Eutrophication and restoration in temperate lakes

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Abstract. Eutrophication affects many lakes and reservoirs worldwide. It is caused by excessive amounts of nutrients entering waterbodies from their catchments, mainly due to human activity. The main sources of these nutrients are discharges from industry and wastewater treatment systems, and agricultural runoff. The water quality problems caused by eutrophication, such as harmful algal blooms, affect the sustainable use of lakes for agriculture, fisheries, recreation, tourism and water supply. They also degrade habitat quality and threaten biodiversity. A range of methods for improving lake water quality are explored, including catchment management and in-lake restoration measures. The potential impacts of these on lake biodiversity are explored, including species interactions and ecosystem feedbacks that may confound the recovery process. A particular challenge is the fact that achieving sustainable recovery may take many years, mainly due to the impact of legacy pollution problems. This must be taken into account when planning and implementing eutrophication management options, because these slow recovery periods can exceed the timescales that people are willing to accept. While this review focuses on the many well documented studies of restoration and recovery processes in temperate lakes, it also highlights the need for similar research on tropical and sub-tropical systems.

1. Introduction

Eutrophication (or nutrient enrichment) is one of the most important anthropogenic pressures on lake ecosystems across the world [1-3]. It is caused by excessive amounts of nutrients entering waterbodies from their catchments (watersheds) due to increased levels of human impact. The main sources of these nutrients (mainly nitrogen (N) and phosphorus (P)) are usually agricultural runoff, and nutrient-laden discharges from industry and wastewater treatment systems. However, fish farming may also contribute to eutrophication problems.

The negative impacts of eutrophication on lakes occur, mainly, when the ecological balance changes to favor higher levels of primary production in the water column (phytoplankton) and lower levels in the benthos (macrophytes) [4]. The ecological consequences of this can result in ecosystem degradation problems that have societal impact, with the rate of change being dependent upon many complex interactions [4]. The water quality issues that arise from this problem, such as harmful algal blooms, affect the sustainable use of lakes and provision of the ecosystem services that we depend on. These include agriculture, fisheries, recreation, tourism and water supply [5-7]. Over recent decades, government agencies have invested considerable amounts of resources in controlling nutrient inputs to lakes and restoring of their ecosystems [7]. This is because eutrophication has negative economic

impacts on drinking water supplies, fisheries, public health, revenue from tourism and the value of waterfront properties, with Dodds *et al*. [5] estimating that eutrophication of freshwaters in the US costs USD 2.2 Bn per year while Pretty et al. [6] have estimated values for the UK to be about USD 101-105 M per year. Mitigation costs are also high; in England and Wales, alone, USD 77 M per year are spent on removing nutrients from point sources, adopting new farming practices and monitoring/enforcing appropriate policy measures [6].

The capacity of a lake to recover to its original state when restoration measures are put in place depends upon a sufficiently high reduction in the most widespread and dominant pressure, i.e. nutrient enrichment [8]. In addition, it may also be necessary to control secondary pressures on these systems, such as pesticides or non-native species, as these may confound the recovery process. Evidence from long-term monitoring studies has often highlighted the interactive nature of these primary and secondary pressures and provided insights into the likely consequences of managing any of these pressures in isolation [9]. A major aim of making restoration 'sustainable' is to ensure that future interventions are not required [10].

The key aims of this study were to review, for temperate waters, (1) the methods available for restoring lakes affected by eutrophication; (2) the nutrient and ecological responses to reductions in nutrient availability; (3) biological and nutrient response times following management intervention; and (4) the most common secondary pressures that confound biological and nutrient recovery processes.

2. Methods Available for Reducing Nutrient Availability

Restoring lakes that have been adversely affected by eutrophication problems is a global scale challenge [8,11]. Where availability of P is the main factor limiting algal growth, improvements in water quality can often be achieved by reducing P inputs from the catchment [12]. Typically, managers identify an acceptable level of phytoplankton and predict the external reduction in P load that is needed to achieve that target using models such as that of Dillon and Rigler [13]. However, evidence suggests that reducing external inputs of P may not lead to the changes in P concentrations and phytoplankton biomass that are predicted by these models [7,14]. Deviations from expected responses have two main causes, top down biological control and internal nutrient load [7]. In the former situation, the food-web structure of a lake can markedly affect how it responds to changes in nutrient inputs, with the sudden appearance of large populations of herbivorous zooplankton, for example, profoundly altering the algal biomass and, consequently, the transparency of the lake. In the latter situation, internal nutrient loading can also make predicting eutrophication effects much more complex. For example, when exploring the effect of three decades of nutrient input reductions to Lake Lugano, Italy, Lepori and Roberts [15] found that recovery of warm meromictic lakes may be slower than expected due to the development of internal loadings, which are not included in these classical P and chlorophyll *a* models. These results, and those of others [12], indicate that the traditional paradigm for eutrophication management may be flawed. In particular, it highlights that the recovery trajectory is not necessarily the reverse of the degradation trajectory when nutrient inputs to lakes are reduced [16]. Indeed, recovery from eutrophication can also show hysteresis effects in the relationship between loads and concentrations [17]. Below, we introduce the most common approaches to lake restoration that are reported in the literature for temperate lakes, with a brief commentary on their effectiveness.

2.1. Reducing external sources of nutrient inputs

There are many examples of lakes where reductions in P inputs have resulted in improvements in water quality, including lower levels of phytoplankton. However, few studies have investigated the effects of reducing P and N inputs at the same time, and some studies have shown that concentrations of algae can increase when N inputs were reduced [18,19]. Although there has been considerable progress in controlling nutrient discharges from point sources, controlling those from diffuse sources remains a major challenge [20]. These sources include runoff from land, seepage from on-site sewage treatment systems and waste material from cage fish farms.

2.2. Reducing internal sources of nutrients
Most of the P in lake ecosystems is stored in the bottom sediments and recycles into the water column under certain conditions, such as deoxygenation at the sediment-water interface [21,22]. A range of methods have been used to reduce the amount of P that recycles from these sediments, including sediment removal, chemical treatment and artificial aeration.

Sediment removal involves the physical removal of P-laden sediment from the bottom of the lake, reducing the likelihood of internal P release. However, although this may be practical for small waterbodies, large-scale sediment removal is an expensive process that requires access to large areas of land for disposing of the sediment that has been removed [23,24]. If the sediment is contaminated (e.g. with heavy metals), there may be additional costs associated with its safe disposal. Given global concerns about exhaustion of phosphate rock, it has also been suggested that it might be better to remove and recycle this accumulated P [25].

The release of P into the water from lake sediments can also be reduced by chemical inactivation, for example with aluminium (Al), iron (Fe) or lanthanum (La) based products [26,27]. However, it is unclear how long such treatments are effective for. Huser et al. [27], for example, reviewed the results from 114 lakes in Denmark, Germany, Sweden and the USA that had been treated with Al salts and concluded that the average time over which water quality improvements continued after treatment was about 15 years. However, the authors found that, at individual sites, this timescale was affected by lake depth, Al dose, watershed:lake area ratio and (in shallow polymictic systems) the presence of benthivorous fish. In general, although they can last for decades, the period over which these chemical treatments have a positive effect on water quality is usually much shorter [26,27].

Despite not providing long-term, sustainable solutions to eutrophication problems, the use of chemical treatments has increased around the world in recent years. This trend tends to reflect the increasing demand for rapid improvements in water quality to meet regulatory requirements [28], and fails to take into account the fact that sediments play an essential role in aquatic ecosystems [29]. That said, in some cases, restoration efforts that compromise sediment quality may be justified, for example where drinking water supplies are under threat. So, each lake needs to be assessed on its own merit [28].

Artificial aeration and oxygenation have also been used to address the problem of releases from lake sediments [30,31], although P release problems recur as soon as anoxic conditions return [32]. Although the positive effects of artificial aeration on water quality are, usually, relatively small, these approaches are popular because of their functional versatility and their seemingly unproblematic applicability [33-35].

3. Chemical and Ecological Responses to Reductions in Nutrient Availability
3.1. Phosphorus
The management of eutrophication problems through P-reduction makes the assumption that algal production and biomass accumulation is P-limited. There is compelling evidence that, in some situations, controlling of eutrophication problems by reducing P inputs, alone, can be very successful. However, there is also evidence that other factors can influence the development of algal blooms, leading to unexpected ecosystem recovery trajectories when P levels are reduced. Often, these have been attributed to N-limitation under P-replete conditions [36]. However, there has been controversy over the role of N- and P-limitation in lakes and the potential effectiveness of reducing just one of these nutrients to improve water quality [37,38]. For example, in a Policy Forum Review, Conley et al. [39] indicated that control of the negative impacts of nutrient enrichment effectively should involve reducing the availability of both N and P. However, based on a meta-analysis of existing data, [20,40] concluded that there was no difference in the recovery rates or restoration end points of lakes that had been subjected to single or dual nutrient reduction approaches.

In shallow lakes, biological responses are determined by in-lake biogeochemical processes that affect P concentrations when external inputs are reduced. These can lead to changes at seasonal, annual and decadal scales. Changes in water column TP concentrations during the transient period

often reflect changes in the relative sizes of external and internal P loading, causing subtle changes in seasonality [41].

3.2. Nitrogen

The responses of N concentrations to external nutrient load reductions also follow seasonal trends that are driven by sediment processes and changes in the biological structure of the lake. For example, Jeppesen et al. [12] found that it took up to 10 years for steady state N concentrations to be achieved in lakes where external inputs of N had been reduced. The authors found that summer total nitrogen (TN) concentrations had decreased, and that the ratio of dissolved inorganic nitrogen (DIN) to TN (DIN:TN) had increased, after recovery. This was probably caused by a reduction in summer phytoplankton biomass and, as a result, a decrease in the organic N content of the water column. Similar reductions in TN were reported by Sondergaard et al. [41] although, in this case, N load reductions were not considered to be the main driver of the reduction in in-lake N concentration. Instead, phytoplankton biomass had decreased due to reductions in TP load, coupled with a reduction in water column TN concentrations due to denitrification and the uptake of dissolved N by macrophytes. These estimates of the transient period for recovery from high N inputs are in general agreement with the results of Jensen et al. [42], who found that steady state TN conditions were reached within a year of a 30% reduction in external N loading to Lake Søbygaard, Denmark.

Weyhenmeyer et al. [43] undertook a comprehensive meta-analysis of the factors that were controlling the rate of nitrate (NO_3-N) loss between spring and summer in 100 lakes from across Europe. In the past, this reduction has been attributed to a combination of denitrification and biological uptake, both of which are expected to increase with rising temperatures [42,44]. However, Weyhenmeyer et al. [43] found that (1) NO_3-N loss rate increased with decreasing lake depth; (2) NO_3-N loss rate was positively correlated with spring NO_3-N concentrations in lakes of less than 12.5m deep; and (3) reductions in external N loading and an increase in water temperature had resulted in an increase in the occurrence and duration of NO_3-N depleted conditions in 16 European lakes.

3.3. Bacterioplankton

Changes in the bacterioplankton of lakes recovering from eutrophication have been reported to be induced by changes in zooplankton grazing behaviour and reductions in phytoplankton biomass. In turn, these have resulted from lower P concentrations, an increase in dissolved oxygen (DO) concentrations and a decrease in dissolved organic carbon (DOC) concentrations that have arisen due to lower levels of primary production in the water column. In a long-term study of Lake Ladoga (Russia), bacterioplankton abundance and dark carbon dioxide (CO_2) fixation were found to have increased from 0.54×10^6 cells mL^{-1} to 1.02×10^6 cells mL^{-1}, and from 0.49 μg C L^{-1} d^{-1} to 2.4 μg C L^{-1} d^{-1}, respectively, as TP concentrations increased [45,46]. The observed increases in bacterioplankton abundance and CO_2 consumption were linked to 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 the 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 and allochthonous TOC. This observation suggests that bacterioplankton production was being limited by resources other than TOC availability in Lake Ladoga, prior to its eutrophication. This agrees with other studies where P-limitation of bacterioplankton has been observed. For example, Spears and Lesack [47] reported an increase in bacterioplankton production in mesocosm nutrient (N and P) amendment bioassays that were performed on natural communities from three lakes in the Mackenzie Delta, Canadian Arctic, especially when soluble reactive phosphorus (SRP) concentrations were less than 10 μg L^{-1}.

Bacterioplankton production and abundance were measured, and grazing by zooplankton was modelled, in Lake Søbygaard, Denmark, after a reduction in the external load of N and P [48]. Although no significant decrease was observed in bacterioplankton production, abundance varied as a

result of zooplankton grazing pressures (from *Daphnia*) that were associated within a recovery-induced trophic cascade. An increase in the biomass of cyprinid fish at the site resulted in a shift in the dominant zooplankton taxa, from *Bosmina longinostris* and ciliates to *Daphnia* sp*.,* the latter being responsible for increasing 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% [49]. In addition, Work and Havens [50] found evidence of bacterioplankton ingestion by 35 micro- and macro-zooplankton species in Lake Okeechobee, Florida, USA, and suggested that ingestion may be the result of (1) unavoidable entrainment whilst filter feeding due to the high density of bacterioplankton, and (2) a requirement to supplement their diet with more "edible" food sources, such as cryptophytes and small chlorophytes.

3.4. Phytoplankton

The main drivers of changes in phytoplankton communities during recovery from eutrophication are decreases in P concentrations, and corresponding alterations to N and silica (Si) concentrations. These changes occur as a result of reductions in the external nutrient load to the lake and alterations to in-lake biogeochemical cycling processes.

Bellinger and Sigee [51] summarise the changes in phytoplankton communities that are likely to occur in different types of lakes as a result of decreasing trophic status. In hypertrophic lakes, small unicellular cyanobacteria and green algae that have short life cycles will tend to dominate the phytoplankton throughout the year. In eutrophic lakes, a short, spring diatom bloom will usually be followed by a mid-summer bloom of large unicellular (e.g. *Ceratium* spp.), filamentous (e.g. *Anabeana* spp.) and globular algae (e.g. *Mycrocystis* spp.). In mesotrophic lakes, the spring diatom bloom will be longer and followed by a more diverse summer peak of dinoflagellates, green algae and cyanobacteria. Oligotrophic lakes will be characterised by a long spring diatom bloom, with diatoms dominating the growing season or co-existing with chrysophytes and desmids. In deep, stratifying lakes, cyanobacterial species that are capable of vertical migration and able to access sediment P stores (e.g. *Gleotrichia* spp. [52]) may also occur. This agrees with the results from a multi-lake (27 lakes) analysis of phytoplankton community responses to reductions in nutrient load undertaken by Jeppesen et al. [12]. In that study, the authors observed changes that included an increase in the relative importance of chrysophytes, chryptophytes and diatoms with decreasing P concentrations in shallow lakes, a decrease in the relative abundance of cyanobacteria, and an increase in dynophytes and chrysophytes in deep lakes. A meta-lake analysis of Danish lakes confirmed a lower percentage of cyanobacteria at P concentrations below 600 µg L^{-1}, with cyanobacteria tending to dominate at P concentrations of between 500 µg L^{-1} and 1000 µg L^{-1} [53]. When cyanobacterial levels are high, there is an increased risk of toxin producing species occurring; this limits the amenity value of the system.

3.5. Zooplankton

Changes in the zooplankton community of lakes during the recovery process were caused, mostly, by an increase in macrophytes, which offer a refuge from fish predation [54]. In general, cladoceran body size and species richness increased as nutrient concentrations decreased. This resulted in higher relative abundances of large cladocera (e.g. *Daphnia hyalina*, *Daphnia galeata*) compared to smaller taxa (e.g. *D. galeata*, *Daphnia ambigua*, *Ceriodaphnia pulchella*), and especially in relation to rotifers. In addition, the zooplankton:phytoplankton ratio increased due to lower phytoplankton biomass and its reduced quality as a food source, and as a result of the lower level of predation on the zooplankton.

Jeppesen et al. [55] reported a decrease in zooplankton biomass (especially of rotifers, cyclopoid and calanoid copepods, small cladocera and *Daphnia* spp.) from about 1 mg dry weight (DW) L^{-1} to <0.5 mg DW L^{-1} across a P gradient of > 400 µg L^{-1} to < 50 µg L^{-1}. The relative contribution of each zooplankton group also varied across the P gradient, with *Daphnia* spp. increasing and calanoid copepods decreasing as P concentration decreased. An increase in total zooplankton biomass, and in the zooplankton:phytoplankton ratio, was observed at P concentrations ranging from <100 µg L^{-1} to 150 µg L^{-1} in 27 lakes after the external nutrient load had been reduced [56]. In a similar analysis of

long-term recovery data in eight shallow lakes in Denmark, an increase in zooplankton biomass was observed in November and December, only. During summer and autumn, the biomass of small cladocera declined, *Daphnia* spp. and total cladoceran body weights increased, and the *Daphnia*:total cladoceran biomass ratio increased; these changes indicate an increase in the potential for phytoplankton to be removed by grazing zooplankton [56].

3.6. Macroinvertebrates
There are few comprehensive studies on the recovery of macroinvertebrate communities from eutrophication; most studies have focused on specific groups, habitats or species. The main changes responsible for alterations in the macroinvertebrate community have been found to be reduction in organic matter content, improvements in dissolved oxygen (DO) concentration in the benthos, increased macrophyte cover in deeper habitats and changes in grazing pressure associated with changes in the fish community [54]. These factors resulted in an overall decrease in community abundance, a shift towards taxa that are more characteristic of meso-oligotrophic conditions (i.e. gastropods, Hydracarina), an increase in the chironomid:oligochaete ratio, and a general expansion of macroinvertebrate communities into deeper habitats.

3.7. Macrophytes
The responses of macrophyte to eutrophication management have been shown to include increases in maximum colonisation depth (MCD), species richness, the number of nutrient intolerant species and species distribution, as P concentrations decrease. Full recovery of species composition has rarely been recorded. This may be due to physical barriers to establishing wider distribution and/or the loss of nutrient intolerant seed banks in areas where eutrophic conditions have been prevalent for many years. Increased water clarity is the most commonly reported change that has led to improvements in macrophyte communities, although reductions (and increases) in TN concentrations were also found to be important. At a structural level, MCD was observed to change relatively quickly (i.e. < 5 years) after P load had been reduced. However, at a community composition level, recovery times for macrophytes were reported to be much longer (i.e. up to 40 years) [57]. A general shift from macroalgae (e.g. hypertrophic: *Cladophora* spp. and *Enteromorpha* spp.) through tall angiosperms (e.g. eutrophic: *Myriophyllum spicatum* and *Potamogeton pectinatus*) 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 to occur as nutrient concentrations were reduced and lake status moved from hypertrophic to oligotrophic.

Although a general increase in macrophyte species richness with decreasing P concentrations has been reported, a meta-analysis of 71 shallow Danish lakes showed that the relationship is unimodal showing peaks at 100 µg P L^{-1} and 400 µg P L^{-1} [55]. Macrophyte percentage cover and percentage volume of water inhabited increased markedly at P concentrations below 100 µg L^{-1} – 200 µg L^{-1}, and 50 µg L^{-1}, respectively [58]. In a similar meta-analysis of 204 Danish lakes, a decrease in macrophyte cover was reported where TN concentrations were greater than 2 mg N L^{-1} [59]. Together, these studies tend to suggest that macrophyte cover and community composition will be low if P concentrations are between 130 µg L^{-1} and 200 µg L^{-1}, when TN concentrations are greater than 2 mg L^{-1} [59]. It has been suggested that the decrease in macrophyte cover at high TN concentrations is caused by shading as a result of epiphyton and phytoplankton growth. This hypothesis is supported by a meta-analysis of data from 60 shallow lakes in Poland and the UK, which showed that macrophyte species richness increased from <5 at winter NO$_3$-N concentrations of greater than about 6 mg N L^{-1} to between 5 and 16 at winter NO$_3$-N concentrations approaching 0 mg N L^{-1} [60]. Under high TN conditions, macrophyte communities were typically dominated by fast growing eutrophic species, such as *Ceratophyllum demersum*, *Lemna minor*, *L. trisulca* and *Potamogeton pectinatus*, [60].

Macrophyte MCD is widely recognised as a simple, yet useful, proxy of macrophyte abundance in lakes. As phytoplankton concentrations increase, light levels in deeper water decrease and submerged

macrophytes are restricted to shallower water. MCD is sensitive to a number of anthropogenic pressures, especially level of eutrophication [61-63].

Few long-term data exist with which the relationship between eutrophication and macrophyte community structure can be assessed at relatively high temporal frequency (i.e. years to decades) and over long time spans, apart from those from the studies of Dudley et al. [64] and Sand-Jensen et al. [57]. Both studies showed that recovery was very slow, and that decreases in MCD, species richness and species distribution that had occurred during the eutrophication phase had not been reversed completely 20-30 years after P inputs had been reduced. Shifts in community composition from small angiosperms, mosses and characeous macroalgae (unimpacted, mesotrophic state) to tall angiosperms (impacted, eutrophic state) were observed over the period of eutrophication. During the recovery phase, submerged vegetation only partially recovered in terms of species richness and depth penetration, with many of the smaller species failing to re-appear.

3.8. Fish

Eutrophication alters lake fish communities in a number of ways. Trout fishery performance is negatively affected by high P concentrations (in excess of 100 µg P L^{-1} [65]) through the reduction of DO concentrations associated with decomposing phytoplankton blooms, and higher turbidity caused by increased phytoplankton biomass. Decreases in fish catches have also been reported [12]. Jeppesen et al. [55] observed a unimodal response in fish species richness in relation to P concentration in 71 Danish lakes, with a peak occurring at between 100-400 µg P L^{-1}. In the same study, the number of cyprinids (bream (*Abramis brama* and roach (*Rutilus rutilus*)) increased, while their individual body mass decreased with increasing P levels. In a similar study, the percentage of carnivorous fish increased sharply at P concentrations below about 100 µg P L^{-1} [49]. This agrees with the results of Jeppesen et al. [12], who analysed contemporary, long-term fish data from 22 lakes that had undergone a reduction in external nutrient load.

Shifts in the fish community, excluding those induced by biomanipulation or non-native invasions, are predominantly driven by changes in the ecosystem structure of lakes. When macrophyte cover increases, the relative abundance of littoral fish species (e.g. gudgeon (*Gobio gobio*), pike (*Esox lucius*) and rudd (*Scardinius erythrophthalmus*)) tends to increase relative to that of pelagic species (e.g. pikeperch (*Stizostedion lucioperca*), ruffe (*Gymnocephalus cernua*) and smelt (*Osmerus eparlanus*)). This spatial partitioning has been confirmed by Jeppesen et al. [66], who investigated the biomass ratio of littoral to pelagic fish along a P 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 P concentration and water clarity. In the same study, long-term data indicated a rapid recovery (≤ 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 P concentrations decreased.

Shifts in the fish communities have been attributed to behavioural responses, increases in macrophyte cover, improvements in water clarity, and decreases in the biomass of phytoplankton and zooplankton. The functional changes associated with recovery from eutrophication include (1) more extensive areas of refugia offered by macrophytes for large bodied cladocera; (2) clearer water and larger macrophyte hunting grounds, which benefit piscivorous fish; (3) a shift from pelagic primary production to benthic primary production, decreasing the energy flow through the pelagic food webs; and (4) improved water clarity, providing a competitive advantage for fish that hunt using visual cues. This is supported by the experimental results of Winfield [67], who reported a decrease in the feeding efficiency of roach and rudd compared to perch (*Perca fluviatilis*) in the presence of artificial macrophytes, with roach being most successful under "no-macrophyte" conditions. Williams and Moss [68] quantified the predation rates of bream, common carp (*Cyprinus carpio*), roach and tench (*Tinca tinca*) and their impacts on water quality and phytoplankton community structure. They found (1) an increase in the abundance of small zooplankton and edible phytoplankton as the biomass of bream, roach and tench increased from 200 kg ha^{-1} to 700 kg ha^{-1}; and (2) an increase in the biovolume

of cyanobacteria at intermediate levels of carp biomass (200 kg ha^{-1}) and high levels of roach biomass (700kg ha^{-1}).

3.9. Waterfowl

The abundance and species richness of waterfowl tends to increase with increasing lake surface area and P concentrations [69]. However, species specific responses to deterioration of water quality are more complex, and depend on waterfowl behaviour and feeding habits. For example, strong correlations have been observed between numbers of Bewick's swan (*Cygnus columbianus bewickii*), coot (*Fulca atra*), gadwall (*Mareca strepera*), mute swan (*Cygnus olor*), pintail (*Anas acuta*), pochard (*Aythya ferina*), red crested pochard (*Netta rufina*) and tufted duck (*Aythya fuligula*) and the abundance of various sources of food, including *Chara* spp., macroalgae, pondweeds and zebra mussels, in Lake Veluwemeer, the Netherlands [70]. These correlations were associated with an improvement in water quality. In addition, Carss et al. [71] also observed different long-term trends among different groups of waterfowl at Loch Leven, Scotland, UK, when comparing national- and local-scale population data. Five species showed trends that were coherent with that occurring at the national scale (Eurasian teal (*Anas crecca*), great cormorant (*Phalacrocorax carbo*), mute swan, pink-footed (*Anser brachrhynchus*) and greylag geese (*Anser anser*)), while another five (coot, great crested grebe (*Podiceps cristatus*), mallard (*Anas platyrhynchos*), pochard and tufted duck) showed distinct differences between local and national trends.

Specific assessments of waterfowl responses to eutrophication management are rare. In Lake Finjasjön, Sweden, eutrophication management included (1) reduction of P load from 63 t yr^{-1} to 5 t yr^{-1}, (2) sediment dredging and (3) reduction in the abundance of planktivorous fish [72]. For 10 years after external loads were reduced, the cyanobacterial biomass remained high and macrophytes did not recolonise the lake, mainly as a result of internal P release from the sediments. Cyanobacterial dominance decreased, water clarity increased and macrophytes began to recolonise the lake (increasing from 1% to 20% areal coverage) only after biomanipulation of the fish community, which increased the piscivorous:planktivorous fish ratio to 1. This recovery was also characterised by an increase in the abundance of herbivorous waterfowl (i.e. goldeneye, pochard), which was assumed to be associated with an increase in macrophytes (*Elodea canadensis Myriophyllum spicatum* and *Potamogeton* spp.). A similar recovery trend was observed in Lake Veluwemeer, the Netherlands, where an increase in benthivorous and herbivorous waterfowl was delayed for about 20 years, following catchment nutrient load reduction and an increase in flushing rate. This was probably due to a high abundance of bream in the lake [73]. Waterfowl abundance increased dramatically when a reduction in bream density 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, the Netherlands. Here, reductions in rudd density and an increase in pike, had caused a rapid reduction of phytoplankton biomass, and an increase in *Daphnia* spp. densities, macrophyte cover and coot abundance within two years of the biomanipulation [74]. However, this recovery was short-lived, with macrophyte and coot abundance declining to pre-management conditions after about five years [73]. The same recovery scenario recurred after each subsequent reduction in rudd abundance [74].

4. Nutrient and Biological Response Times of Lakes to Management Intervention

It is unrealistic to assume that disturbances caused over decades can be corrected in a much shorter time [75,76] and it is not uncommon for restoration to take longer than degradation [77,78]. For shallow lakes, in particular, a new state of equilibrium is often reached after 10-15 years for P and after <5-10 years N [12,79]. However, in some lakes, internal loading has delayed recovery for up to 20 years (e.g. Lake Søbygård, Denmark [58]) when external loads have been reduced. A critical aspect of recovery time is the release of legacy P that has accumulated in the lake sediments, which can delay recovery for many years [58,80].

In terms of biological recovery times, those of macrophytes are some of the best documented. For example, at Loch Leven, macrophyte species richness, species evenness and MCD was very slow to respond when external P loads were reduced over a 20-year period Dudley et al. [64]. Similarly, an equally slow response was observed by Sand-Jensen et al [57], who found that decreases in MCD, species richness and species distribution that had occurred during the eutrophication phase in Lake Fure, Denmark, had not been reversed completely even 30 years after P inputs had been reduced by 95 per cent.

5. Complicating Factors That Confound Biological and Nutrient Recovery Processes

Lake depth affects biological and nutrient recovery processes in lakes. For example, the effects of grazing pressure are likely to be higher in deep lakes, where zooplankton grazers can avoid predatory fish through vertical migration into deep water refuges [81]. Also, the recovery of deep lakes is less likely to be affected by internal P load than shallow lakes, because deep lakes dilute the P released from the sediments into larger volumes of water [82]. In addition, Weyhenmeyer et al [43] found that NO_3-N loss rate increased with decreasing lake depth. In large lakes, more generally, species richness is unlikely to be reduced due to species replacement, especially in large lakes where species extinctions are rare due to the presence of *refugia* [83,84].

Recovery of phytoplankton communities can be confounded by a range of biological and nutrient conditions. In shallow lakes with summer N-limitation, a decrease in non-heterocystous cyanobacteria species (e.g. *Limnothrix redeki*, *Oscillatoria* spp. and *Planktothrix agardhii*) was reported relative to N_2-fixing species (e.g. *Aphanizomenon flos-aquae*) when P concentrations are reduced [85-87]. Also, natural or anthropogenically induced alterations in the community composition of fish can cause changes in top-down pressures that alter phytoplankton responses to changes in nutrient availability [48,88,89]. Climate change has rarely been considered to be an important driver of recovery processes, however, several studies have reported that climate change affects phytoplankton communities more generally over a range of time-scales [90,91].

Recovery of zooplankton communities may be confounded by fish in terms of insufficient stock reduction, natural or human induced re-colonisation of target fish species, and/or low survival of stocked fish, all of which were found to lead to a reversal of improvement trends in zooplankton due to trophic cascades [58,92]. In addition, it has been rported that increases in predatory zooplankton could result from biomanipulation/fish stocking [74] or changes in toxic cyanobacteria [93], leading to a reversal of the general recovery processes outlined above. In contrast climate change, especially an increase in spring water temperatures, may enhance the response of *Daphnia* to recovery from eutrophication [94], while phenological shifts can favour earlier occurrence of *Daphnia* in spring [95]. In general, cladocerans are likely to benefit from higher temperatures more than copepods, which may lead to a change in dominance patterns within zooplankton communities in spring [96]. In addition, acidification may result in a drop in fecundity in *Daphnia* spp. and unbalance the zooplankton response to favour eutrophic community structures [97].

Recovery of macroinvertebrate communities is confounded by habitat specific responses, with communities in deeper areas responding more slowly to restoration efforts (e.g. up to 10 years in Lake Ladoga, Russia; Viljanen et al. [98]) than those in littoral habitats. It has been suggested that this is due to sustained deposition of organic matter and reduced DO concentrations, because there is a negative relationship between organic matter deposition and oligochaetes in more oligotrophic conditions [99,100]. Colonisation by invasive non-native dreissenid mussels (i.e. Zebra mussel (*Dreissena polymorpha*)) during the recovery process can enhance the recovery of deposit-feeding organisms, small gastropods and small predatory macroinvertebrates, by increasing resource availability [101,102], although they can also cause adverse changes in community composition, such as the decline of native molluscs [101]. Changes in the fish community that alter predation levels on specific groups within the benthic macroinvertebrate community, may affect their recovery rates as demonstrated by an increase in predation by perch and roach and whitefish in Lake Ring, Denmark, which reduced the density of *Chaoborus* and Chironomidae [103].

In terms of macrophyte recovery, this is often confounded by preferential grazing of species by herbivorous waterfowl and fish, leading to variations in end point community composition. Invasion by more competitive species may also be a problem, leading to loss, or suppression, of native species and persistent habitat disturbance (e.g. by wind and waves), can "re-set" the recovery trajectory of the whole system to favour the turbid state in shallow lakes (e.g. Lake Apopka, USA [104]). The existence of seed banks, the availability of distribution networks and pathways, and species distribution and growth traits, will determine the recovery trajectory of the macrophyte community. More generally, it is likely that, after 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) will appear as nutrient concentrations decrease [105].

Recovery of the fish community is affected by many things. For example, fish communities in lakes where biomanipulation has been conducted do not necessarily respond as expected [106]. In addition, changes in the inorganic sediment load from manipulated catchments can cause high loads of total suspended sediment (TSS) to enter lakes and their feeder streams, adversely affecting local fish populations. In general, it has been found that TSS concentrations of more than 100 mg L^{-1} pose a medium to high risk to both fish and their habitat [107]. Invasion by non-native fish (e.g. chub (*Leuciscus cephalus*)) can also cause problems for native fish populations during the recovery process [108], through competition, environmental degradation and predation [109,110]. Finally, extreme variations in water level during the recovery process have been shown to damage eggs and limit habitat availability for young of the year fish, leading to reduced recruitment success [111,112].

6. Conclusions

The successful restoration of a lake from eutrophication is a complex process that requires a comprehensive understanding of the impacts of multiple primary and secondary pressures. Without this, undesirable deterioration of nutrient and biological water quality may occur as a result of the numerous feedback mechanisms that exist within a lake ecosystem. What is apparent from this review is that restoration case studies that were deemed "successful" have been underpinned by long-term monitoring of pressures and responses throughout the phases of degradation and recovery [20,28]. The review found little reference to detailed lake restoration studies in tropical and sub-tropical systems in the published literature, which highlights the need for further research on these systems.

Very few studies have reported pre-defined ecological restoration targets aligned to the relevant legislative drivers of restoration. Also, at present, there are insufficient data available in the literature to undertake multi-lake meta-analyses of the ecological recovery trajectories that lakes followed after mitigation strategies were put in place to reduce eutrophication problems. This is especially true of sub-tropical and tropical systems, which behave differently to temperate systems and are under represented in the current literature.

In general, the duration of the recovery period is driven by a range of primary pressures and sensitivity factors, including lake depth, pollution history, retention time, and sediment P composition and concentrations [113]. In addition, species interactions and feedback mechanisms complicate recovery processes making it difficult to predict restoration trajectories and outcomes. It is clear, however, that sustainable recovery takes many years, if not decades, to achieve. It is important to take this into account when planning and implementing eutrophication management options [20], because these slow recovery periods can exceed the timescales that humans are willing to understand and accept [76]. This highlights some of the societal and political considerations that need to be taken into account when selecting management actions to restore impacted lakes [28].

7. References

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