic conditions	Increase in *refugia* for benthic and planktonic organisms.	Macrophyte control by humans using mechanical harvesting or herbicides.
	Reduction in herbivorous waterfowl and fish	Macrophyte abundance decreases above about 2 mg N l^{-1} due to competition for light with epiphytes	Decrease in water column NO_3-N concentrations through direct uptake and enhanced denitrification	Invasive species ingress or extinction of regional seed bank or blocked distribution pathways
	Reduction in periphyton shading		Increase in food supply for waterfowl and fish	
Fish (2-10+ years)	Decrease in TP concentrations	Shift from cyprinids to percids to coregonids to salmonids with decreasing TP	Competitive advantage for visual predators	Biomanipulation and/or invasive non-native species
	Increase in water clarity	Fish species richness increases towards 0.1 to 0.4 mg TP l^{-1}	Increased predation pressure on zooplanktovorous fish	Persistent internal loading
	Increase in macrophyte abundance	Increase in littoral fish species (e.g. gudgeon, rudd, and pike) relative to pelagic species (e.g. pikeperch and ruffe)	Increased energy transfer through littoral habitats	Climate change related temperature increases, especially in winter and spring
	Decrease in zooplankton biomass	Decrease in fish abundance with decreasing TP	Increase in chlorophyll:phosphorus ration as a result of trophic cascade	Blocked distribution pathways
Waterfowl (2-21+ years)	Reduction in TP concentrations	Increase in herbivorous bird species including coot, goldeneye, and pochard	Increased energy transfer to waterfowl	Competition for food with bream
	Reduction in benthivorous fish species	Increased benthivorous birds	Increased grazing on macrophytes	Persistence of internal loading delaying recovery of macrophytes and macroinvertabrates
	Increase in macrophyte abundance		Increased nutrient inputs to lakes	Extreme fluctuations in water level
	Increased abundance of macroinvertebrates		Increased nutrient cycling from macrophytes through waterfowl to water column	

4.4. Ecological recovery following eutrophication management

4.4.1. Ecological recovery of the bacterioplankton community

The responses of the bacterioplankton community following eutrophication management (Table 5) were summarised from only 3 publications. Meta-analyses and data from long-term studies documenting eutrophication and recovery were used to describe temporal responses.

Very few studies have considered the effects of eutrophication and recovery on bacterioplankton. In a long-term study of Lake Ladoga (Russia), bacterioplankton abundance and dark CO_2 fixation were observed to increase (0.54 – 1.02 x 10^6 cells ml^{-1} and 0.49 µg C l^{-1} d^{-1} – 2.4 µg C l^{-1} d^{-1}, respectively) with increasing TP concentrations (Kapustina, 1996 & 1999). The observed increases in bacterioplankton abundance and CO_2 consumption were coupled with a decrease in total organic carbon (TOC) from 9 mg l^{-1} to 6.3-8.3 mg l^{-1} with no apparent change in external loading of TOC. Whole lake TOC mass balance estimates indicated that bacterioplankton consumed more TOC than could be produced by phytoplankton alone, leading to the conclusion that bacterioplankton production was supported by both autochthonous (low molecular weight) and allochthonous (high molecular weight) TOC. This observation suggests that bacterioplankton production was limited by resources other than TOC availability in Lake Ladoga prior to eutrophication. This is in agreement with other studies in which P-limitation of bacterioplankton has been observed. For example, Spears and Lesack (2006) reported an increase in bacterioplankton production in mesocosm nutrient (N and P) amendment bioassays using natural communities from three lakes in the Mackenzie Delta, Canadian Arctic, particularly at low SRP concentrations of less than 10 µg l^{-1}.

Bacterioplankton production and abundance were measured, and grazing by zooplankton modelled, in Lake Søbygaard (Denmark) following external N and P load reduction (Jeppesen et al., 1998). Although no significant decrease was observed in bacterioplankton production, abundance was reported to vary as a result of zooplankton grazing (by *Daphnia*) pressures associated with a recovery-induced trophic cascade. An increase in the cyprinid fish community biomass resulted in a shift in the dominant zooplankton taxa from *Bosmina longinostris* and ciliates to *Daphnia,* the latter being observed to be responsible for much higher rates of bacterioplankton removal. This trophic cascade resulted in an increase in the contribution of bacterioplankton to energy transfer through the food web from 1% to around 8% (Jeppesen et al., 1996). Work and Havens (2003) provide evidence of bacterioplankton ingestion by both micro- and macro-zooplankton species (35 species in total) in Lake Okeechobee (Florida, USA) and suggest that ingestion may be the result of (1) unavoidable ingestion whilst feeding due to the high density of bacterioplankton and (2) a requirement to supplement more “edible” food sources, such as cryptophytes and small chlorophytes.

4.4.2. Ecological recovery of the phytoplankton community

The responses of the phytoplankton community following eutrophication management (Table 5) were summarised from 226 publications. Meta-analyses and data from long-term studies documenting eutrophication and recovery were used to describe temporal responses and nutrient thresholds.

The resource requirements of phytoplankton vary at the species specific level. In general, phytoplankton require light energy within a wavelength of 400-700 nm and readily accessible supplies of the nutrients (in general order of importance) C, N, P, Si, K, Ca, Mg, S, Fe, Mn, Cu, Zn, Cl, Mo, and Co (Raven & Maberly, 2005). Limitation by any of these elements can, theoretically, occur (Tilman et al., 1982). However, carbon limitation is unlikely to control phytoplankton production in shallow, high alkalinity, lakes where CO_2 inputs from the atmosphere can supplement phytoplankton uptake.

P, N, and Si (generally in that order) are the major limiting nutrients in freshwater lakes. Available sources of dissolved N include nitrate (NO_3^-), nitrite (NO_2^-) and ammonium (NH_4^+), although certain species of cyanobacteria can also “fix” N gas (N_2) directly from the atmosphere. The dominant available forms of P and Si are dissolved orthophosphate (PO_4^{3-}; also known as soluble reactive phosphorus [SRP]) and silicate (SiO_2), respectively. Silicate availability mainly limits diatom growth, whereas that of N and P can limit all phytoplankton. Studies of both marine and freshwater phytoplankton have suggested that ‘balanced’ growth occurs at molar ratios of 106C:16N:1P (Redfield, 1958). Seasonal variability in the main limiting nutrients is strong in lakes that are recovering from eutrophication, where sediment processes and biological uptake regulate stoichiometry to favour P or Si limitation in winter and spring and N limitation in summer (Figure 15; Spears et al., 2009b).

At the multi-lake scale, a clear correlation is commonly observed between TP concentration and phytoplankton biomass (expressed as chlorophyll *a* concentration) (e.g. Figure 16). However, in many cases, water quality targets for phytoplankton are not simply a reduction in chlorophyll *a* concentration. They are often aimed at reducing the public health risk by controlling the accumulation of potentially harmful cyanobacteria. It is, therefore, important to understand the drivers and responses of both phytoplankton biomass and community composition.

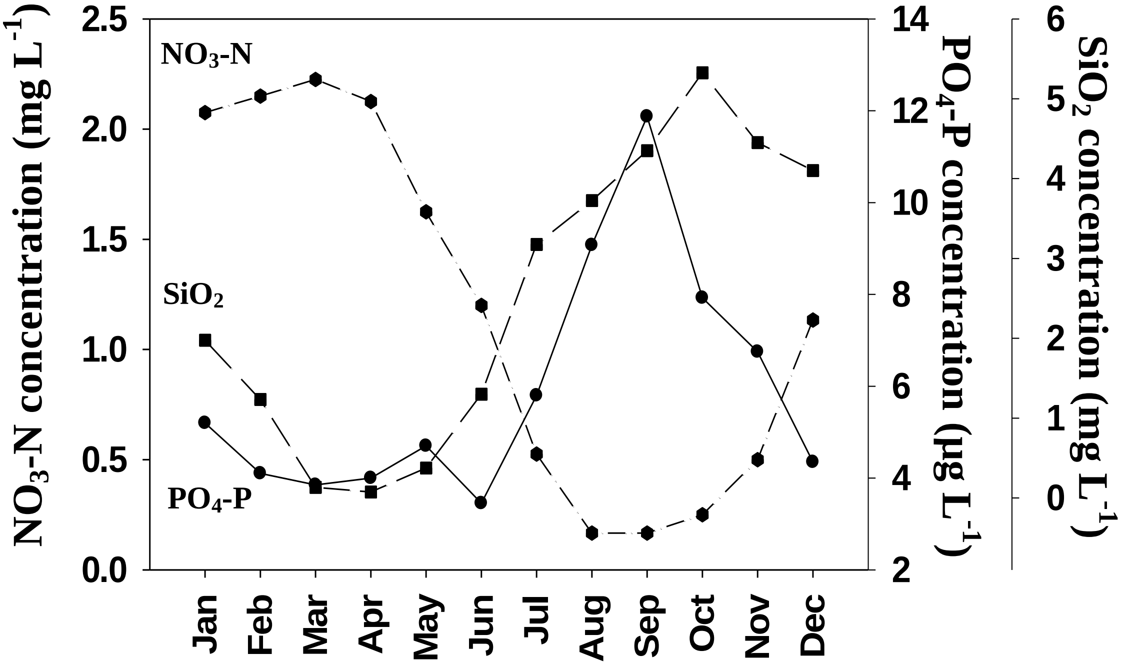


Figure 15. Average monthly water column concentrations of PO_4-P, NO_3-N, and SiO_2 during the recovery period in Loch Leven. Years included in the average values are 1997, 1998, 1999 and 2000 (after Spears et al., 2009b).

Bellinger and Sigee (2010) outline the general community level changes expected to occur with decreasing trophic status in lakes. Hypertrophic lakes are expected to be dominated throughout the year by small unicellular cyanobacteria and green algal taxa with short life cycles. In eutrophic lakes, a short, spring diatom bloom is expected to be followed by a mid-summer bloom of large unicellular (e.g. *Ceratium* spp.), filamentous (e.g. *Anabeana* spp.) and globular cyanobacteria (e.g. *Mycrocystis* spp.). In mesotrophic lakes, the diatom spring bloom will be longer and followed by a more diverse summer peak of dinoflagellates, green algae and cyanobacteria. Oligotrophic lakes are usually characterised by a long spring diatom bloom and diatoms may continue to dominate throughout the growing season or co-exist with chrysophytes and desmids. In deep, stratifying lakes, cyanobacteria species capable of vertical migration (i.e. capable of accessing sediment P stores, such as *Gleotrichia* spp.; Karlson-Elfgren et al., 2003) may also occur. This general model is in agreement with the results of multi-lake (27 lakes) analyses of phytoplankton community responses following nutrient load reduction (Jeppesen et al., 2005b). These observed changes included an increase in the importance of diatoms, chryptophytes and chrysophytes with decreasing P concentrations in shallow lakes (mean depth <5 m or polymictic), and a decrease in the relative contribution of cyanobacteria and an increase in dynophytes and chrysophytes in deep lakes following reduction of nutrients, especially TP. Meta-lake analyses of Danish lakes indicate a decrease in percentage cyanobacteria at TP concentrations below 0.6 µg l^{-1}, with peak cyanobacterial dominance occurring in the range of 500 µg l^{-1} to 1000 µg l^{-1} (Jeppesen et al., 1991). These general community shifts, and the TP ranges over which these shifts were found to occur, are summarised in Figure 17.

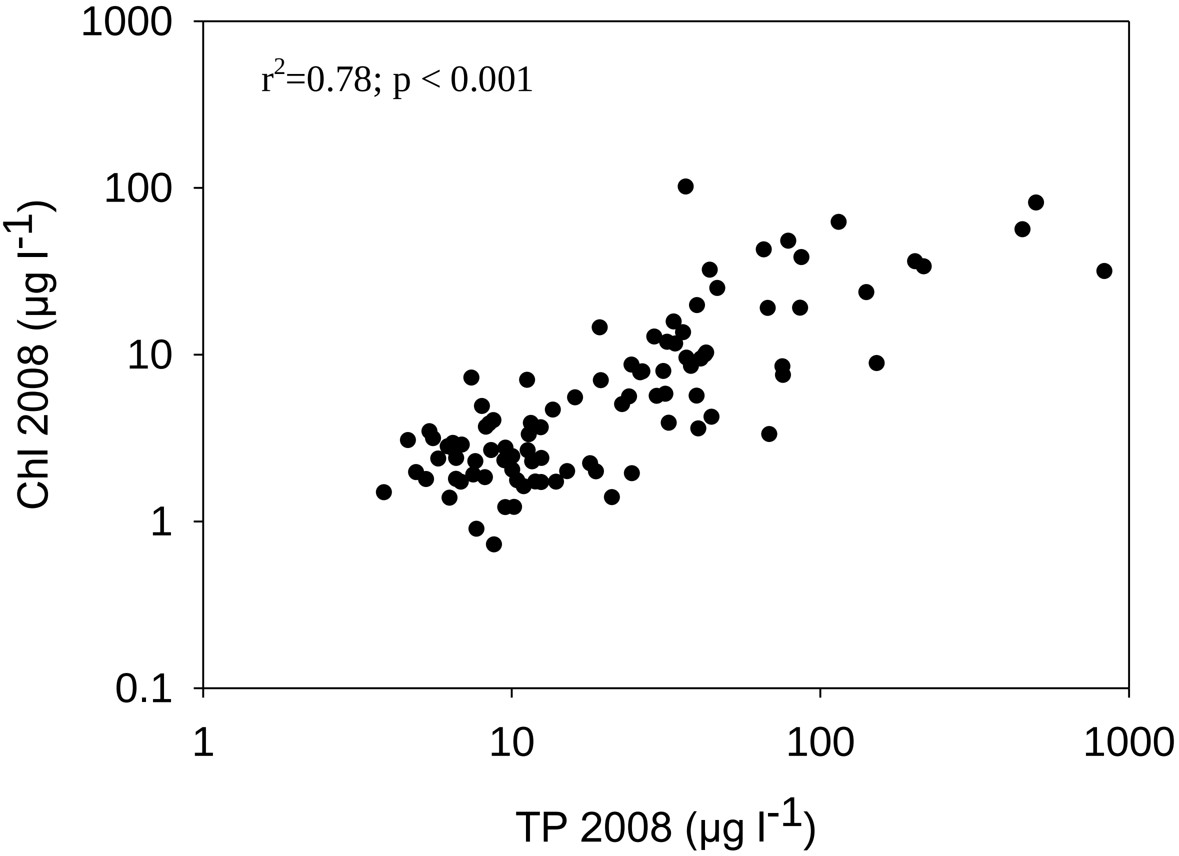
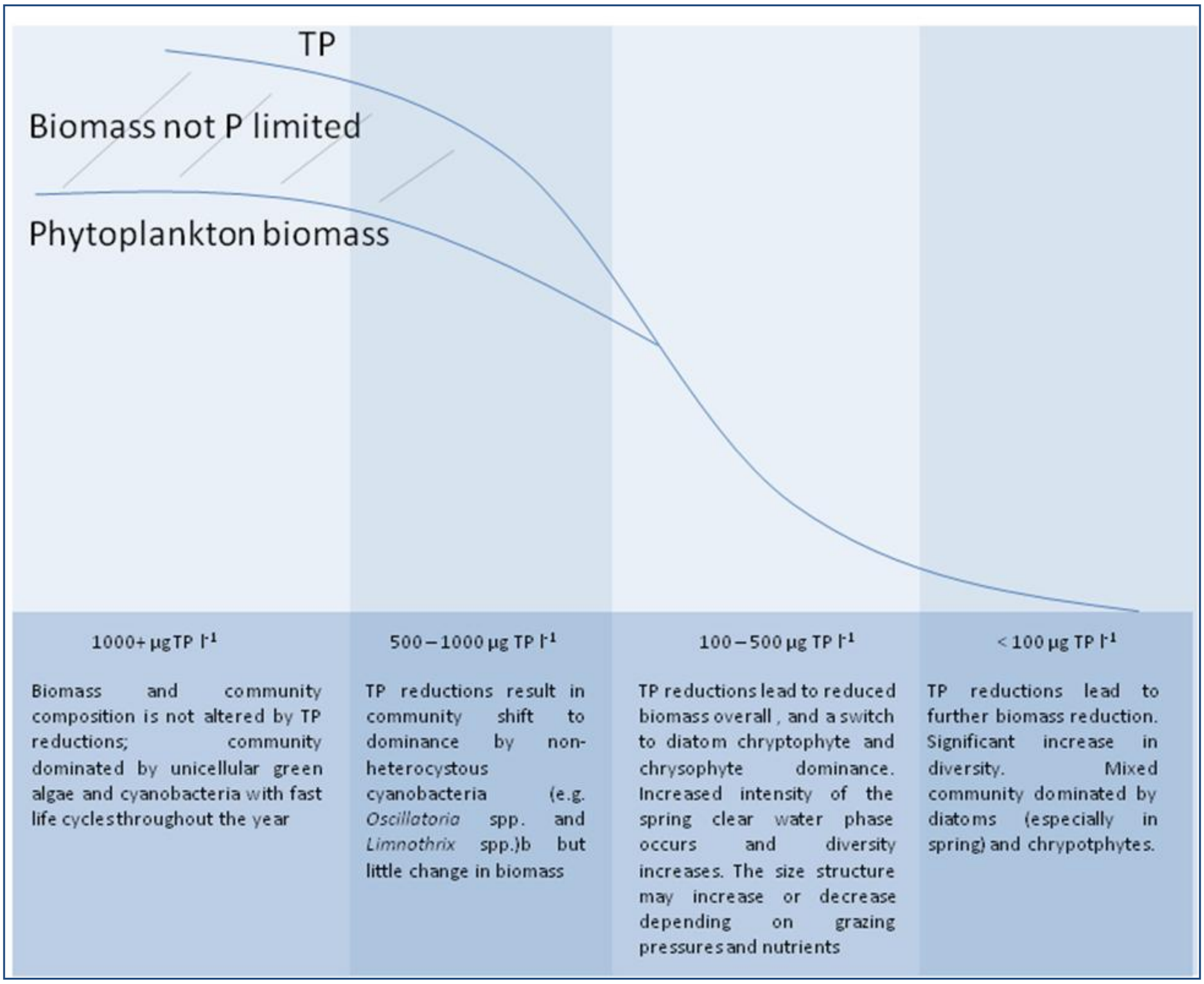


Figure 16. Plot of annual mean total phosphorus (TP) and chlorophyll a (Chl) concentrations from 95 Scottish lochs in 2008, showing results of correlation analysis. Data provided by SEPA. Note log scales.

A range of lake-specific responses were also reported that were not consistent with the general responses outlined above. This may have been due to the following reasons:

- end point TP concentrations varied (*ca*. 6 to > 250 µg TP l^{-1}), resulting in a range of phytoplankton recovery end points,
- in shallow lakes, where summer N-limitation was apparent, a decrease in non-heterocystous cyanobacteria species (e.g. the *Oscillatoria* spp., *Limnothrix redeki* and *Planktothrix agardhii*) was reported relative to N_2-fixing species (e.g. *Aphanizomenon flos-aquae*) when P concentrations were moderate (e.g. Keto & Tallberg, 2000; Kohler et al., 2005; Phillips et al., 2005),
- natural or human induced alteration in fish community composition can alter the response of the phytoplankton community as a result of top-down pressures (e.g. Jeppesen et al., 1998; Sarvala et al., 2000; Ruuhijärvi et al., 2010),
- climate change is rarely considered as a driver in restoration studies, although a range of studies have reported changes in the phytoplankton community over short and long time-scales (e.g. Anneville et al., 2005; Kernan et al., 2010; Box 3), and

- in large lakes, species richness is unlikely to be reduced due to species replacement, especially in large lakes where species extinctions can be rare due to the presence of *refugia* (Dokulil & Tuebner, 2005; Padisak & Reynolds, 1998; Box 3).



1000+ µg TP l^{-1}	500 – 1000 µg TP l^{-1}	100 – 500 µg TP l^{-1}	< 100 µg TP l^{-1}
Biomass and community composition is not altered by TP reductions; community dominated by unicellular green algae and cyanobacteria with fast life cycles throughout the year	TP reductions result in community shift to dominance by non-heterocystous cyanobacteria (e.g. *Oscillatoria* spp. and *Limnothrix* spp.)b but little change in biomass	TP reductions lead to reduced biomass overall , and a switch to diatom chryptophyte and chrysophyte dominance. Increased intensity of the spring clear water phase occurs and diversity increases. The size structure may increase or decrease depending on grazing pressures and nutrients	TP reductions lead to further biomass reduction. Significant increase in diversity. Mixed community dominated by diatoms (especially in spring) and chrypotphytes.

Figure 17. Conceptual diagram relating changes in the phytoplankton community reported in the literature with the TP concentration ranges generally associtaed with the change. Adapted from Sas (1989).

The dominance of cyanobacteria in eutrophic lakes is regulated by a range of factors. Multi-lake studies have indicated that cyanobacterial biomass increases as N and P concentrations increase (Downing et al., 2001), and under low N:P ratios combined with low light levels (i.e. light-/N-limitation; Levine & Schindler, 1999). The latter are attributed to the ability of a range of cyanobacterial species to exist under low light conditions, to fix atmospheric N_2 when the supply of dissolved N is low, and to persist in dormant states in surface sediments (Head et al., 1999). However, a range of site specific physical attributes are also known to be important drivers. For example, cyanobacterial biomass is known to be inversely related to flushing rate in European lakes (Tyler et al., 2010), and to increase with decreasing water turbulence (Steinber

& Hartmann, 1988). Manipulation studies have also suggested that creating artificial turbulence may be an effective, physical means of controlling cyanobacterial blooms (e.g. Coldingham Loch; Bailey-Watts et al., 1987). Cyanobacteria may also dominate under conditions of strong zooplankton grazing, where more "edible" phytoplankton groups such as diatoms and green algae are preferentially removed from the community (Chow-Fraser et al., 1994).

BOX 3: LAKE BALATON, HUNGARY

Lake type

Large (596 km^2), shallow (mean depth 3.2m; maximum depth 11.2m), well-mixed, lake with a water retention time of *ca*. 3-8 years; predominantly phosphorus (P) limited throughout the year.

Catchment characteristics

River Zala is the main inflow draining about half of the catchment (total catchment area: 5775 km^2) with 51 minor inflows (20 permanent) draining the remainder.

Driver

Increasing population density, agricultural intensification and industrial development increased the P input to about 4 g P m^{-2} yr^{-1} in 1980-1988. Poor water quality conditions persisted between 1975 and 1981.

Pressure

Nutrient enrichment, invasion of non-native fish species (including silver and common carp; 60% of annual commercial catch in 1990s); commercial fishing pressures.

State

Annual mean TP concentrations increased to >100 µg l^{-1} (basin 4; 1980s). More than 90% of the predatory fish (pikeperch and pike) were removed as a result of commercial fishing; integrated catch per unit effort (CPUE) rank was white bream>roach>common bream>bleak. Biomass of total fish stock was estimated to be 120-194 kg ha^{-1} (+/- 45-63% S.D.) during 1996-2000.

Impact

Mean annual chlorophyll *a* concentrations were maintained at about 50 µg l^{-1} during the 1980s in the hypertrophic western basins of Lake Balaton. Cyanobacterial dominance increased in summer in terms of biomass. No obvious change in eukaryotic phytoplankton community structure was observed, probably due to wide overlaps in the ecological requirements of individual species (e.g. 23 Thalassiosiracean species were recorded in Lake Balaton in 1980). In contrast, a general shift in the cyanobacterial community was observed to favour Nostocalean algae, including species characteristic of tropical and sub-tropical areas, and *Aphanizomenon* spp., *Anabaena* spp., *Cylindrospermopsis raciborskii* and other filamentous species of *Planktothrix, Limnothrix and Pseudanabaena*.

Response

A series of sewage treatment improvements and diversions within the catchment, coupled with the inundation of a nutrient retention wetland, reduced external nutrient load to 2 mg TP m^{-2} yr^{-1} by 1989-2002. This resulted in a reduction of TP to <40 µg l^{-1} within 10 years of the onset of management.

Phytoplankton recovery

Mean annual chlorophyll *a* concentrations in the hypertrophic western basin decreased from > 50 µg l^{-1} (1980s) to <20 µg l^{-1} by 2000. During this period, no significant changes were observed in the eukaryotic phytoplankton community composition. In contrast, the cyanobacterial community shifted towards more northern-temperate species, including *Anabaena compacta*, *A. circinalis* and *Aphanizomenon gracile*. The contribution of cyanobacteria to total phytoplankton biomass gradually decreased (from about 100% in 1983 to about 80% in 1997) in the hypertrophic western basin over about a 15 year period post management. Responses in the less productive eastern basin suggested an increase in cyanobacterial dominance in summer. In 1997, phytoplankton biomass in the eastern basin exceeded that recorded in the western basin for the first time in the documented water quality history. The delay in the response of the phytoplankton community was attributed to internal P loading. A general decrease in heterocystous N-fixing cyanobacteria species was observed and attributed to an inability to fix N under P-limited conditions. Sporadic blooms of the N-fixing *Cylindrospermopsis raciborskii*, a sub-tropical cyanobacterium, were observed during the recovery period, although, only during specific environmental conditions when water temperatures reached 22-24°C. This was the optimum range for akinete germination of this species whereas it is 17-26°C for other heterocytous cyanobacteria. The fish community was dominated by cyprinids both before and after the reduction in TP concentrations and no significant changes in the abundance of crustacean zooplankton or the cladocera/copepoda ratio were observed. These results indicate that the responses in the phytoplankton community were the result of nutrient reduction, primarily, with anomalous high temperature weather events causing sporadic blooms of rarer taxa.

References

Padisak & Reynolds, 1998; Tatrai et al., 2008

4.4.3. Ecological recovery of the zooplankton community

The responses of the zooplankton community after eutrophication management have been summarised from a review of 71 publications (Table 5) and by using meta-analyses and site specific studies with long-term data on eutrophication and recovery. The main changes in environmental state associated with the zooplankton community response were reduction in TP concentration, increased macrophyte cover leading to larger areas of *refugia*, improvement in food quality of the phytoplankton community, and a decrease in zooplanktivorous fish abundance relative to piscivorous fish. The key structural cause of changes in the zooplankton community is clearly the increase in the extent of macrophyte beds which offer a refuge from fish predation by (1) providing a physical *refugia* for larger bodied zooplankton, and (2) providing hunting habitat for piscivorous fish (e.g. Pike), which leads to a reduction in zooplanktivorous fish and a release of predation pressure on zooplankton. In general, an increase in cladoceran body size and species richness was reported as nutrient concentrations decreased, with an increase in the relative abundances of *Daphnia* spp. and large cladocera (e.g. *D. hyalina* and *D. galeata*) in relation to smaller taxa (e.g. *D. galeata*, *D. ambigua*, *Ceriodaphnia pulchella*), and especially in relation to rotifer biomass. As a result of the decrease in phytoplankton biomass, its reduced quality as a food source, and the decreased risk of predation, the zooplankton:phytoplankton ratio increases.

In a meta-analysis of 71 Danish lakes, Jeppesen et al. (2000) reported a decrease in zooplankton biomass (specifically, rotifers, cyclopoid copepods, calanoid copepods, small cladocera and *Daphnia* spp.) from about 1 mg DW l^{-1} to <0.5 mg DW l^{-1} across a TP gradient of > 400 µg l^{-1} to <50 µg l^{-1}. The relative contribution of each zooplankton group also varied across the TP gradient, with a general increase in *Daphnia* spp. and calanoid copepods being observed as TP concentration decreased. The range and maximum species richness of crustacean and total zooplankton also increased to maxima of about 25 and 60, respectively, as TP concentration decreased, increasing markedly between 50 µg l^{-1} and 100 µg l^{-1}. An increase in total zooplankton biomass and the zooplankton:phytoplankton ratio was observed at TP concentrations of <100 µg l^{-1} to 150 µg l^{-1} in a meta-analysis of contemporary long-term data from 27 lakes after the external nutrient load had been reduced (Jeppesen et al., 2005b). In a similar study involving a comprehensive analysis of long-term recovery data in 8 Danish shallow lakes, an increase in zooplankton biomass was observed only in November and December. During summer and autumn, small cladoceran biomass declined, *Daphnia* spp. and total cladoceran body weight increased, and the ratio of *Daphnia*:total cladoceran biomass increased (Jeppesen et al., 2005a). These results are in agreement with the general responses reported in the literature review outlined above.

The zooplankton community were particularly sensitive to secondary pressures including:

- failure of biomanipulation due to insufficient fish stock reduction, natural or human induced re-colonisation of target fish species, and low survival of stocked fish; all of these were found to lead to a reversal of the above general zooplankton responses through trophic cascades (Søndergaard et al., 2007; 2008),
- increased occurrence of predatory zooplankton may be caused by a range of factors, including biomanipulation/fish stocking (e.g. occurrence *Neomysis integer* following removal of perch in Lake Wolderwijd, Gulati & van Donk, 2002) and changes in toxic cyanobacteria (e.g. occurrence of *Neomysis integer* following reduction in *Prymnesium parvum* in the brackish Hickling Broad, UK; Bales et al., 1993); this can lead to a reversal of the general recovery processes outlined above,
- climate change, especially an increase in spring water temperatures, may enhance the response of *Daphnia* to recovery from eutrophication through increased abundance (Carvalho & Kirika, 2003), while phenological shifts can favour earlier occurrence in spring (Thackeray et al., 2010), and
- acidification may result in a drop in fecundity in *Daphnia* spp. and unbalance the zooplankton response to favour eutrophic community structures (Havens et al., 1993).

4.4.4. Ecological recovery of the macroinvertebrate community

The responses in the macroinvertebrate community to eutrophication management were summarised following a review of 68 publications (Table 5) and using long-term data from eutrophication management studies. Although a large number of papers were returned, few reported comprehensively on recovery in the macroinvertebrate community as a whole, instead focusing on specific groups, habitats or species. The main changes in environmental state caused by eutrophication management, and responsible for alterations in the macroinvertebrate community, were reduction in organic matter content, improvements in dissolved oxygen concentration in the benthos, increased cover of macrophytes in deeper habitats and changes in grazing pressure related to alteration in the fish community. These resulted in an overall decrease in the abundance of the community coupled with a shift towards taxa that are more characteristic of meso-oligotrophic conditions (e.g. gastropods and hydracarina). An increase in the ratio of chironomids to oligocheates and a general expansion of range into deeper habitats was also reported.

The following pressures were reported to confound the above general recovery responses:

- habitat specific responses, where communities in deeper areas respond more slowly (e.g. up to 10 years in Lake Ladoga, Russia; Viljanen et al., 2008) than communities in littoral habitats, probably due to sustained deposition of organic matter and reduced dissolved oxygen (DO) concentrations. For example, a negative correlation between organic matter deposition and oligocheate species characteristic of oligotrophic conditions has been demonstrated in Lake Geneva, Switzerland (Lang & Reymond, 1995; Lang, 1998),

- at high biomass, colonisation by non-native invasive dreissenid mussels (e.g. Zebra mussel; *Dreissena polymorpha*) may enhance the recovery of small deposit feeding gastropods and small predatory macroinvertebrates relative to large gastropods and filter feeders (Ricciardi et al., 1997); this reduces the explanatory power of current WFD ecological metrics such as percentage taxa sensitive to TP, and the TP Score and Indicator Taxa Metric (Atalah et al., 2010), and
- natural or human induced changes in the fish community may alter predation levels on specific groups within the benthic macroinvertebrate community, thereby altering their recovery (e.g. reduction in the density of *Chaoborus* and Chironomidae as a result of an increase in predation by whitefish, perch and roach in Lake Ring, Denmark; Berg et al., 1994).

BOX 4: LOCH LEVEN, SCOTLAND

Lake type

Large (13.3km^2), shallow (mean depth 3.9m; maximum depth 25.5m), well mixed, alkaline lake with a water retention time of *ca*. 0.5 years; predominantly phosphorus (P) limited.

Catchment characteristics

Catchment area 145km^2; mainly lowland agriculture with some forestry in upland areas.

Driver

Increasing population density, agricultural intensification and industrial development increased the P input to the lake from *ca*. 5 t y^{-1} in the early 1900s to *ca*. 20 t y^{-1} by 1985.

Pressure

Nutrient enrichment.

State

Winter P concentrations of *ca*. 40 µg l^{-1}; P retention coefficient of 0.61; accumulated organic sediments with high nutrient content.

Impact

Problem algal blooms, high turbidity and loss of macrophytes.

Response

Improved control of nutrient rich sewage effluent discharges, cessation of P inputs from industry, and better farm management reduced P inputs by *ca*. 60% between 1985 and 1995.

Macroinvertebrate recovery

Following the reduction in P input to the lake, the number of macroinvertebrate taxa in the littoral benthos increased significantly from 41 taxa in 1966-1973 to 153 taxa in 1993-2006. Of the latter, 45 taxa had not been recorded in the lake before and two of these were pollution intolerant insect species. The number of insect species increased dramatically between the eutrophication (1966-1973) and recovery (1998-2006) phases, with the number of Trichoptera Coleoptera, Plecoptera and Ephemeroptera species increasing by 225, 400, 550 and 700 percent, respectively. This probably reflects the fact that insects only spend part of their life cycle in the water and, as winged adults, are much more able to colonise new areas than many other macroinvertebrate species that do not have a life stage that lends itself to rapid dispersal. Although the number of macroinvertebrate taxa increased, there was an accompanying decline in overall macroinvertebrate abundance during the recovery phase. This is believed to have resulted from a decline in the amount of organic matter falling to the sediments as the productivity of the lake declined. As detailed sampling only began when the lake was already impacted, it is difficult to assess the extent to which recovery has been a complete reversal of degradation in relation to the macroinvertebrate community. However, it is interesting to note that the number of taxa found in the most recent surveys (i.e. 153) is higher than the number found in the pre-1966 surveys (i.e. 96), when the lake was beginning to experience a rapid acceleration in the eutrophication process.

References

Gunn et al, submitted.

4.4.5. Ecological recovery of the macrophyte community

The responses of the macrophyte community following eutrophication management have been summarised from a review of 76 publications (Table 5) and using long-term data from oligotrophication case studies. These responses included an increase in colonisation depth, species richness (including relative characean abundance), number of nutrient intolerant species and species distribution as TP concentrations decreased. Full recovery of species composition was rarely recorded, potentially as a result of physical barriers to distribution and/or the loss of nutrient intolerant seed banks in cases where eutrophic conditions had been prevalent for many years. Increased water clarity was the most commonly reported state change that lead to macrophyte community responses, although reductions (and increases) in TN concentrations were also reported to be important. At a structural level, macrophyte colonisation responses were observed relatively quickly (i.e. less than 5 years) after reductions in TP load. However, at a community composition level, recovery timescales for macrophytes (i.e. 2 to 40+ years) were reported to be greater than the transient period estimates outlined above. A general shift from macroalgae (e.g. hypertrophic: *Cladophora* spp. and *Enteromorpha* spp.) through tall angiosperms (e.g. eutrophic: *Potamogeton pectinatus*; *Myriophyllum spicatum*, etc.) and short angiosperms (e.g. mesotrophic: *Eleocharis acicularis* and *Littorella uniflora*) to characean macrophytes (e.g. oligotrophic: *Chara globularis* and *Nitellopsis obtusa*) and mosses (e.g. *Fontinalis antipyretica*) was reported as nutrient concentrations were reduced from hypertrophic to oligotrophic.

The response in macrophyte community composition to changes in nutrient availability is confounded by contrasting responses to TN and TP concentrations. Although a general increase in macrophyte species richness was commonly reported with decreasing TP concentration in the literature, a meta-lake analysis of 71 shallow Danish lakes reported the relationship to be unimodal with a peak between 100 µg TP l^{-1} and 400 µg TP l^{-1} (Jeppesen et al., 2000), macrophyte percentage cover and percentage volume of water inhabited increased markedly at TP concentrations below 100 µg l^{-1} – 200 µg l^{-1} and 50 ug l^{-1}, respectively (Søndergaard, 2007). In a similar meta-analysis of 204 Danish lakes, a decrease in macrophyte cover was reported at TN concentrations above about 2 mg TN l^{-1} (Gonzalez-Sagrario et al., 2005). In combination, these reports suggest that macrophyte cover and community composition will be low at TP concentrations of <130 µg l^{-1} to 200 µg l^{-1} when TN concentrations are greater than 2 mg l^{-1} (Gonzalez-Sagrario, 2005). It is likely that the decrease in macrophyte cover at high TN concentrations is the result of shading by epiphyton and phytoplankton. An increase in macrophyte species richness was reported in a meta-analysis of 60 shallow lakes in Poland and the UK where species number increased from <5 at winter NO_3-N concentrations of greater than about 6 mg l^{-1} to >5 and less than about 16 at winter NO_3-N concentrations approaching 0 mg l^{-1} (James et al., 2005). Under high TN conditions, macrophyte communities were typically dominated by fast growing eutrophic species including *Ceratophyllum demersum*, *Potamogeton pectinatus*, *Lemna minor* and *Lemna trisulca* (James et al., 2005).

Macrophyte maximum colonisation depth (MCD) is widely recognised as a simple proxy of macrophyte abundance in lakes. As phytoplankton concentrations increase, so light levels at the sediment surface decrease and macrophyte growth is restricted to shallower water. MCD is sensitive to a number of anthropogenic pressures, including eutrophication (Jupp & Spence, 1977; Søndergaard et al., 2005b; May & Carvalho, 2010).

The responses of the macrophyte community varied at the lake specific scale, probably because of a combination of the following factors:

- preferential grazing of species by herbivorous waterfowl and fish, leading to variations in end point community composition,
- invasion by more competitive species leading to loss or suppression of native species,
- insufficient sampling effort leading to inaccuracy in community composition and cover estimation (Spears et al., 2009a; Gunn et al., submitted),
- persistent habitat disturbance (e.g. wind induced wave disturbance), potentially linked to climate change and the NAO (Spears & Jones, 2010), which can “re-set” the recovery trajectory to favour the turbid state in shallow lakes (e.g. Lake Apopka, USA; Havens et al., 2001), and
- seed banks, available distribution networks and pathways, and species distribution and growth traits will dictate the recovery trajectory of the macrophyte community. It is likely that, following initial macrophyte colonisation by c-strategists (i.e. fast growth rate; canopy forming; tall vegetation) s-strategists (slow biomass growth, luxury resource uptake, high root:shoot ratio, small, long lived vegetation) then appear as nutrient concentrations decrease (Riis & Biggs, 2001).

Few long-term data exist with which the pressure-impact-response relationship between eutrophication and macrophyte community can be assessed at relatively high temporal frequency (i.e. years to decades) over long time spans. However, in Loch Leven, observations over a 40 year period revealed a decrease in species richness, species evenness and MCD associated with increasing eutrophication, followed by a slow improvement in these parameters associated with reductions in external TP load that lasted more than 20 years Dudley et al., (submitted). A similar macrophyte response to eutrophication was observed by Sand-Jensen et al. (2008; Box 5), who analysed 100 years of data from Lake Fure (Denmark). In this study, the observed decreases in MCD, species richness and species distribution during the eutrophication phase had still not been reversed completely 30 years after P inputs had been reduced by 95 per cent. A shift in community composition from small angiosperms, mosses and characeous macroalgae (unimpacted, mesotrophic state) to tall angiosperms (impacted, eutrophic state) was observed over the period of eutrophication in both studies. Also, during the recovery phase, the submerged vegetation only partly recovered in terms of species richness and depth penetration, with many of the small species that had been lost during eutrophication failing to re-appear.

Shifts in community composition can be characterised mathematically to give an index of change based on the sensitivity of a given species to nutrient conditions. This method of assessment is currently being investigated for use across Europe under the WFD (Penning et al., 2008). For the UK, Willby et al. (2006) outline a method of numerically classifying macrophyte species according to their sensitivity to eutrophication and using these numerical classifications to calculate a whole lake Trophic Rank Index (TRI). The TRI has been shown to vary with TP on an annual scale (Penning et al., 2008). TRI may, therefore, be a useful metric for assessing changes in macrophyte community composition that can be used alongside MCD, which is a measure of community distribution or extent.

BOX 5: LAKE FURE, DENMARK

Lake type

Large (9.4km^2), deep (mean depth 7.4m; maximum depth 38m), dimictic, alkaline lake with a water retention time of *ca*. 10 years.

Catchment characteristics

Catchment area 69.6km^2; mainly agricultural land & forest.

Driver

Increasing population from 4,400 in 1900 to 35,000 in 1970; associated increase in nutrient pollution from domestic sewage (from 1.3 tonnes P y^{-1}/19 tonnes N y^{-1} in 1900 to 37.4 tonnes P y^{-1}/237 tonnes N y^{-1} in 1970).

Pressure

Nutrient enrichment.

State

Winter P concentrations of 300 µg l^{-1} by 1970; P retention coefficient of 0.76; accumulated organic sediments rich in P and N.

Impact

Problem algal blooms, high turbidity and loss of macrophytes.

Response

Better management of nutrient rich sewage effluent, which reduced P input by 87% and N input by 77% in 1975.

Macrophyte recovery

The reduction in nutrient input led to lower levels of phytoplankton biomass within the lake and associated improvements in mean summer water transparency (1.6 m in 1977; 4.1 m in 2001). This, in turn, resulted in macrophytes returning to deeper water. Both deep growing characean species, which had disappeared from the lake by the mid 1980s, and taller angiosperms, whose depth limits had been restricted to a maximum of 3 m by the mid 1990s, had returned to depths of about 7.5 m by 2005. However, at the species level, recovery was incomplete. While the reduction in species distribution and richness that had occurred during eutrophication was found to be reversible, the associated reduction in abundance and species composition was not. Various reasons are suggested. These include (1) historical legacy of community composition has a stronger effect on recovery than changes in nutrient availability and water transparency, (2) oligotrophic species have become relatively rare across Denmark, reducing the chance of these species recolonising the lake, and (3) although external inputs have reduced, nutrient rich sediments in the lake may discourage oligotrophic species from re-establishing at the site.

Reference
Sand-Jensen et al. (2008)

4.4.6. Ecological recovery of the fish community

The response in the fish community to eutrophication management was summarised from 61 publications (Table 5), and from meta-analyses and site specific studies with long-term data documenting community responses to eutrophication and recovery.

Eutrophication alters lake fish communities in a number of ways. Trout fishery performance is known to be negatively affected by high TP concentrations (in excess of 100 µg l^{-1}; Burnet & Wallace, 1973) through the reduction of dissolved oxygen concentrations associated with decomposing phytoplankton blooms, and the higher turbidity caused by increased phytoplankton biomass. Decreases in fish catch were also reported by Jeppesen et al (2005b). Jeppesen et al (2000) observed a unimodal response in fish species richness in relation to TP concentration in 71 Danish lakes, with a peak occurring between 100-400 µg l^{-1}. In the same study, the size of the cyprinid population (roach, *Rutilus rutilus* and bream, *Abramis brama*) increased, while their individual body mass decreased with increasing TP. In a similar study, the percentage of carnivorous fish was observed to increase sharply below concentrations of about 100 µg l^{-1} (Jeppesen et al., 1996). This is also in agreement with results of Jeppesen et al (2005b) who analysed contemporary, long-term fish data from 22 lakes that had undergone external nutrient load reduction. A general increase in dominance from cyprinids to cyprinids and percids was observed in shallow lakes, and from cyprinids to percids or coregonids to salmonids, with decreasing TP concentration.

Shifts in the fish community, excluding those induced by biomanipulation or non-native invasions, are predominantly driven by changes in the structure of lakes. Where macrophyte cover increases with decreasing nutrient concentrations, the relative abundance of littoral fish species (e.g. gudgeon, rudd and pike) tends to increase relative to pelagic species (e.g. pikeperch, smelt and ruffe). This spatial partitioning was confirmed by Jeppesen et al. (2006) who investigated the ratio of littoral to pelagic fish in terms of their biomass along a TP gradient in 34 Danish lakes. The relative proportion of large fish (>10 cm; with the exception of pikeperch and bream) increased in the littoral zone with increasing TP and water clarity. In the same study, long-term data following eutrophication recovery indicated a rapid recovery (within about 10 years) in the spatial distribution of the fish community, with small perch and roach returning to pelagic areas. In general, shifts in fish community composition tended to follow the series cyprinids→percids→coregonids→salmonids as TP concentrations decreased.

The shift in the fish community has been attributed to behavioural responses, increased macrophyte cover and water clarity, and decreased biomass of phytoplankton and zooplankton. The functional changes associated with eutrophication recovery include (1) more extensive areas of *refugia* offered by macrophytes for large bodied cladoceran; (2) clearer water and larger macrophyte hunting grounds, which benefit piscivorous fish; (3) a shift from pelagic primary production to benthic primary production, which leads to a decrease in energy flow through pelagic food webs; (4) improved water clarity, which provides a competitive advantage for fish species that hunt using visual cues. For example, in an experimental study, Winfield (1986) reported a decrease in the feeding efficiency of roach and rudd in comparison to perch in the presence of artificial macrophytes. Roach were most successful under "no-macrophyte" conditions. These changes were related to swimming speeds within structured habitats and behavioural changes related to predator avoidance and feeding habit. Feeding rates for all species were higher in synthetic lily beds than reed stands. The spatial distribution of many fish species and the drivers of this distribution have been comprehensively reviewed by Winfield (2004; Table 6). Williams and Moss (2003) quantified grazing rates and impacts on water quality and phytoplankton community structure of common carp, bream, tench and roach, and reported (1) an increase in small zooplankton and edible phytoplankton abundance as bream, tench and roach biomass increased from 200 kg ha^{-1} to 700 kg ha^{-1}; and (2) an increase in cyanobacteria biovolume at intermediate levels of carp biomass (200 kg ha^{-1}) and high levels of roach biomass (700kg ha^{-1}).

Table 6. Summary of littoral zone use by the typical fish community of European lakes. Table adapted from Winfield (2004).

Timing of use	Duration of use	Purpose of use	Example species	Example studies
Diel	Hours	Feeding	Bream; perch; roach	Hölker et al., (2002); Kubecka et al. (1998)
Diel	Hours	Avoidance of predators	Roach	Brabrand & Faafeng (1993); Hölker et al., (2002)
Seasonal	Weeks or months	Exploitation of environmental conditions	Bleak; bream; burbot; chub; dace; eel; perch; roach; ruffe; tench; three-spined stickleback	Fischer & Eckman (1997); Wang & Eckman (1994)
Seasonal	Hours, days or weeks	Reproduction	Arctic charr; European whitefish; pike; vendace	Fortin et al. (1982); Frost (1965); Lahti (1992); Salojarvi (1982)
Ontogenic	Months or years	Feeding	Bullhead; burbot; perch	Fischer (1999); Wang & Eckman (1994); Wanzenböck et al. (2000)

The following pressures were reported to confound general recovery responses outlined above:

- in catchments with intensive agriculture, an increase in inorganic sediment load may occur. The effects of high total suspended sediments (TSS) load on fish have been well documented and concentrations of less than 100 mg l^{-1} TSS pose a "low" (25-100 mg l^{-1}) or "very low" (<25 mg l^{-1}) risk to fish and their habitat (Birtwell, 1999),

- obvious pressures result from an unbalanced fish population; fish community responses in lakes where biomanipulation has been conducted should not be expected to respond in line with the general response outlined above (Hosper, 1998),
- invasion by non-native fish species (e.g. chub, Cafrae et al., 2008) may alter the recovery of native fish species through competition, environmental degradation and predation,
- invasion by other non-native species (e.g. crayfish, Rosenthal et al., 2006), and their control leading to loss of habitat structure (Kovalenko et al., 2010), present a potential threat to the recovery of native, especially "littoral", fish species, and
- extreme variations in water level, as a result of climate change or human resource management, may damage eggs and limit habitat availability for young of the year fish, which leads to reduced recruitment success (Winfield et al., 1998; Kahl et al., 2008).

4.4.7. Ecological recovery of the waterfowl community

In general, abundance and species richness of waterfowl increase with TP concentrations and lake surface area (Hoyer & Canfield, 1994). However, species specific responses to deterioration of water quality are more complex than this simple productivity relationship and depend on waterfowl behaviour and feeding habits. For example, strong correlations have been observed between numbers of mute swan, pochard, tufted duck, coot, gadwall, Bewick's swan, red crested pochard, and pintail, and the abundance of various sources of food, including chara, pondweeds, macroalgae, and zebra mussels in Lake Veluwemeer, the Netherlands (Noordhuis et al., 2002). These correlations are associated with an improvement in water quality. It should be noted, however, that the response to changes in water quality is likely to be species specific. For example, Carss et al. (submitted) observed contrasting long-term trends among groups of waterfowl at Loch Leven (Scotland) when comparing population data at both national and local scales. Five species showed trends that were coherent, or broadly so, with that at the Scottish scale (Eurasian teal, mute swan, great cormorant, pink-footed and greylag geese), while another five species (mallard, coot, great crested grebe, tufted duck and pochard) all showed distinct differences between the local trends and those at the Scottish scale. However, the likely drivers of either local or national trends were untested.

Specific assessments of waterfowl responses to eutrophication management responses are rare. In Lake Finjasjön (Sweden), eutrophication management included (1) reduction of catchment TP load (63 t TP yr^{-1} to 5 t TP yr^{-1}), (2) sediment dredging, and (3) reduction of planktivorous fish abundance (Annadotter et al., 1999). Macrophytes did not recolonise the lake and cyanobacterial biomass remained high for 10 years after external loads were reduced, mainly as a result of internal loading. Sediment dredging was deemed unsuccessful, with insufficient change in water quality being recorded for 3 years post management. Cyanobacterial dominance decreased, water clarity increased and macrophytes began to recolonise the lake (increasing from 1% to 20% cover) only after biomanipulation of the fish community, which increased the piscivorous:planktivorous fish ratio to 1:1. This recovery was also characterised by an increase in the abundance of herbivorous waterfowl (i.e. goldeneye and pochard), which was assumed to be related to the increased abundance of macrophytes (*Myriophyllum spicatum*, *Elodea canadensis* and *Potamogeton* spp.). A similar recovery scenario was observed in Lake Veluwemeer (the Netherlands), where an increase in benthivorous and herbivorous waterfowl abundance was delayed for about 20 years, following catchment nutrient load reduction and increased flushing, as a result of high bream abundance (Ibelings et al., 2007). Waterfowl abundance increased dramatically following a reduction in bream density that resulted in an increase in charophyte and zebra mussel abundance. Finally, the importance of the planktivorous fish community in maintaining low coot abundance was demonstrated in Lake Zwemlust. Here, reductions in rudd density and an increase in pike, alone, led to a rapid reduction of phytoplankton biomass and increases in *Daphnia* spp., macrophyte cover and coot abundance within 2 years of biomanipulation (Gulati & van Donk, 2002). However, this recovery was short lived, with macrophyte and coot abundance declining again to pre-management conditions after about 5 years. The same recovery scenario occurred again after each subsequent reduction in rudd abundance (Gulati & van Donk, 2002).

BOX 6: LOCH LEVEN, SCOTLAND

Lake type

Large (13.3km^2), shallow (mean depth 3.9m; maximum depth 25.5m), well mixed, alkaline lake with a water retention time of *ca*. 0.5 years; predominantly phosphorus (P) limited.

Catchment characteristics

Catchment area 145km^2; mainly lowland agriculture with some forestry in upland areas.

Driver

Increasing population density, agricultural intensification and industrial development increased the P input to the loch from *ca*. 5 t y^{-1} in the early 1900s to *ca*. 20 t y^{-1} by 1985.

Pressure

Nutrient enrichment.

State

Winter P concentrations of *ca*. 40 µg l^{-1}; P retention coefficient of 0.61; accumulated organic sediments with high nutrient content.

Impact

Problem algal blooms, high turbidity and loss of macrophytes.

Response

Improved control of nutrient rich sewage effluent discharges, cessation of P inputs from industry, and better farm management reduced the P input by *ca*. 60% between 1985 and 1995.

Waterfowl response

The reduction in P inputs to the lake resulted in greater water clarity and a corresponding increase in macrophyte growing depth and abundance. In comparison with Scottish trends, bird counts at the lake over the periods of pre-nutrient reduction (1967 to 1995) and recovery (1995 to 2006) suggested that responses to eutrophication and recovery were species specific. Some species (i.e. mallard duck, pink footed geese, cormorants) were unaffected by changes over the recovery period, while others (i.e. Eurasian teal, mute swan, coot, great crested grebe, tufted duck, pochard) responded positively. Those that responded positively tended to be species that were dependent upon macrophytes as a food source than those that were not. Of the latter, mallard ducks and pink footed geese are less dependent on macrophytes because they tend to supplement their in-lake diets by grazing crops on local farmland, while cormorants have even less dependence on macrophytes because they feed on fish. As there are no pre-eutrophication bird counts for this site, it is impossible to say whether the bird populations that are approaching their pre-eutrophication levels.

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May & Carvalho, 2010; Carss et al, submitted; Carvalho et al., submitted; Dudley et al., submitted

5. Potential for cross-ecosystem linkages

5.1. Nutrient delivery to downstream ecosystems

There is a need to consider linkages between ecosystems when assessing recovery after eutrophication management. This need is explicitly stated within the Water Framework Directive. Howarth and Marino (2006) review the importance of nutrient limitation in estuaries and conclude that N-limitation is most prominent in temperate estuarine waters. However, changes in the supply of P may also alter the ecological structure of estuaries. For example, reductions in TP may limit the benthic diatom community and favour a shift in primary production from the desirable eelgrass towards undesirable macro-algae (*Enteromorpha* sp. and *Ulva* sp.; Sand-Jensen & Borum, 1991). Flindt et al (1999) describe the shift in ecological structure and function with increasing TN concentration in estuaries as being from a grazing and/or nutrient limited stable system to detritus/mineralisation systems that are ecologically unstable. Although a full review of the ecological responses of estuaries is not within the scope of this report, we provide evidence from a case study of seasonal changes in downstream nutrient supply and stoichiometry before and after reductions in TP loading to an upstream lake (Loch Leven, Scotland; Figure 18).

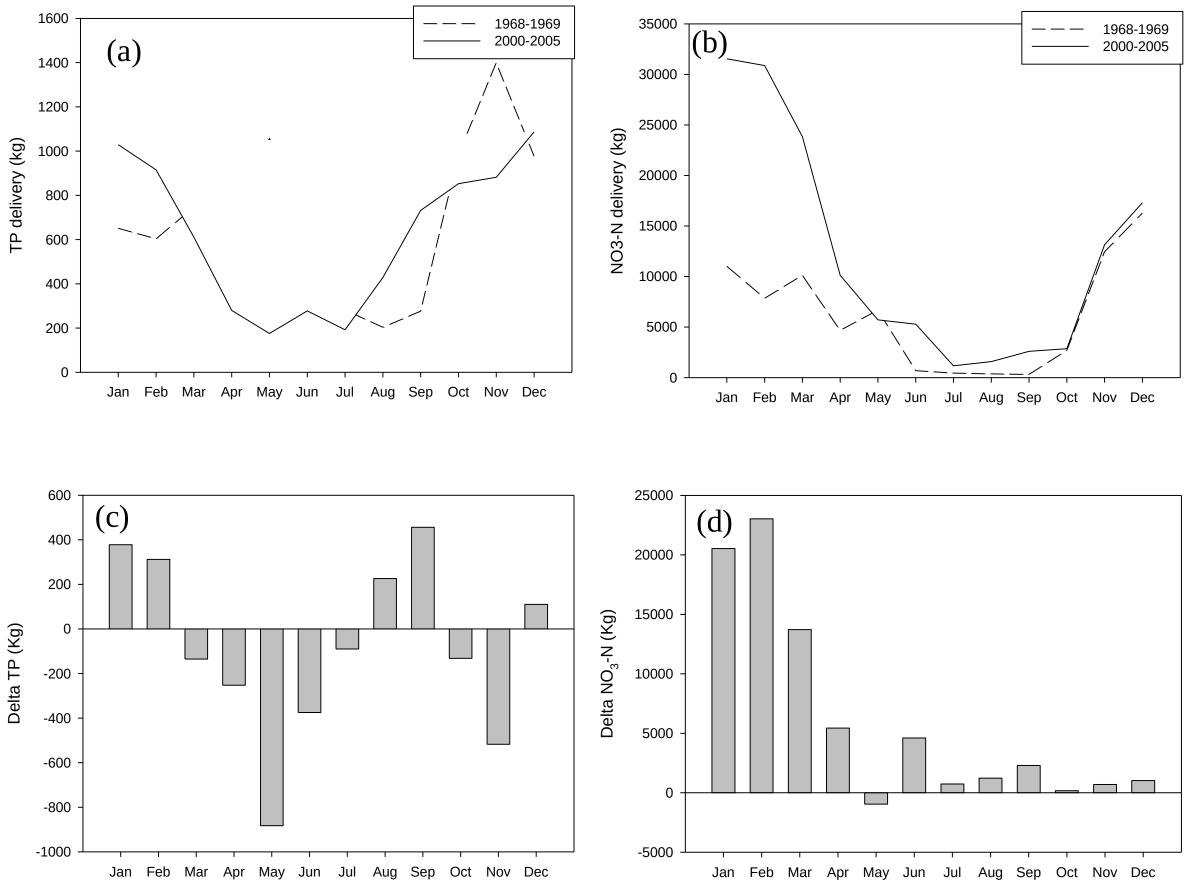

Figure 18. Delivery of (a) TP and (b) NO_3-N from Loch Leven during the pre-management (1968-1969) and post-management (2000-2005) periods. The change ('delta') in post-management monthly delivery of (c) TP and (d) NO_3-N relative to pre-management estimates, is also shown.

As outlined above, responses to changing nutrient concentrations in lakes following eutrophication management are complex and seasonally distinct. However, nutrient delivery from recovering lakes to downstream ecosystems is also affected by changes in flushing rate. Loch Leven provides a good case study with which the impacts of eutrophication management can be assessed because the outflow discharge has been controlled by a series of sluice gates over the period of P abatement and monitored at a daily frequency (May & Carvalho, 2010). Also, only reductions in TP load (from 20 t TP yr^{-1} to 8 t TP yr^{-1}) were targeted at Loch Leven over the management period and water chemistry measurements were made at roughly fortnightly intervals.

Changes in downstream TP load from Loch Leven varied seasonally between the pre-management (1968-1969) and post-management/recovery (2000-2005) periods (Figure 18). A strong decrease in the TP load was observed during spring and a moderate increase was observed during winter, summer and autumn. These changes reflect changes in the in-lake TP concentrations reported in Box 2, with the exception of the winter increase which was apparently due to elevated flushing and not an increase in TP concentration. A strong increase in NO_3-N delivery was observed in winter, post-management, probably as a result of an increase in the external N loading. In this case, eutrophication management altered both the magnitude and timing of downstream nutrient delivery. These changes will change the stoichiometry of nutrients delivered to downstream ecosystems, the ecological impacts on which will depend on the relative importance of the upstream lake as a nutrient source within the catchment.

6. Synthesis

The key aim of this report was to describe the ecological recovery of lakes from eutrophication by conducting a systematic meta-analysis of the peer reviewed literature in combination with reviews of peer-reviewed multi-lake meta-analyses and site-specific case studies with long-term data spanning recovery periods. The key results, in line with the specific questions posed by the working group of WP 6.4 were as follows:

- *What are the most common pressure scenarios in eutrophic lakes?*

The key primary eutrophication pressures were related to agricultural sources (e.g. animal waste, fertiliser applications, soil erosion), discharges from industry (e.g. aquaculture, paper mills, food manufacturing) and the infrastructure associated with areas of high population density (e.g. waste water treatment works, housing, roads). Acidification and fishery management were the most commonly reported secondary pressures (29% and 20%, respectively), followed by industrial pollution (16%), climate change (13%), pesticide application (9%), salinisation (7%), ingress of invasive species (7%), alkalisation (4%), water level fluctuation (2%), boating (2%) and sediment dredging (2%). About 83% of the published case studies reported on the effects of eutrophication alone, whereas 15% documented responses to multiple pressures. We expect the occurrence of secondary pressures (especially invasive species ingress) to be significantly underrepresented in the literature.

- *What are the most common management approaches?*

A range of approaches to eutrophication management were documented. That most commonly reported was a reduction of external nutrient loading (88% of returned publications). In contrast, in-lake management with or without external loading reduction, received relatively little attention (19% and 6% of returned publications, respectively). Of these, fish biomanipulation (41% of reported in-lake management cases) was the most commonly reported measure, followed by sediment phosphorus (P) capping (16%), drawdown (12%), sediment dredging (13%), flushing (6%), aeration/circulation (5%) and waterfowl/macrophyte biomanipulation (2%).

- *What WFD BQEs and other organism groups are most commonly reported?*

Responses to eutrophication management were reported for phytoplankton (44% of case studies reporting ecological recovery), macrophytes (15%), zooplankton (14%), macroinvertebrates (13%), fish (12%), waterfowl (2%) and bacterioplankton (<1%).

- *What are the structural and functional changes in end point biological communities when compared to impacted states?*

In general the ecological responses of phytoplankton, macrophytes, macroinvertebrates and fish were well reported and we consider the general responses identified in this report for these BQEs to be of relatively high accuracy. For these BQEs, responses included an increase (i.e. of macrophytes) or decrease (i.e. of phytoplankton, fish, zooplankton and macroinvertebrates) in biomass and an increase in species richness. The responses of waterfowl and bacterioplankton were unclear due to a lack of peer reviewed literature. The functional changes at the whole lake scale included a shift from open water pelagic to benthic littoral production leading to similar shifts in the transfer of energy through the food web. These changes were generally associated with an increase in the extent of the macrophyte community and a decrease in phytoplankton biomass and turbidity as a result of decreased TP concentrations. Significant changes in the community composition for each of the BQEs were returned (not tested for bacterioplankton), apparently resulting in an overall increase in biodiversity at the whole lake scale.

- *What confounding processes are important in determining response trajectories and end points?*

Although a wide range of confounding pressures were identified for each BQE, persistent internal loading of P, ingress of non-native invasive species and changes in weather patterns associated with climate change were common across all BQEs. It should be noted that non-native invasive macrophyte species were not always reported as a negative response but more commonly as a positive response associated with an increase in macrophyte extent. The importance of in-lake biogeochemical cycling was reported to be the most important factor delaying recovery. Responses of TP and TN concentrations, driven mainly by sediment processes, were reported to take years to decades and were the main drivers of ecological responses across all BQEs. Emerging research highlighted the importance of managing these processes for enhancing ecological recovery of lakes, especially shallow lakes, following external nutrient load reduction. Issues related to metapopulation dynamics, specifically associated with blockages of species distribution, were apparently more important for macrophytes and fish compared to other BQEs.

- *Will the recovery of lakes from eutrophication potentially impact downstream ecosystems?*

Changes in nutrient dynamics and discharge from lakes following eutrophication control varied following external nutrient load reduction. In Loch Leven, where P reduction was targeted alone, changes in the stoichiometry of nutrients delivered to downstream ecosystems were seasonally distinct and favoured P limitation, especially during winter, spring and autumn during the transient period.

The successful restoration of lakes from eutrophication is complex and requires a comprehensive understanding of multiple and site-specific primary and secondary pressures. Without this, undesirable deterioration of non-target BQEs may inadvertently be achieved as a result of the numerous feedback mechanisms known to occur in these complex ecological systems. What is apparent is that those case studies where restoration has been labelled “successful” have been underpinned by long-term monitoring of target pressures and BQEs throughout the degradation and recovery phase. Also apparent, is that very few studies report pre-defined ecological restoration targets in line with WFD metrics. At present, insufficient data are available in the literature with which multi-lake meta-analyses of ecological recovery following eutrophication management can be conducted in line with WFD targets. Efforts should be made to identify groups of case studies where the responses of multiple BQEs can be retrospectively assessed in line with WFD targets, as they come online.

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