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Success of lake restoration depends on spatial aspects of nutrient loading and hydrology



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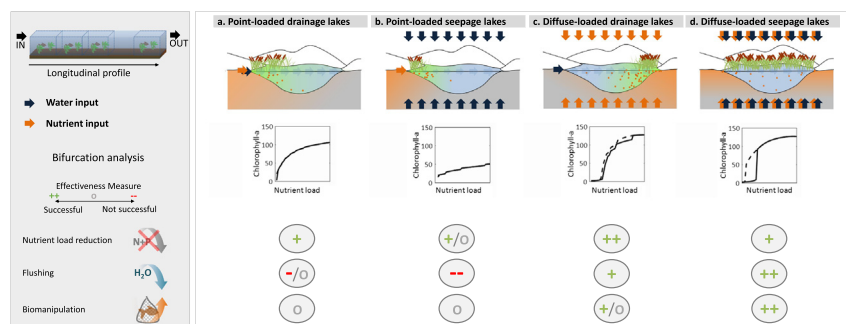
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HIGHLIGHTS

- Many aquatic ecosystems are deteriorated and their restoration is often troublesome.
- Four lake types can be distinguished with contrasting nutrient loading and hydrology.
- Long-term restoration by reducing nutrient loading is effective in all cases.
- Biomanipulation (fish removal) only works in diffuse-loaded seepage lakes.
- Lake flushing will be counterproductive in lakes with nutrient point sources.

GRAPHICAL ABSTRACT



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ABSTRACT

Many aquatic ecosystems have deteriorated due to human activities and their restoration is often troublesome. It is proposed here that the restoration success of deteriorated lakes critically depends on hitherto largely neglected spatial heterogeneity in nutrient loading and hydrology. A modelling approach is used to study this hypothesis by considering four lake types with contrasting nutrient loading (point versus diffuse) and hydrology (seepage versus drainage). By comparing the longterm effect of common restoration measures (nutrient load reduction, lake flushing or biomanipulation) in these four lake types, we found that restoration through reduction of nutrient loading is effective in all cases. In contrast, biomanipulation only works in seepage lakes with diffuse nutrient inputs, while lake flushing will even be counterproductive in lakes with nutrient point sources. The main conclusion of the presented analysis is that a priori assessment of spatial heterogeneity caused by nutrient loading and hydrology is essential for successful restoration of lake ecosystems.

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1. Introduction

Globally, the water quality of aquatic ecosystems is increasingly degraded by excessive nutrient loading and changes in natural hydrology (Fink et al., 2018; Kroeze et al., 2013; Tong et al., 2019; Tonkin et al., 2018). For instance, increased coastal water runoff, sediments and nutrients underlie the deterioration of coral reefs (D'Angelo and Wiedenmann, 2014), and increased nutrient enrichment causes the emergence of harmful algal blooms in lakes (Paerl and Otten, 2013; Tong et al., 2019). Human-alterations to the natural hydrology and changed pathways of allochthonous nutrient input are underlying this widespread degradation of aquatic ecosystems (Beusen et al., 2016; Doughty et al., 2016; Tonkin et al., 2018). Ample attempts are made to restore deteriorated ecosystems by controlling the allochthonous nutrient input, for instance in coastal regions (Riemann et al., 2016), as well as by addressing the transport by water, for instance by restoring the natural hydrology (Kong et al., 2016; Perry, 2008). Unfortunately, restoration of deteriorated aquatic ecosystems has only been partly successful (Elliott et al., 2007; Qin et al., 2010; Søndergaard et al., 2007) and it remains a challenge to reach UN Sustainable Development Goals (SDG) such as clean water as described in SDG6 (Griggs et al., 2013; Nations, 2009).

Nutrient loading originates from external sources (allochthonous nutrient input) as well as from the recycling of nutrients within the ecosystem (autochthonous nutrient input) (Doi, 2009). Sources of allochthonous nutrient inputs are numerous and include atmospheric wet and dry deposition, loading via water flows such as groundwater, rivers and tide (Beusen et al., 2016). Additionally, an often overlooked source of nutrients originates from animal motility such as fish and bird migration (Doughty et al., 2016). These various sources of allochthonous nutrient inputs are commonly categorised into two main load types; point and diffuse nutrient sources (Rissman and Carpenter, 2015). Here we define point sources of nutrients as local foci of nutrient input into lakes, which include nutrient inputs by rivers or pipelines. We defined diffuse sources as broadly dispersed nutrient input to lakes, resulting in spatially more homogeneous nutrient input. Examples of diffuse sources of nutrients are atmospheric nutrient deposition and nutrients input via groundwater seepage. The difference between point and diffuse sources is thus that the first enters a lake at one location and the latter is spatially spread over the whole lake. This difference affects the spatial heterogeneity in resource availability within ecosystems, which in turn creates spatial patterns in the aquatic food web (Doi, 2009).

Hydrology also affects the spatial heterogeneity of nutrients through transport processes (Oldham et al., 2013; Tong et al., 2019). Relative high transport rates limit the biological conversion of nutrients and allow nutrients to be spread further (Schmadel et al., 2018). Relative low transport rates allow high local nutrient retention and leave less nutrients to be spread further in the aquatic ecosystem (Schmadel et al., 2018). As with nutrients, the sources of water entering the ecosystem can be local foci or broadly dispersed and this determines the eventual distribution of resources in the waterbody. For water, this difference in hydrology types is commonly designated by classifying them as drainage and seepage, respectively (Driscoll and Newton, 1985).

It is important to disentangle the different nutrient and hydrology types to fully understand the biological and physical dynamics in lakes (Brock et al., 1982; Corman et al., 2018). A study by Van Gerwen et al. (2016) suggests that differences in hydrology and nutrient input can have important implications for water quality. Moreover, Hilt et al. (2011) showed that the water flow velocity determines how local regime shifts propagate through aquatic systems. Yet, a thorough study that elucidates the effect of different types of nutrient load and hydrology is, to our knowledge, still lacking. Here we hypothesise that the effectiveness of lake restoration measures critically depends on hitherto largely neglected spatial heterogeneity in nutrient availability, caused by different nutrient loading and hydrology types.

Importantly, a successful restoration measure promotes desired primary producers, such as macrophytes in shallow lakes, at the expense of undesired primary producers such as cyanobacteria (Hilt et al., 2018). Primary producers show spatial heterogeneity in their response to restoration (Janssen et al., 2017). Since primary producers rely on available nutrients, this can possibly be explained by spatial heterogeneity of resources within lakes, which differs for point and diffuse sources of nutrients and is affected by hydrology.

With a modelling approach, we tested how the effectiveness of lake restoration measures depends on spatial heterogeneity in nutrient availability, using lake types with contrasting nutrient loading (point versus diffuse) and hydrology (seepage versus drainage). First, we explore how spatial patterns in loading and transport of incoming nutrients within lakes affect the spatial heterogeneity in primary producers and the presence of (lake-wide) alternative-stable states. Next, we compare the effect of common lake restoration measures (load reduction, flushing, and biomanipulation) in the contrasting lakes. Finally, we give real-world examples of these lake types to illustrate the predicted patterns and the effectiveness of restoration measures. With this approach, we show that assessment of the loading type and transport of nutrients is essential for planning successful restoration of lake ecosystems. For visualisation of our study please watch the explanatory movie (see video attached to this publication or at <https://www.youtube.com/watch?v=FJ2pAWjOcok>).

2. Materials and methods

2.1. Study design: 4 lake types

We used a full factorial design to explore the effects of type of allochthonous nutrient source in combination with the transport processes of nutrients within lakes. For the allochthonous nutrient load types, we distinguished point and diffuse nutrient sources. With respect to the transport of nutrients within the lake, we used lake hydrology. As lake hydrology types we distinguished drainage and seepage lakes, which are determined by the type of water input. Lakes receiving water primarily from rivers are referred to as drainage lakes. According to the law of conservation of mass, the main water flow in drainage lakes with one water inflow point and one outlet will constitute a spatially uniform mass flux of water between the inflow and outlet. In contrast, lakes that receive water mainly from diffuse sources like groundwater and precipitation are referred to as seepage lakes (Driscoll and Newton, 1985). The main water flow in seepage lakes will build up mass flux of water towards the outlet, as new water is added over the entire spatial extent of the lake. The difference between drainage and seepage lakes is thus the way the main water flow develops towards the outflow point, which is expected to affect nutrient transport and distribution.

Combining the two allochthonous nutrient load types with the two hydrology types leads to four different lake types (Fig. 1). We will simulate these four lakes using lake types at the extreme of the nutrient and hydrological spectrum but discuss the implications for lakes that do not fit into these discrete and rigid categories in the discussion. Below, each of these lake types is described and an example of a real-world lake is provided. We will use these real lakes as examples to illustrate the horizontal patterns found for the four lake types used in our model study.

The first lake type represents drainage lakes that receive nutrients, along with water, primarily from allochthonous point sources like an inflowing river, stream or ditch (Fig. 1a, 'point-loaded drainage lakes'). These point-loaded drainage lakes are, for example, lowland lakes that are part of a river catchment with rivers that are nutrient rich due to urban, industrial and agricultural activities. For example, Lake Taihu (China) can be characterised as a point-loaded drainage lake since the majority of nutrients originate from point sources (90%) and water input is mainly from rivers (75%) (Kelderman et al., 2005; Wang et al., 2019).

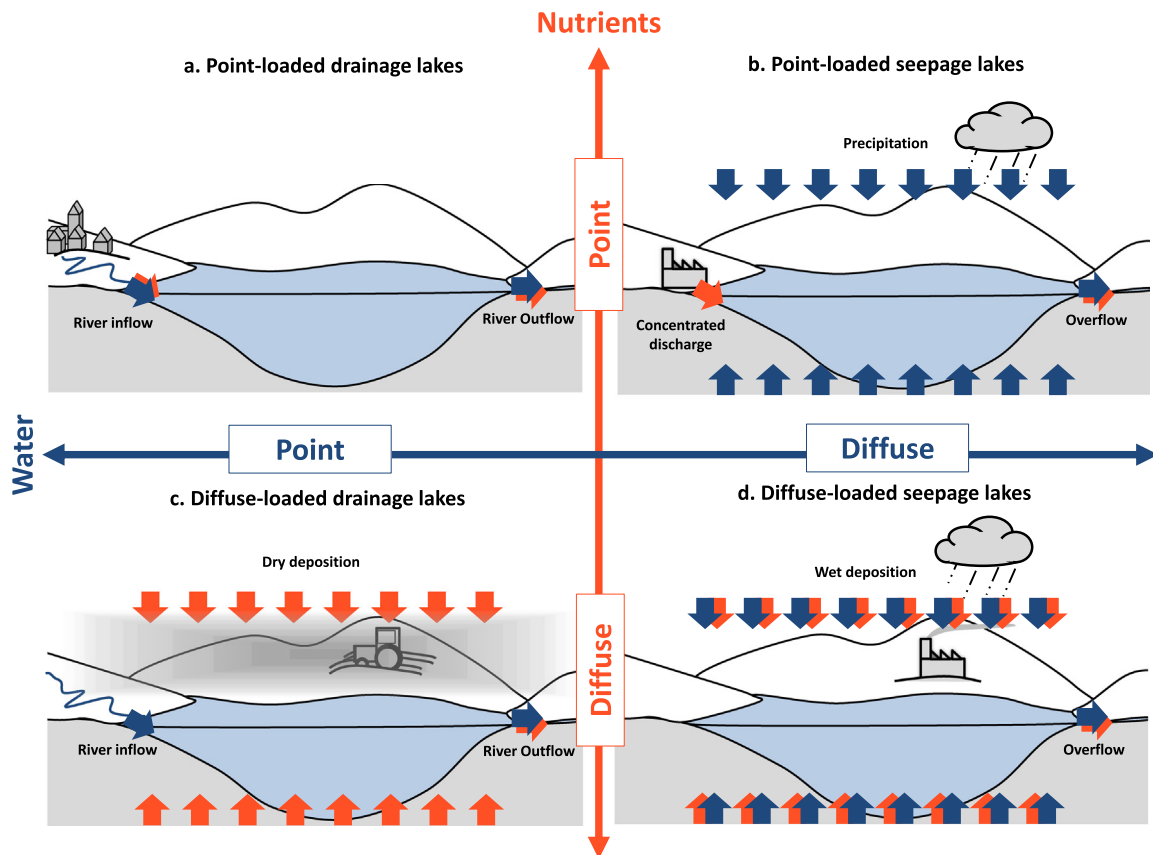


Fig. 1. Textbook examples of four different lake types characterised by spatial patterns of nutrient loading (point versus diffuse; horizontal axis; red arrows) and by nutrient distribution through hydrological dispersal (drainage versus seepage; vertical axis; blue arrows).

The second lake type comprises seepage lakes, receiving water mainly via groundwater and precipitation, whereas the majority of nutrient loading originates from a point source, such as industrial wastewater or untreated sewage water (Fig. 1b, ‘point-loaded seepage lakes’). Point-loaded seepage lakes could be urban lakes that are naturally fed by groundwater, but due to human development receive a relatively large amount of nutrients that are directly funnelled into this lake. An example of such a point-loaded seepage lake is Lake Pátzcuaro in Mexico. The main water source of Lake Pátzcuaro (Mexico) is rainwater, while point loadings from wastewater to the south of the lake have become the main nutrient load (Bernal-Brooks et al., 2003; Chacón-Torres and Múzquiz-Iribe, 1997).

The third lake type represents drainage lakes (Fig. 1c, ‘diffuse-loaded drainage lakes’), which differ fundamentally from the first type, in that they receive nutrients from diffuse allochthonous sources such as dry atmospheric nutrient deposition or agricultural leaching. Diffuse-loaded drainage lakes could, for instance, be lakes located in a valley heavily used for agriculture resulting in high levels of dry atmospheric nutrient input, but for which the main water source is relatively clean because it originates from the mountains. An example is the alpine Lake Tahoe (USA), which receives water that mainly originates from watershed runoff, whereas the majority of allochthonous input of nutrients is atmospheric deposition from combustion emissions, agricultural fertiliser and industrial waste (Jassby et al., 1994; Schuster and Grismer, 2004).

The fourth lake type comprises seepage lakes, which receive both nutrients and water from diffuse sources such as wet atmospheric deposition or nutrient-rich groundwater (Fig. 1d, ‘diffuse-loaded seepage lakes’). Diffuse-loaded seepage lakes are, for example, peat lakes that are groundwater or rainfed and receive their nutrients mainly through the same pathway as water. An example is Lake Loosdrecht in the

Netherlands. Since Lake Loosdrecht naturally received groundwater together with nutrients from an elevated sand ridge and input from rainwater it can be characterised as a diffuse-loaded seepage lake (Van Liere, 1986; Van Liere et al., 1991).

2.2. Model setup

To study the success of lake restoration measures we used a modelling approach. While field studies are essential where and when possible, modelling approaches have a key role and have the advantage of enabling outcome comparisons under strictly controlled conditions for many simulation repetitions. A large spectrum of aquatic ecosystem models exists (Janssen et al., 2015). In this study, we sought a model based on fundamental limnological processes, so that it is applicable to study the restoration of diverse lakes. Additionally, the model should be linked with a hydrological model to simulate the distribution of transportable substances, such as nutrients. We selected the ecosystem model PCLake because it has shown broad applicability to different shallow lakes (Janse et al., 2010; Nielsen et al., 2014). Moreover, the model stands out in its ability to estimate critical nutrient loadings at which a lake in a turbid state turns to the clear state (Janse et al., 2010; Janssen et al., 2015). We ran the model code of PCLake in R by using the Database Approach To Modelling (DATM) (Mooij et al., 2014; Van Gerven et al., 2015). DATM is an approach in which a model is specified in mathematical terms in a database, and by which framework-specific code can be generated using automated code generators (Janssen et al., 2015). This allows for linking PCLake to hydrological models (Mooij et al., 2014; Van Gerven et al., 2015).

The aquatic ecosystem model PCLake includes both water column and sediment layer food webs, with functional groups comprising three phytoplankton types, zooplankton, zoobenthos, planktivorous

and piscivorous fish (Janse, 2005; Janse et al., 2008; Janse et al., 2010). The interactions between these functional groups, together with conversions of detritus, nutrients (nitrogen, phosphorus and silica) and inorganic matter in sediment and water, are the biogeochemical processes simulated in this study. Variable nutrient burial and release from the sediments are included in these biogeochemical processes. See Fig. 2 for a schematic of PCLake. For the simulations, we chose to use a default lake as defined by Janse et al. (2010). This default lake is based on an ‘average’ temporal lake that has been calibrated and validated with a dataset of nearly 40 lakes in northern Europe (Janse et al., 2010). The average lake has a depth of 2 m, a fetch of 1000 m and the sediment is slightly clayish. Except for the settings for hydrology (Q_{in}) and nutrient load, the parameter settings for each of the lake types were equal, using the parameter values as defined in Appendix A.

We schematised each hypothetical lake into a one-dimensional chain of (N = 10) segments (Fig. 3). For each segment, biogeochemical processes were simulated using PCLake (Fig. 2). A spatially explicit hydrodynamic model was adopted to simulate the transport of nutrients for each lake type (Van Gerven et al., 2016). To guarantee a fair comparison between the modelled lakes, each lake type received an equal total amount of water (20 mm·d⁻¹) and allochthonous nutrients, yet the distribution over the segments depended on the nutrient source type and lake hydrology (see Table 1). In the case of point-loaded and drainage lakes, all nutrients or water, respectively, enters the lake in the first segment (n = 1). In diffuse-loaded and seepage lakes, each segment receives one Nth of the total amount of nutrients or water respectively. In each case, part of the nutrients is retained due to biogeochemical processes taking place in each segment. The remaining nutrients and other transportable substances are passed onto the next segment as autochthonous load by the main water flow. This procedure was repeated until the last segment discharged the water via an out- or overflow.

2.3. Model analysis

First, we performed a *spatial response analysis* to identify the effect of lake type on the spatial heterogeneity of nutrients and primary producers within lakes. To this end, we repeatedly ran the model to equilibrium, each time evaluating the equilibrium response of primary producers and nutrient concentrations along the longitudinal profile to a given temporally constant nutrient load. For each run, the constant nutrient loads were chosen from a range of loading levels that varied between 0.002 and 0.05 g P·m⁻²·d⁻¹ with 40 intervals each of 0.0012 g P·m⁻²·d⁻¹. Similar to previous studies (Janse et al., 2010), we adopted a constant nutrient load N:P ratio of 10, which is close to the median ratio of nutrient loads to lakes reported in the database of the International Lake Environment Committee (ILEC, 1999) and is in the range of what has been found for rivers (Beusen et al., 2016).

Next, we performed a *bifurcation analysis* to identify the possible lake-wide presence of alternative stable states (that is, hysteresis). For this, we averaged the equilibrium responses to each nutrient load along the longitudinal profile. We repeated this procedure twice, once starting with a clear oligotrophic state and once with a turbid eutrophic state. In the case of alternative stable states, the lake-wide outcomes for oligotrophication and eutrophication differ.

2.4. Set up of restoration scenarios

We analysed the effect of the three types of commonly used lake restoration measures on the equilibrium responses of bifurcation analysis (Fig. 4). These lake restoration measures include nutrient load reductions, flushing and biomanipulation (e.g. Ibelings et al., 2016; Janse et al., 2008). These measures should move the equilibrium outcome for a given nutrient load towards the preferred clear state. The success of these measures to sufficiently reduce phytoplankton concentrations thus critically depends on 1) whether the lake is currently in an

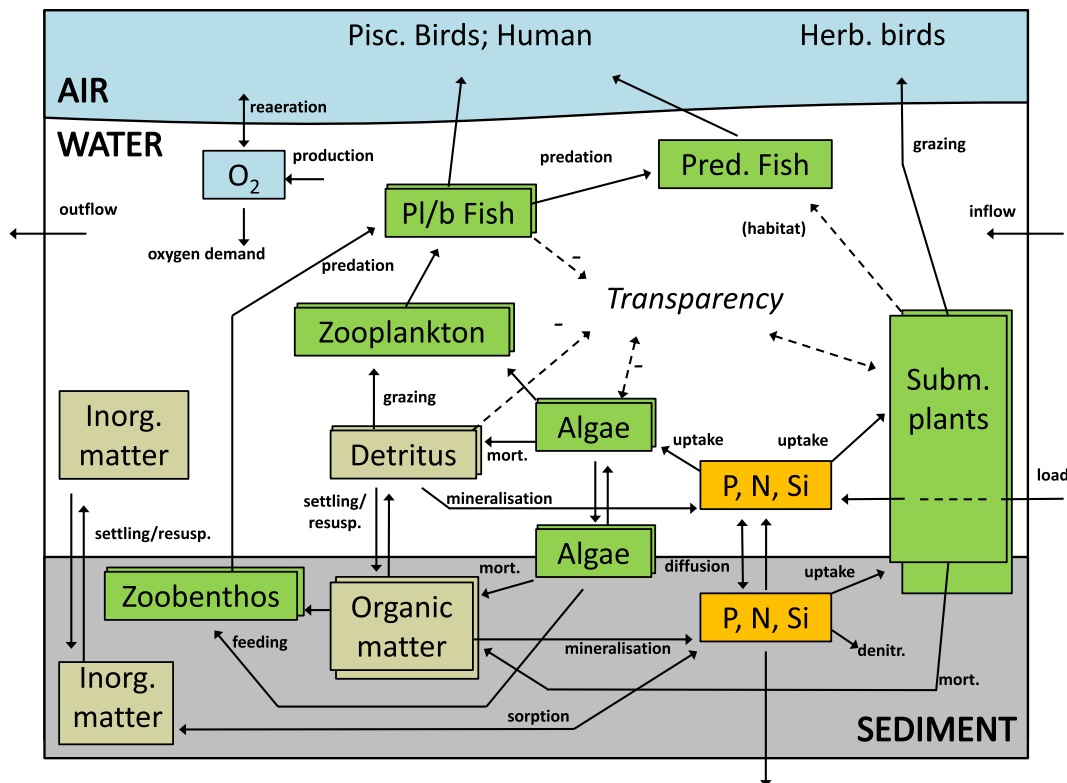


Fig. 2. Schematic of PCLake showing its biogeochemical processes, including interactions between functional groups and conversions of detritus, nutrients (nitrogen, phosphorus and silica) and inorganic matter in sediment and water (Van Gerven et al., 2015).

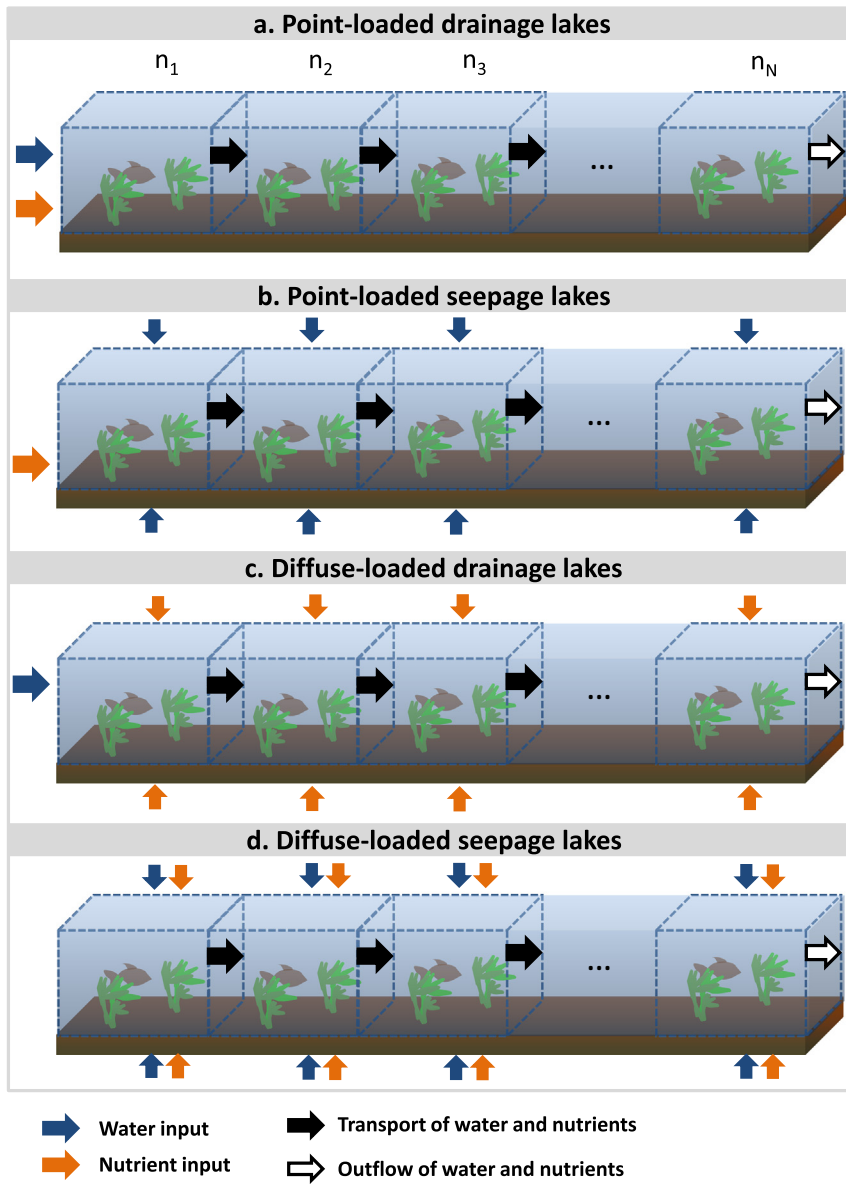


Fig. 3. Schematisation of the model setup of the four lake types.

oligotrophic or eutrophic state, 2) the required nutrient load reduction and 3) whether or not alternative stable states are present. For each of the lake restoration measures, we simulated the long-term outcome of the lake as described below.

First, we simulated the long-term effect of allochthonous nutrient load reduction over the full range from eutrophic to oligotrophic. Allochthonous nutrient load should be sufficiently reduced to ensure that phytoplankton growth is no longer sustained by an excess of

Table 1
Dynamics of substances in the four lake types.

Lake type ^a	Nutrient balance ^b
Point-loaded drainage lakes	$V \frac{dC_{i,n}}{dt} = \begin{cases} L - QC_{i,1} - rVC_{i,1} & \text{if } n = 1 \\ QC_{i,n-1} - QC_{i,n} - rVC_{i,n} & \text{if } n > 1 \end{cases}$
Point-loaded seepage lakes	$V \frac{dC_{i,n}}{dt} = \begin{cases} L - \frac{Q}{N}C_{i,1} - rVC_{i,1} & \text{if } n = 1 \\ (n-1)\frac{Q}{N}C_{i,n-1} - n\frac{Q}{N}C_{i,n} - rVC_{i,n} & \text{if } n > 1 \end{cases}$
Diffuse-loaded drainage lakes	$V \frac{dC_{i,n}}{dt} = \begin{cases} \frac{L}{N} - QC_{i,1} - rVC_{i,1} & \text{if } n = 1 \\ \frac{L}{N} + QC_{i,n-1} - QC_{i,n} - rVC_{i,n} & \text{if } n > 1 \end{cases}$
Diffuse-loaded seepage lakes	$V \frac{dC_{i,n}}{dt} = \begin{cases} \frac{L}{N} - \frac{Q}{N}C_{i,1} - rVC_{i,1} & \text{if } n = 1 \\ \frac{L}{N} + (n-1)\frac{Q}{N}C_{i,n-1} - n\frac{Q}{N}C_{i,n} - rVC_{i,n} & \text{if } n > 1 \end{cases}$

^a See for schematisation of the lake types Fig. 1 and for the schematisation of model setup of the four lake types Fig. 3.

^b C (g·m⁻³) is the concentration of substance i in the nth segment, V (m³) is the volume of a segment (assumed constant), t is the time (d), L (g·d⁻¹) is the loading of substance i, N is the number of segments and n the index of the nth segment, Q (m³·d⁻¹) is the total discharge to the lake and r is the biochemical conversion factor.

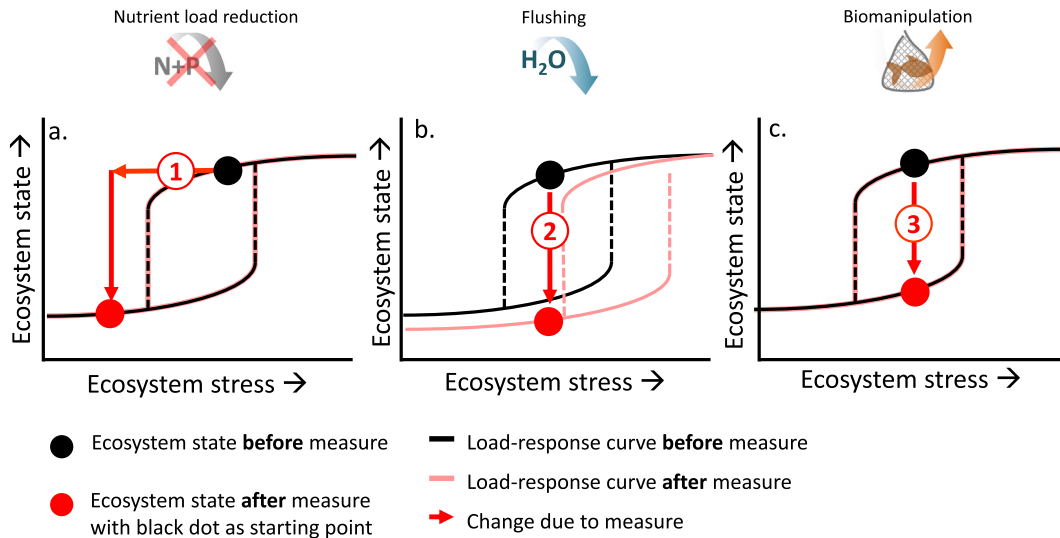


Fig. 4. Options for lake restoration: a) nutrient load reduction b) flushing c) biomanipulation. Modified after Janse et al. (2008).

nutrients. Its effect is often delayed due to internal loading which, especially in the short term, could be high, but in the long run becomes less important after the sediment has released the excess amount of nutrients (Jeppesen et al., 2007).

Second, we simulated flushing ('retention time reduction') by a 50% increased water input via a permanent water pipeline that continuously adds water with a negligible amount of nutrients. By permanently increased water input, flushing aims to increase the water flow in the lake so that the phytoplankton biomass is washed out of the lake (Li et al., 2011; Romo et al., 2013).

Lastly, biomanipulation, by a single catch of 90% of all planktivorous fish that directly feed on zooplankton like *Daphnia*, was modelled as a perturbation aiming to push the lake to the alternative clear state. Biomanipulation is a measure that alters the food web by adding or removing species to trigger biological mechanisms in the food web that reduces phytoplankton growth. A list of biomanipulation options exists (e.g. Jeppesen et al. (2012)) for which an up to 100% removal of planktivorous fish is a commonly used measure (Meijer et al., 1999), although with mixed results (Søndergaard et al., 2007). In our model example, the single removal of planktivorous fish should promote the reestablishment of macrophytes that can support a permanent reduction of predation pressure on zooplankton like *Daphnia* by offering refuge. As a result, zooplankton species can grow in large numbers and graze down phytoplankton biomass.

3. Results

We will first interpret the spatial response of different nutrient loading and hydrology types. Results of this first step are used to interpret the effect of nutrient loading and hydrology types on the success of lake-wide restoration measures.

3.1. Spatial response analysis of nutrient load type

The spatial distributions of both nutrient concentrations and primary producers within lakes depend on whether the allochthonous nutrients came from diffuse or point sources (Fig. 5). At the water outlet, the total nutrient load is highest in lakes with diffuse nutrient sources (Fig. 5c and d), whereas it is lowest for lakes with nutrient point sources (Fig. 5a and b). The difference between allochthonous point and diffuse sources can explain this: with an allochthonous point source, nutrients enter in bulk form at the inlet point, promoting in situ luxurious growth of either macrophytes (low allochthonous nutrient load) or

phytoplankton (high allochthonous nutrient load) (Fig. 5a and b). Towards the water outlet, nutrient depletion leads to a decrease in primary production. In contrast, lakes with a diffuse nutrient load receive allochthonous nutrients homogeneously. Since only a fraction of these nutrients are retained at any location along the longitudinal profile, diffuse nutrient loading leads to spatial accumulation of total nutrient load towards the outlet (Fig. 5c and d, total nutrient load). In the diffuse-loaded drainage lakes, therefore, increasing in-lake nutrient concentrations and phytoplankton biomass are observed towards the outlet in Fig. 5c. Interestingly, diffuse nutrient loading in seepage lakes leads to completely homogeneous in-lake nutrient, phytoplankton and macrophyte distributions (Fig. 5d). This homogeneity follows from a constant ratio between the incoming water and the allochthonous nutrient load, which keeps the in-lake nutrient concentrations at a constant level.

3.2. Spatial response analysis of lake hydrology type

Effects of hydrology type on the spatial pattern of nutrient concentrations and primary producers are subtler than the effect of nutrient load type. Hydrology type skews the spatial pattern of in-lake nutrient concentrations and primary producers rather than determining their general locations (Fig. 5). Comparing lakes with nutrient point sources reveals that the nutrient and algal concentrations are skewed towards the inlet in case of seepage compared to drainage lakes (Fig. 5a and b). This emerges from the relative high flow-driven nutrient transport rate close to the inlet of drainage lakes. In contrast, seepage lakes experience lower transportation rates at these locations, resulting in a high degree of in situ nutrient retention. The same process has a contrasting effect in diffuse-loaded lakes due to the positioning of the highest total nutrient loads (Fig. 5c and d). Here the relatively high flow-driven nutrient transport at the inlet of drainage lakes prevents high nutrient concentrations from emerging at the inlet. Therefore nutrient and algal concentrations are skewed towards the outlet in case of diffuse-loaded drainage lakes.

3.3. Bifurcation analysis of lake-wide effects

Spatial heterogeneity in phytoplankton, resulting from different nutrient load and hydrology types, has consequences for the lake average phytoplankton chlorophyll-*a* values. Alternative stable states, phytoplankton versus macrophyte dominance for the same nutrient loading, are only present if the load-response curve for eutrophication (black

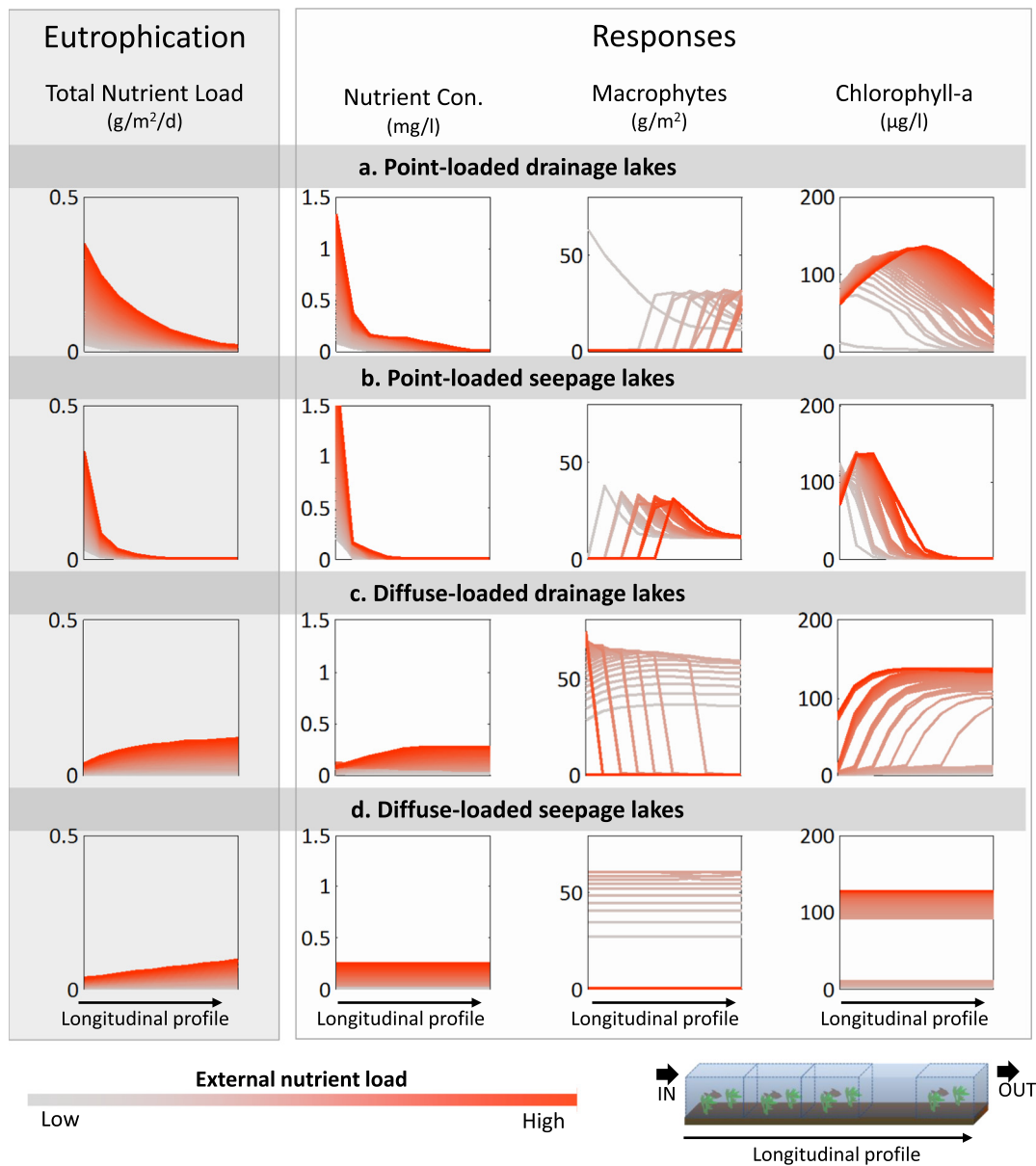


Fig. 5. Spatial response analysis: model results for each of the four lake types, showing the response of nutrients and primary producers in lakes along the longitudinal axis, which extends from the inflow point towards the outflow point of the lake, to different amounts of allochthonous nutrient loads. Results with low nutrient loads are shown in grey and results with high nutrient loads are shown in red. The variables from left to right are the total nutrient load defined as the sum of allochthonous (external nutrient load) and autochthonous (internal nutrient load) nitrogen load per segment ($\text{g N} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) (graphs for total P-loading are similar), surface water nutrient concentrations of NH_4 ($\text{mg} \cdot \text{L}^{-1}$) (graphs for other nutrients are similar), biomass of macrophytes ($\text{g} \cdot \text{m}^{-2}$) and chlorophyll-a concentration as a proxy for phytoplankton biomass ($\mu\text{g} \cdot \text{L}^{-1}$).

solid line) differs from the load-response curve for oligotrophication (black dashed line) (Fig. 6A). Importantly, the occurrence of alternative stable states is prominent in the modelled diffuse-loaded seepage lakes (Fig. 6A.d) and present in the diffuse-loaded drainage lakes (Fig. 6A.c). However, alternative stable states were absent in point-loaded lakes since their load-response curves for eutrophication coincided with the one of oligotrophication (Fig. 6A.a and A.b). Our results suggest that this is due to the fundamental difference between the fixed position of rooted macrophytes and the mobility of free-flowing phytoplankton. Once phytoplankton is growing at high densities at the inlet in the point-loaded lakes, they are also being dispersed by water movement across the lake. This transport of phytoplankton into initially macrophyte-dominated areas negatively affects the competitive strength of macrophytes. Thereby, strong positive feedbacks, which otherwise would maintain the macrophyte-dominated state, are weakened.

In lakes with a diffuse nutrient load, however, positive feedbacks that maintain macrophytes are less affected by transport of phytoplankton, since significant phytoplankton concentrations appear first close to the lake outlet (diffuse-loaded drainage lakes) or are homogeneous throughout the entire lake (diffuse-loaded seepage lakes). Consequently, feedbacks that enable alternative stable states are unaffected by phytoplankton transport in diffuse-loaded lakes. Still, there are differences between diffuse-loaded lakes. In the case of diffuse-loaded seepage lakes, one shift between alternative stable states occurs at the same time across the whole lake (Fig. 6A.d). In diffuse-loaded drainage lakes (Fig. 6A.c), such shifts are weaker and are based on successive local shifts, each successively farther from the outlet as nutrient input increases.

Finally, note that the load-response curve in point-loaded drainage lakes (Fig. 6A.a, black solid line) resembles the oligotrophication curve of diffuse-loaded seepage lakes (Fig. 6A.d, black dashed line). This

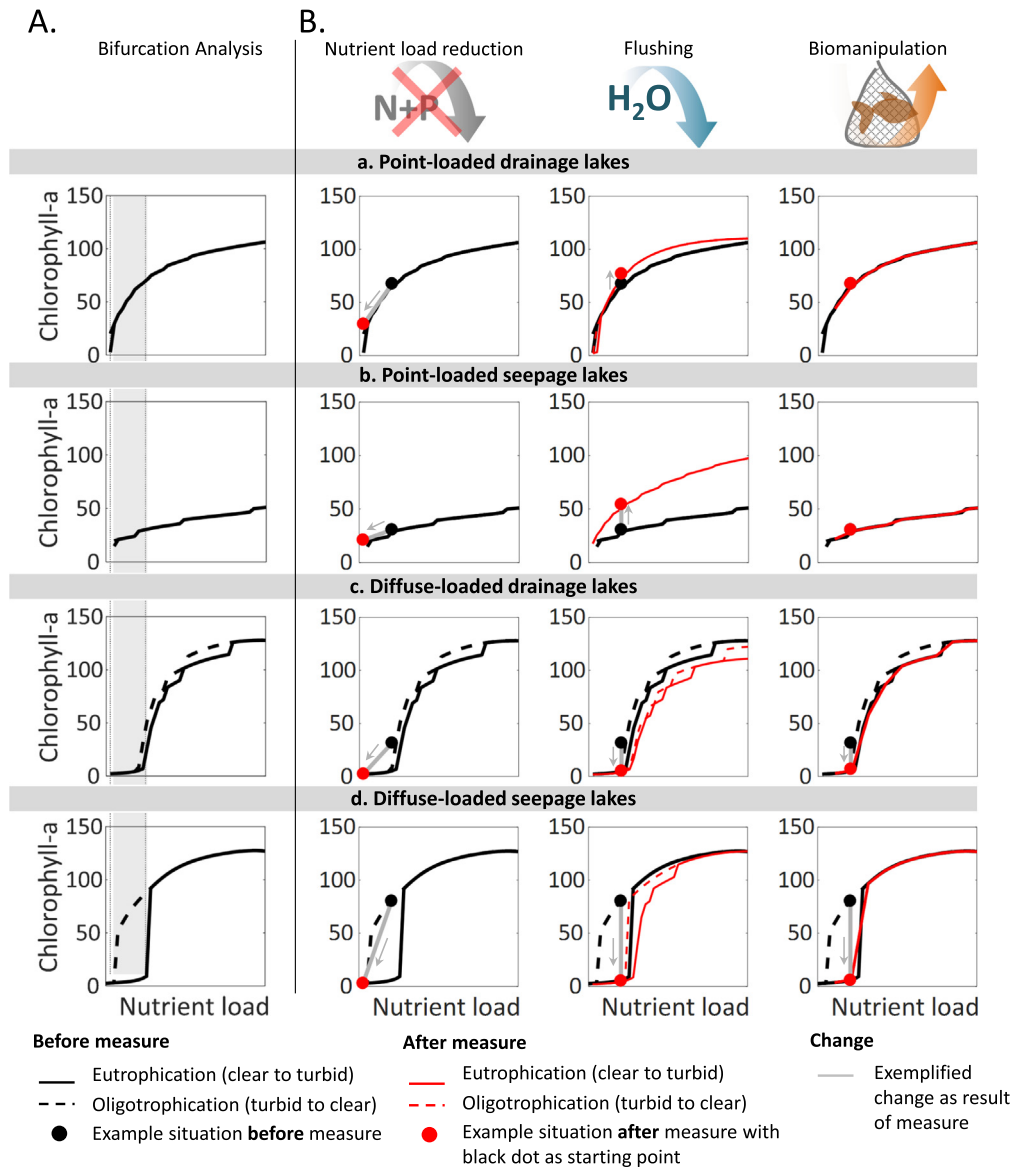


Fig. 6. Bifurcation analysis of lake-wide effects: A) Spatially-averaged load-response curves resulting from bifurcation analysis showing the total allochthonous nutrient load for each lake type on the horizontal axis and the lake average chlorophyll-a ($\mu\text{g}\cdot\text{L}^{-1}$), as a proxy for phytoplankton biomass, on the vertical axis. B) Spatially-averaged load response curves for three restoration measures, from left to right: nutrient load reduction, flushing and biomanipulation. The effect of each measure is illustrated by the change indicated by the grey line between an initial equilibrium (black dot) and a new equilibrium that established after the intervention (red dot). The measure improves the situation if it leads to lower chlorophyll-a concentrations (red dot is located below the black dot).

suggests that phytoplankton controls the transition from clear to turbid state and vice versa in point-loaded drainage lakes. Additionally, the load-response curve of diffuse-loaded drainage lakes (Fig. 6A.c) is similar to that of the load-response curve for eutrophication of diffuse-loaded seepage lakes (Fig. 6A.d, black solid line). In this case, macrophytes appear to control the transition from clear to turbid and vice versa in diffuse-loaded drainage lakes, which could again be explained by the spatial positioning and motility of phytoplankton. Thus, in drainage lakes, nutrient load type determines the position of the load-response curve, both during eutrophication and oligotrophication.

3.4. Lake type's effect on the success of restoration measures

For the four lake types, we modelled scenarios for restoration measures aimed at phytoplankton biomass reduction. Fig. 6B presents the load response curves before (black lines) and after (red lines) the intervention for both eutrophication (solid lines) and oligotrophication

(dashed lines). The load-response curves after the intervention show the long-term effect of these three measures.

Our results show that the effect of *nutrient load reductions* was different for each lake type. We show that point-loaded drainage lakes and diffuse-loaded seepage lakes return to the clear oligotrophic state at the same level of nutrient loading (Fig. 6B.a and B.d, left column, dashed line). However, in case of diffuse-loaded seepage lakes, this involves a much larger nutrient load reduction compared to the level at which the system turned into the turbid eutrophic state. Our results suggest that this is because of alternative stable states occurring in diffuse-loaded seepage lakes. Compared to the two former lake types, diffuse-loaded drainage lakes require a considerably smaller nutrient load reduction to return to the oligotrophic state (Fig. 6B.c, left column). Finally, point-loaded seepage lakes respond most gradually to nutrient load reduction (Fig. 6B.b, left column). While such limited response to nutrient load reduction may be perceived as a lake restoration failure, it should be noted that point-loaded seepage lakes were least affected by the nutrient load compared to all other lake types.

Surprisingly, our analysis highlights that *flushing* is not necessarily beneficial towards restoring lakes to a clear state. Further deterioration is even likely in the case of point-loaded lakes (Fig. 6B.a and B.b, middle column). For these lake types, flushing distributes nutrients farther through the lake instead of retaining them close to the inlet. Increasing the nutrient distribution rate caused higher phytoplankton biomass levels away from the inlet. This paradox does not apply to diffuse-loaded lakes (Fig. 6B.c and B.d, middle column). Phytoplankton biomass drops to lower levels when these lakes are flushed, because of the negative effects of washout to phytoplankton growth. Additionally, higher nutrient distribution rates could result in an abrupt shift to the clear state in diffuse-loaded lakes. This happens when the allochthonous nutrient load becomes lower than the newly established critical nutrient load (Fig. 6B.c and B.d, middle column, red dashed line).

Biomanipulation is only a temporary perturbation, therefore the existence of alternative stable states is required for it to have a long-lasting impact. Otherwise, the lake will eventually return to its initial state given the unaltered allochthonous nutrient load. Accordingly, a long-term effect of biomanipulation can only be observed in diffuse-loaded seepage lakes and to a lesser extent in diffuse-loaded drainage lakes, provided that the allochthonous nutrient load lies between the lower and higher critical nutrient loads (Fig. 6B, right column).

4. Real lake examples

We have shown that nutrient load type (point versus diffuse) determines the spatial position of primary producers, while the lake hydrology type (drainage versus seepage) skews the spatial pattern of primary

producers (Fig. 5). These spatial differences are crucial to the success of restoration measures (Fig. 6). We will illustrate the predicted horizontal patterns and the effectiveness of restoration measures in four lakes around the world that are representative of each of the four lake types used in our model study. The comparison between the model results and real lake examples is summarised in Fig. 7.

4.1. Point-loaded drainage lakes

Lake Taihu (China) is a point-loaded drainage lake. In accordance with our predictions, highest concentrations of algal biomass appear in the northern and central parts of the lake where the point sources and major water inputs are located, while algal biomass and nutrient levels are lowest at the outflow (Janssen et al., 2017; Wang and Liu, 2005). In contrast, macrophytes biomass is highest at the outlet and lowest near the inlet (Janssen et al., 2014). Nutrient reduction was attempted as a restoration measure but could not keep up with the rapid socio-economic development in the region (Janssen et al., 2014). In an attempt to reduce the nuisance of increasingly recurring algal blooms, the lake was flushed with Yangtze River water (Qin et al., 2010). While this measure temporarily reduced phytoplankton biomass at the inlet, the transport of phytoplankton resulted in higher chlorophyll-a levels elsewhere in the lake (Qin et al., 2010). Our model results indeed show a plausible negative impact of flushing this type of lake. Additionally, the Yangtze River water contained high nutrient concentrations, which likely negatively affected the measure's outcome (Qin et al., 2010).

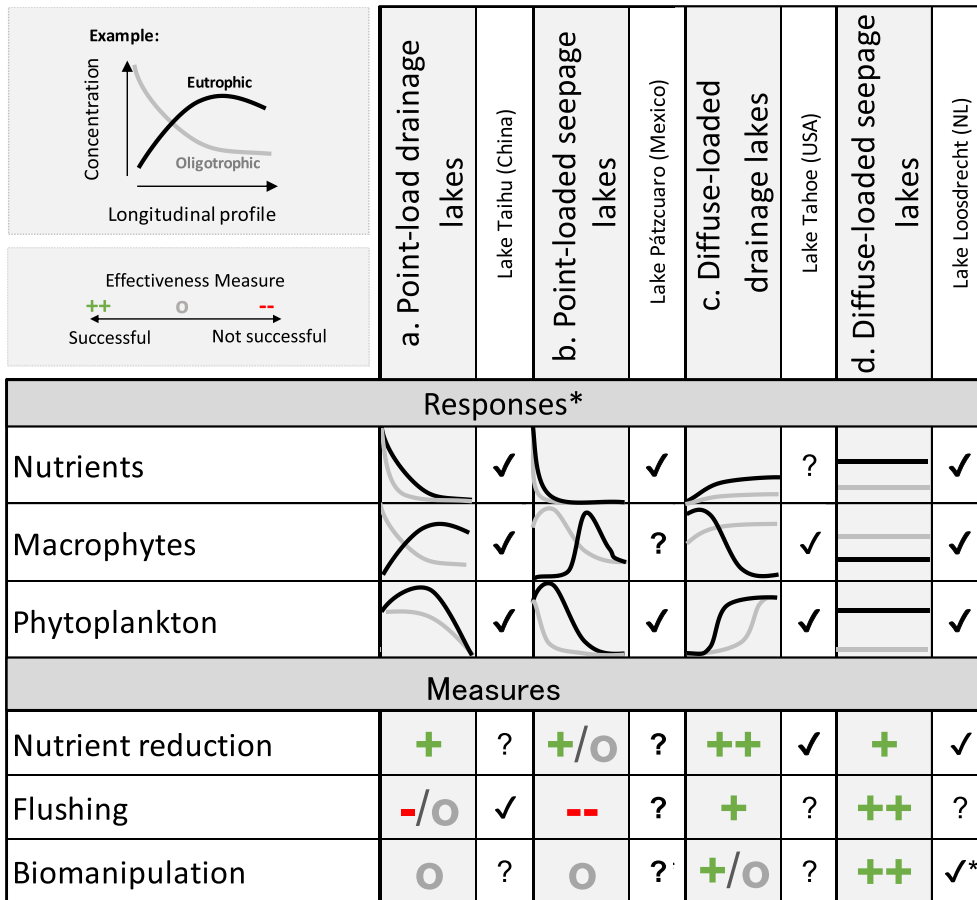


Fig. 7. Comparison between model results and empirical data. The graphs depicted under the title 'responses' show the spatial pattern deduced from Fig. 4 (outlet on the right). The pluses, zeros and minuses depicted under the title 'measures' indicate the effectiveness of restoration measures according to the model simulations. A tick-mark indicates confirmation through empirical observations. A question mark indicates missing values since the restoration measure either has not been carried out or information on the results is lacking. * In Lake Loosdrecht biomanipulation has not been applied; however, in a nearby, smaller, diffuse-loaded seepage lake (Lake Zwemlust), biomanipulation has been applied successfully.

4.2. Point-loaded seepage lakes

Lake Pátzcuaro (Mexico) can be characterised as a point-loaded seepage lake. Observations show decreasing nutrient concentrations, macrophyte biomass and chlorophyll-*a* away from the main input at the south and towards northern regions (Bernal-Brooks et al., 2003; Rosas et al., 1993). This pattern fits well with our predictions for point-loaded seepage lakes. We are not aware of restoration plans to reduce the impact of eutrophication on the ecology of Lake Pátzcuaro.

4.3. Diffuse-loaded drainage lakes

Lake Tahoe (USA) is a diffuse-loaded drainage lake. Historically, the highest eutrophication levels are found near the outlet of the lake (Abrahamsson and Goldman, 1970) and recent reports show that macrophytes only resist turbidity away from the outlet (Caires et al., 2013). These spatial patterns are consistent with our model results. Eutrophication control focuses on the reduction in atmospheric deposition as well as on reduction of point loading (Schuster and Grismer, 2004). Most restoration projects focusing on nutrient reductions have been successful in reducing the nutrient concentrations (Schuster and Grismer, 2004), yet macrophytes have not recovered to the undisturbed level of the 1960s (Caires et al., 2013).

4.4. Diffuse-loaded seepage lakes

Lake Loosdrecht can be classified as a diffuse-loaded seepage lake. Nutrients and phytoplankton were relatively homogeneously distributed in Lake Loosdrecht, as expected for a diffuse-loaded seepage lake. To prevent too low water levels resulting from reduced seepage, a river water inlet was constructed. However, the high nutrient content of the river water pushed the lake temporarily towards a point-loaded seepage lake (Van Liere et al., 1991). To improve water quality, the allochthonous nutrient loading was drastically reduced (Engelen et al., 1992; Van Liere, 1986; Van Liere et al., 1991), which pushed the lake type back to a diffuse-loaded seepage lake, but unfortunately did not lead to lower phytoplankton concentrations and the reestablishment of macrophytes (Janse et al., 1992). Possibly, this limited success resulted from the existence of alternative stable states, as predicted for diffuse-loaded seepage lakes. Although potentially effective according to our analysis, flushing was not considered in Lake Loosdrecht for practical reasons (Janse et al., 1992). Experience with another diffuse-loaded seepage lake, Lake Zwemlust, confirmed the potential of biomanipulation in this type of lake (Ozimek et al., 1990). However, in Lake Loosdrecht this measure is infeasible because it is impossible to capture a sufficient amount of fish and because high wind-caused resuspension hinders macrophyte reestablishment (Janse et al., 1992; Penning et al., 2013). The most promising restoration measures, therefore, are further allochthonous nutrient load reduction and restoration of the original low-nutrient groundwater flow (Engelen et al., 1992; Janse et al., 1992).

5. Discussion

Our model results indicate that the four lake types affect the success of lake restoration. It is thus important to account for lake types when it comes down to the restoration of real lakes. The four real lakes described above are textbook examples of the studied lake types, yet plenty of lakes do not fit into these discrete and rigid categories. Before interpreting the effect of lake types for successful lake restoration, one should be aware of possible shifts in lake types and the existence of 'subtypes'. Moreover, spatial heterogeneity in primary producers is not exclusively determined by different nutrient loading and hydrology types and is affected by spatial heterogeneity in lake sediment or lake depth as well. Lastly, our study complements the debate on the applicability of the theory of alternative stable states, as it suggests that

alternative stable states are restricted to lakes that can be classified as diffuse-loaded seepage lakes. This insight is important to decide on the application of restoration measures. Each of these points will be discussed in detail below.

5.1. Challenges in interpreting the lake types

The interpretation of the effect of the lake types on the effectiveness of restoration measures faces two major challenges. Firstly, ongoing anthropogenic pressures cause temporal heterogeneity in external nutrient loading and internal nutrient distribution, which could force shifts from one lake type to another. For example, temporal changes caused by socio-economic developments could change the major nutrient load type. As shown, such a change occurred in Lake Loosdrecht. Another example is Conservation Area 2A within The Everglades wetland (USA), which shifted from a diffuse-loaded seepage wetland dominated by atmospheric nutrient load to a point-loaded wetland with nutrient-rich canal inflow as a result of agricultural activities (Chimney and Goforth, 2006; Davis, 1994). The spatial pattern of primary producers shifted in response to these changes in nutrient source and hydrology types. Importantly, awareness of these mechanisms points the way to successful lake restoration. For instance, the restoration of a point-loaded drainage lake can be facilitated by pushing the lake to a diffuse-loaded drainage lake type by minimising the relative contribution of the nutrient point sources or by diverting the nutrient inputs to other places within the lake. The latter, however, will affect ecosystem services such as nutrient retention, and it is likely that more nutrients will leave the lake, increasing the risk of eutrophication problems downstream (Harrison et al., 2009; Hilt et al., 2011).

Secondly, spatial heterogeneity in lake characteristics may lead to 'subtypes' within one ecosystem. For instance, Lake Victoria (East Africa), as a whole, best resembles a diffuse-loaded seepage lake since the majority of both the water and nutrients originate from atmospheric sources (Scheren et al., 2000; Tamatamah et al., 2005). However, point loading has a local high impact inshore and in Victoria's Nyanza Gulf (Guya, 2013; Hecky et al., 2010; Scheren et al., 2000). Therefore, despite Victoria's general classification as a diffuse-loaded seepage lake, locally these bays should be classified as point-loaded drainage 'lakes'. Clearly, this shows the challenge of differentiating between large and small scales, especially in large and heterogeneous ecosystems such as Lake Victoria (Downing et al., 2014) and Taihu (Janssen et al., 2017).

5.2. Other causes of spatial heterogeneity

It is evident that spatial heterogeneity in primary producers is the result of not only different nutrient loading and hydrology types. Also, differences in environmental characteristics such as water depth, temperature and sediment type can cause spatial heterogeneity in primary producers (Kratz et al., 2005). For example, irregularities in a lake's morphometry may result in deviations from the main flow direction. Due to these irregularities, a bay may be relatively isolated from the rest of the lake and less influenced by the main flow. The above-presented case of Lake Victoria's Nyanza Gulf is a good example. Also, Meiliang Bay in Lake Taihu is known as a bay with its own hydrodynamics (Qin et al., 2007; Qin et al., 2010). Such bays may be seen as separate 'lakes' to which our findings may be applied. Another cause of spatial heterogeneity is grazer distribution, as can be seen in Lake IJsselmeer. Lake IJsselmeer is a point-loaded drainage lake, which is reflected in the high nutrient concentrations near its inlets. Yet, least phytoplankton biomass is found near the inlet due to high grazing pressure imposed by zebra mussels that grow best on the coarse substrate near the inlet (Bij de Vaate, 1991). This coarse substrate is absent near the outlet, resulting in lower grazing pressure from zebra mussel and higher phytoplankton biomass near the outlet.

The relative importance of nutrient load and hydrology type compared to other causes of spatial heterogeneity in primary producers is

different for each lake and this might alter the effectiveness of restoration measures. We anticipate that allochthonous nutrient load reduction would probably still be successful in the long term when internal loads are released since it would reduce nutrient concentrations in the entire lake. The effect of flushing depends on how phytoplankton is affected by other causes of heterogeneity. Flushing would presumably still be successful if other causes of spatial heterogeneity would result in a high phytoplankton concentration close to the outlet since flushing would not spread them farther into the lake. Conversely, if the highest phytoplankton concentrations are found away from the outlet, flushing might have less effect than was simulated. Lastly, the chance of success of biomanipulation would possibly decrease since heterogeneity in the lake will weaken the presence of alternative stable states (Van de Leemput et al., 2015). The ability to make use of alternative stable states is fundamentally important for biomanipulation to be successful (Janssen et al., 2008).

5.3. Implications for theory

Alternative stable states are typically associated with shallow lakes that are homogenous in lake characteristics (e.g. depth or sediment type) (Scheffer and Van Nes, 2007; Van de Leemput et al., 2015) and have a relatively high retention time (Hilt et al., 2011). Intriguingly, we demonstrated that alternative stable states are restricted to shallow lakes that can be classified as diffuse-loaded seepage lakes. Consequently, we suggest that alternative stable states are limited to lakes where the allochthonous nutrient load is distributed homogeneously and that have homogeneous lake characteristics. It is therefore not surprising that, to our knowledge, most cases of alternative stable states in ecosystems, also occur in relatively homogeneous ecosystems having diffuse nutrient sources (Van de Leemput et al., 2015). We have to acknowledge here though, that our approach implicitly assumed horizontal dispersion to be relatively small compared to horizontal advection. If dispersion is relatively high though, it could homogenize transportable substances within lakes. Hilt et al. (2011) demonstrated that increased dispersion had only a small effect on critical thresholds. Therefore we expect little effect of dispersion on the alternative stable states.

5.4. Implications for practice

These insights into the applicability of the theory on alternative stable states are important in practice when restoration measures are applied to real lakes. We deem successful application of biomanipulation only possible in diffuse-loaded seepage lakes due to the presence of alternative stable states that are absent in other lake types. For the same reasons, these diffuse-loaded seepage lakes will require more nutrient load reduction to achieve the desired result. In contrast, in all other lake types in which alternative stable states are absent, oligotrophication will follow the same path as eutrophication. Intriguingly, the success of flushing as a measure to restore lake water quality is independent of the presence of alternative stable states but will be counterproductive in lakes with nutrient point sources.

So far we have discussed the applicability of single measures, yet these measures might reinforce each other's effect when applied in combination. At several locations around the world, combinations of these measures have been taken. For instance, nutrient reductions combined with biomanipulation has been applied in the Netherlands (Meijer et al., 1999), Denmark (Jeppesen et al., 2007) and USA (Edmondson, 1994). The individual effects of each of the measures in our study are addable since flushing is the only presented measure that affects the shape of the load-response curve whereas biomanipulation and nutrient load reductions only result in a new position on this load response curve. Our results show that combining nutrient reductions with biomanipulation could indeed be beneficial for lakes with alternative stable states, especially when these lakes are highly eutrophic. In such cases, the nutrient load reduction will move

the lake system to the area of alternative states, whereas the biomanipulation will then perturb the lake in such a way that it will develop a clear state. Similarly, flushing in combination with nutrient load reductions would be beneficial to diffuse loaded lakes since this combination will both increase the lake's resilience and reduce the pressure from high nutrient loads. Our results also suggest that applying all three measures in concert is only beneficial in the case of diffuse-loaded lakes.

Since we demonstrated that the effectiveness of all three lake measures is inextricably linked with the lake type, we propose that a priori assessment of spatial heterogeneity caused by the nutrient loading and hydrology is essential for successful restoration of lake ecosystems. Such assessments should also take into account the possibility of a shift in lake type to reach successful lake restoration. Finally, we think that restoration of deteriorated ecosystems, in general, can potentially benefit from our findings (Appendix B).

6. Conclusion

Restoration of deteriorated aquatic ecosystems has been only partly successful and therewith undermines achieving the UN Sustainable Development goals such as clean water (SDG 6). We showed that the long-term effectiveness of lake restoration measures critically depends on spatial aspects of nutrient loading and hydrology. We found that biomanipulation is only a possible option in diffuse-loaded seepage lakes, because of the prominent presence of alternative stable states that are absent in other lake types. Moreover, continuous flushing might help in diffuse-loaded lakes, but can further deteriorate point-loaded lakes. When sufficiently reduced, allochthonous nutrient load reduction has a positive long-term effect in all cases; however, the degree of success differs for each lake type. Concluding, for successful lake restoration we, therefore, advocate thorough a priori assessments of nutrient source and hydrology types of lakes.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.04.443>.

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