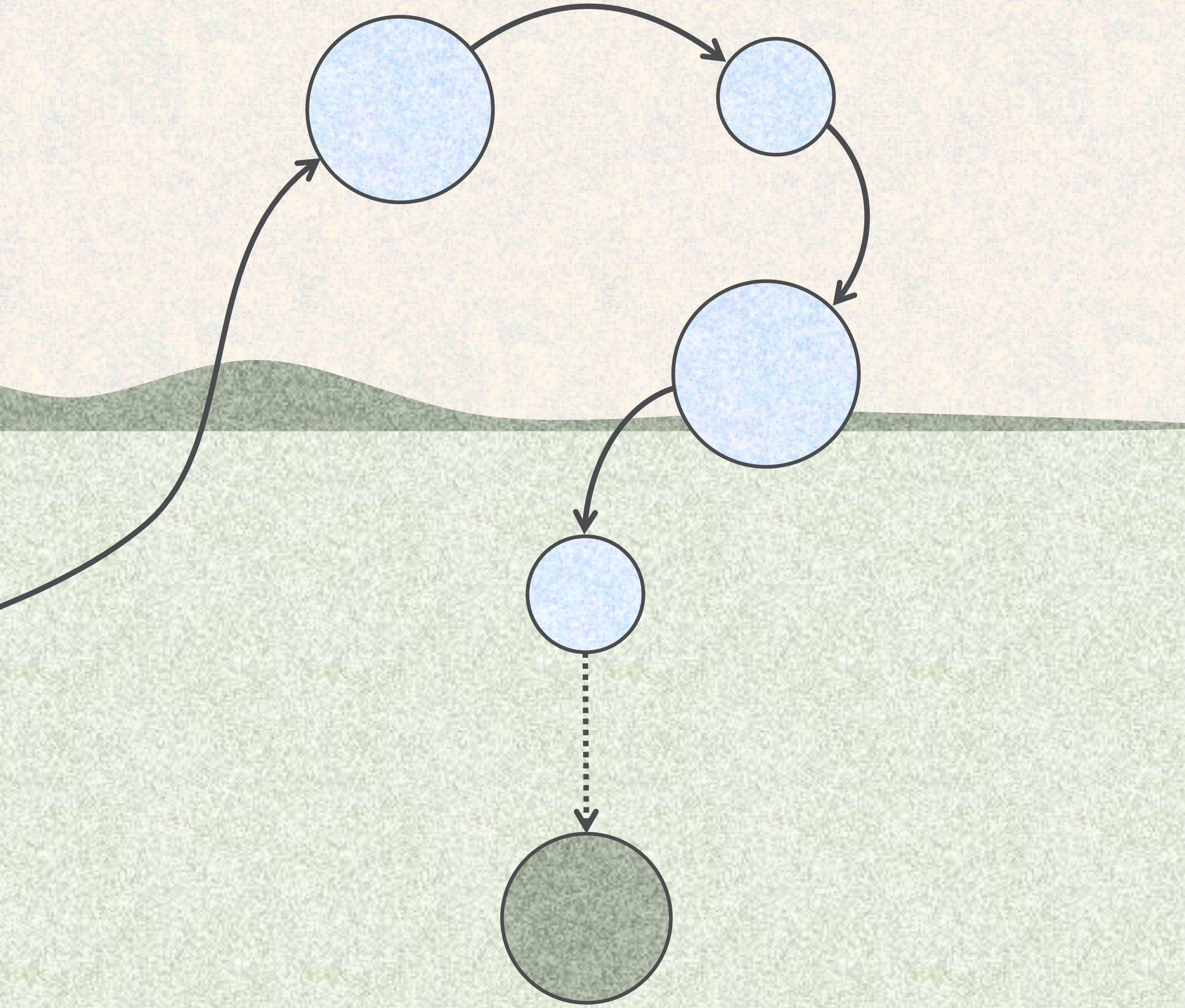
Towards Smart Nutrient Retention Networks to improve water quality:

perspectives, theories and tools



Dianneke van Wijk

Propositions

1. The nutrient retention strength of individual waterbodies dictates their importance for water quality in networks of surface waters.
(this thesis)

2. A world of complexity lies behind relatively simple lake ecosystem models.
(this thesis)

3. The proficiency of scientific generalists lies in their mindsets rather than in their skills.

4. Creative solutions emerge from combinations of existing knowledge.

5. Freedom within safe boundaries is the perfect condition for personal growth.

6. A diversity of perspectives enriches life.

Propositions belonging to the thesis, entitled

Towards Smart Nutrient Retention Networks to improve water quality: perspectives, theories and tools

Dianneke van Wijk

Wageningen, 20 February 2024

Towards Smart Nutrient Retention Networks

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Towards Smart Nutrient Retention Networks to improve water quality:

perspectives, theories and tools

Dianneke van Wijk

Thesis

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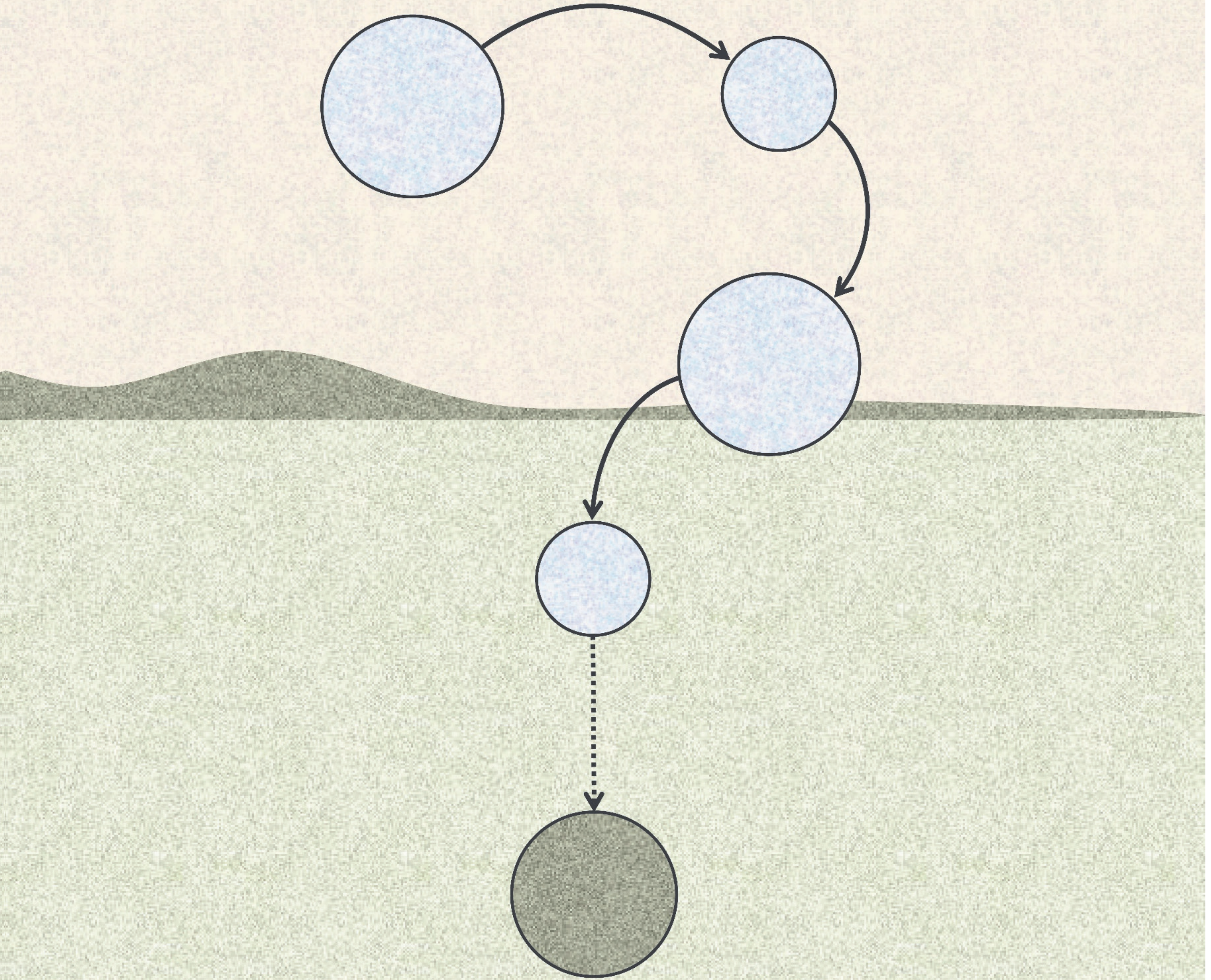
Contents

Chapter 1

General introduction



1.1 Motivation

Water and nutrients are essential to life and wellbeing, which is reflected in the development of the earliest human civilizations in fertile river deltas (Bianchi 2016). In addition to providing basic physiological needs for drinking and food production (Maslow 1954; Denton 1990) as part of the social foundation for a safe and just space for humanity (Raworth 2012), water is used for sanitation (WHO, 2018), hydropower production (Jager and Smith 2008) recreation (Angradi et al. 2018), and has cultural value (Wantzen et al. 2016). Therefore, unsurprisingly, water security is said to underpin all UN Sustainable Development Goals (37th UN-Water Meeting, 2022). Besides supplying water, surface water systems also transport various substances (e.g., nutrients and carbon) (Cardille et al. 2007; Teurlincx et al. 2019). Regionally, hotspots of excess nutrients threaten freshwater and marine systems (Steffen et al. 2015a), resulting in eutrophication problems such as smelly and potentially toxic algal blooms and oxygen depletion (Paerl 1988; Chislock et al. 2013). Moreover, on a global scale, biogeochemical flows of phosphorus (P) and nitrogen (N) have crossed planetary boundaries, presenting high risks of large-scale ocean anoxic events (Steffen et al. 2015a). Besides threatening human and natural health, and services that surface waters provide (Janssen et al. 2020), these excess nutrients eventually also constitute a loss of resources into the deep oceans.

Historically, agriculture benefited from naturally nutrient rich soils originating from slow flowing systems (e.g., floodplains, wetlands, and lakes) where nutrients were retained in the sediment. To further enhance the productivity of soils and to increase food production, agricultural lands are (synthetically) fertilized. Together with other technological developments, this currently lifts human population growth beyond resource scarcity as postulated by Malthus (Downing et al. 2020). Since the 1950s, rapid increases in human population, consumption of fertilizers and nutrient fluxes into the oceans co-occurred (Steffen et al. 2015b).

Additionally, after nutrients from food have passed living systems, humanity tries to get rid of nutrient rich waste (e.g., feces and animal manure) as fast as possible. As already noted in the time Victor Hugo wrote Les Misérables, humanity thereby neglects the valuable potential of nutrients as resource for food production (Hugo 1862). Although the potential to produce fertilizers (e.g., by the Haber-Bosch process) and the efficiency to prevent nutrient losses (e.g., by wastewater treatment technologies) has increased, these essential resources are still lost through transport and storage in networks of waterbodies.

Whereas others have focused on increasing nutrient use efficiency on land and reducing nutrient losses to water systems (e.g., Bouwman et al. (2005) and Withers et al. (2014)), I here focus on management of nutrients in interconnected aquatic ecosystems. First, because some nutrient pollution of surface waters in inevitable (Withers et al. 2014). Second, since by combining management strategies, larger impacts may be achieved (Lürling and Mucci 2020). Third, because I believe the spatial network perspective for water quality management is a promising but relatively novel and growing field in science and practice. In this thesis, I specifically focus on nutrient retention in interconnected waterbodies as a step towards enhanced nutrient conservation by retention and consecutive reuse (Box 1.1), by developing the novel "Smart Nutrient Retention Networks" (SNRNs) concept as a concrete direction for water quality management. By this, I hope to contribute to more sustainable management of water and nutrients (cf., Tammeorg et al. 2023).

1.2 Water quality management approaches

Traditional and contemporary water quality management approaches vary from preventing pollution to acute remediation. Nutrient load reduction can be used as a precautionary or mitigative approach to conserve or restore water quality, for example, by more modest and efficient application and management of fertilizers and manure, erosion prevention, and

Box 1.1: Nutrient retention for nutrient conservation

In this thesis, I use a broad definition of nutrient retention that includes long-term storage and removal of nutrients from waterbodies, for example, by storage in sediment or losses to the atmosphere by denitrification. Temporary storage of nutrients in biomass is also considered nutrient retention when being harvest by humans (e.g., fishing) or naturally removed (e.g., consumption by migrating waterfowl). Thus, nutrient retention in waterbodies is long-term removal of nutrients from the water column, which at equilibrium can simply be expressed in absolute amounts as the nutrient inflow minus the nutrient outflow of the system. Throughout this PhD thesis, nutrient retention fractions (i.e., the absolute amount retained divided by the nutrient inflow) are generally used to show the relative nutrient retention efficiency of various ecosystems. A high nutrient retention fraction means that relatively little of the incoming nutrients is transported to downstream systems, whereas at low nutrient retention fractions hardly any of the nutrients are intercepted by the waterbody. Therefore, the nutrient retention fraction influences how much nutrients are reaching downstream waterbodies and influences their water quality. Furthermore, nutrient retention may contribute to nutrient conservation in the water-food system when being reused, for example, through fish consumption or (processed) aquatic biomass application on agricultural land as organic fertilizer. I define nutrient conservation as the prevention of nutrient losses to the atmosphere and downstream ecosystems by nutrient retention and consecutive nutrient reuse. Exploration of harvesting, processing and reuse strategies of nutrient retaining aquatic ecosystem components for nutrient conservation is beyond the scope of this PhD research. Here, I focus on nutrient retention in waterbodies as an essential part of nutrient conservation.

improvement of connections to sewage systems and consecutive treatment (Boesch 2002; Makarewicz 2009; Seitzinger et al. 2010). Acute remediation options are more adaptive in nature, typically being in-lake interventions to reduce algal blooms instantly. These options include the addition of substances to kill phytoplankton (i.e., algal) cells, remove phytoplankton and P from the water column, or reduce P availability from the sediment (Lürling and Mucci 2020). Such measures typically need to be repeated or require sufficient nutrient load reduction afterwards (Lürling and Mucci 2020). Other approaches influence the ecosystem state and functioning for longer periods, without or in combination with nutrient load reductions. These biomanipulation options, for example, encompass adding or removing fish, supporting mussels, or planting water plants (i.e., macrophytes) (Triest et al. 2016). Additionally, to stimulate occurrence of submerged macrophytes, long-term measures may be employed to increase the littoral marsh zone area, or to reduce the water depth or the effective wind fetch (Van den Berg et al. 2003; Istvánovics et al. 2008; Sollie et al. 2008).

1.2.1 Nutrient retention as a novel management strategy

All the above mentioned water quality management approaches are typically focused on the water quality of single waterbodies, as in line with policy requirements (e.g., the European Water Framework Directive and the US Clean Water Act). However, I think in this way we miss opportunities for larger scale water quality improvements, despite incentives for larger scale and more integrative management (e.g., European River Basin Management Plans (Griffiths 2002)). In the landscape and waterscape context, an additional strategy to reduce eutrophication is to retain nutrients while they are transported downstream (Boesch 2002). Moreover, this offers opportunities to harvest and reuse nutrients from waterbodies (Tammeorg et al. 2023), thus contributing to nutrient conservation (Box 1.1).

By managing factors that influence nutrient retention, the flow of nutrients in connected waterbodies can be manipulated, both as a pollutant and as a resource. For example, hydrological management can alter the hydraulic residence time (i.e., water renewal time), which is one of the most evident drivers of nutrient retention (Jansson et al. 1994; Saunders and Kalff 2001; Vörösmarty et al. 2003; de Klein and Koelmans 2011; Maavara et al. 2015). The role of other factors, such ecosystem state and stratification are less ubiquitous and more case specific. For example, their effect on nutrient retention differs for phosphorus (P) and nitrogen (N), and depends on vegetation characteristics (Nürnberg 1984; Barko and James 1998; Søndergaard et al. 2001; Sollie et al. 2008; Kõiv et al. 2011; Beaulieu et al. 2014; Hilt et al. 2017). The influence of ecosystem state on nutrient retention is complicated because ecosystem state also depends on the nutrient loading entering the ecosystem (Rast and Lee 1978; Ahlgren et al. 1988). This is relevant when raising water quality management perspectives from single waterbodies towards networks of interconnected waterbodies, because changes in ecosystem state may create a domino effect in water quality of downstream systems (Hilt et al. 2011; Teurlincx et al. 2019).

In most chapters of this thesis, I focus on shallow lakes because these are known for the positive feedback loops between primary producers, water turbidity, and nutrient retention, for different ecological states (cf., alternative stable states theory by Scheffer et al. (1993)). Shallow lakes may experience gradual or abrupt transitions (i.e., regime shifts) between a clear, submerged macrophyte dominated state and a turbid, phytoplankton dominated state (Jeppesen et al. 1990; Scheffer et al. 1993; Jeppesen et al. 2007). These ecosystem states amongst others depend on nutrient loading and are known to have distinct nutrient retention capacities (Hilt et al. 2017). Thereby, one may expect a potential spatial feedback between nutrient loading into a lake, the resulting lake ecosystem state and associated in-lake nutrient retention, which in turn affect the nutrient loading and ecosystem state in downstream systems. More effective and novel management strategies may arise when this potential positive feedback of ecological water quality improvement (i.e., macrophyte instead of phytoplankton dominance) for the larger hydrological network is understood, acknowledged, and stimulated.

1.3 Knowledge gaps and missing tools

In this thesis, I build on existing scientific *perspectives*, *theories,* and *tools* to support water quality management. Here, I define *perspectives* as a particular mental viewpoint, for example, considering a specific focus in water quality management. I characterize *theories* as scientifically acceptable general principles to explain phenomena, for instance, resource competition *theory* to explain algal blooms in lakes. Furthermore, I consider *tools* as practical means to help to achieve something, for example, lake ecosystem models to inform water quality management and communication instruments to introduce such models.

Despite the scientific recognition of the importance of hydrological connections for nutrient flows and retention, and the resulting chemical and ecological water quality (Epstein et al. 2013; Carpenter and Lathrop 2014; Teurlincx et al. 2019; Heino et al. 2021), water quality management commonly targets individual waterbodies without consideration of the effect of nutrient retention on downstream systems. Moreover, literature on nutrient retention in surface waters is scattered and generally focused on describing and understanding nutrient cycling in waterbodies (e.g., Saunders and Kalff (2001) and Schulz et al. (2003)), rather than giving insight in management options. A compilation of the existing knowledge on nutrient retention in surface waters from a *theoretical* and an applied angle is missing to inform new water quality management *perspectives* beyond the scale of individual waterbodies. This study aims to fill that gap.

Moreover, both the total and relative amounts of N and P loading into a system matter for ecological water quality (Guildford and Hecky 2000), for example, in terms of harmful algal bloom formation (Paerl et al. 2016). Amongst others, relatively stronger improvements in wastewater treatment for P than for N have contributed to higher N:P ratios of sewage and surface waters (Jeppesen et al. 2005; Tong et al. 2020). Moreover, lakes tend to aggravate the increase in N:P ratios by a relatively greater retention efficiency of P than of N (Wu et al. 2022). The effect of increased N:P ratios on water quality may vary per ecosystem but it seems to enhance toxin contents of phytoplankton (van de Waal et al. 2014) and to increase the risks of algal blooms in N-limited coastal zones (Wu et al. 2022). Despite the abundance of studies on N:P ratios, only a few assessed the relative retention of N and P in waterbodies and its implication for N:P ratios of loading to downstream systems (e.g., Grantz et al. (2014) and Liu et al. (2018)). Increased *theoretical* insights in how N:P ratios of in- and outflows of waterbodies will develop in the future may advance water quality management strategies for connected waterbodies.

Models are useful *tools* to support water quality management strategies, among others, by increasing insight in feedbacks within ecosystems, quantify nutrient budgets, and formulating and testing hypotheses and management options (Janssen et al. 2015). Although catchment transport models and aquatic ecosystem models offer opportunities to simulate ecological feedbacks in networks of surface waters (Teurlincx et al. 2019), thus far, only a few model studies explored the potential cascading effects of ecological water quality and nutrient retention in linearly connected waterbodies (Hilt et al. 2011; van Gerven et al. 2017). Simple, mass-balanced, and process-based lake models would be a useful first step to simulate nutrient retention in relation to ecosystem state in more complex networks to explore hypotheses and management strategies. This calls for a mechanistic understanding of transitions in lake ecosystem state and the associated nutrient retention.

Tilman's (1982) seminal resource competition *theory* provides a mechanistic and mathematical explanation of which species will win competition based on bottom-up control by shared limiting resources. Primary produces in lakes require nutrients and light, and when one or multiple of these resources are insufficiently available, this will limit their growth. Hence, reducing inputs of the limiting nutrient(s) may reduce algal biomass in lakes (Paerl et al. 2016; Schindler et al. 2016). In Tilman's (1982) *theory*, the minimal resource requirements (R^*) of phytoplankton and macrophytes will determine whether one of the species will dominate at a given supply of resources. Indeed, competition for nutrients and light has been used to explain and model regime shifts between macrophyte and phytoplankton dominance in shallow lakes (Scheffer et al. 1993; Janse 1997). However, to my knowledge, fundamental ecological *theory* on resource competition has not yet been captured in fully mechanistic and mass-balanced, yet simple, mathematical models of these regime shifts.

Ultimately, scientific *perspectives*, *theories* and *tools* should feedback into society to stimulate their practical implementation, and thus their impact. Through my PhD research, I would like to inform and engage water managers and others in the field of nutrient and water quality management on new *theoretical* insights, management *perspectives*, modeling *tools* and their results. However, it may be complicated to increase the understanding of model concepts and results by (future) professionals with limited modeling background. This requires an appropriate education or communication strategy. Yet, there is no standard communication strategy because the way to communicate depends on the purpose and complexity of the scientific content and the target audience (Jordan et al. 2018; Bakhanova et al. 2020). Therefore, it would be useful to have *tools* for the scientific community to guide and inspire each other on how to communicate scientific outcomes, especially to bridge the gap between modelers and non-modelers.

1.4 Research objectives and scope

The aim of this thesis is to increase our understanding of nutrient retention in connected surface waters. I build on existing — and develop novel —

perspectives, *theories*, and *tools* to support water quality management with the objective to:

1) Develop the SNRN concept based on existing knowledge of nutrient retention in surface waters.
2) Support the development of SNRNs through relatively simple and versatile dynamic models that are rooted in resource competition *theory*.
3) Increase understanding of how nutrient retention may influence nutrient ratios and their transport to downstream systems.
4) Develop a *tool* to interactively increase the non-modelers' understanding of concepts and results that arise from a lake modeling exercise.

By this, I hope my thesis will contribute to more sustainable management of water and nutrients. Here, I focus on regions with connected (shallow) lakes in the northern temperate zone, such as lowland western Europe. This work may be relevant to better understand water quality developments from the past and present, and to explore scenarios and develop strategies for water quality management in the future. How lake models may help to inform water quality management is exemplified by a scenario analysis of future water quality development in Chinese lakes and a historic case of a European lake.

1.5 Research approach

To fill the gap in the explicit use of inland water networks in water quality management, first, I explain how I define nutrient retention and how it is influenced by natural mechanisms and human interventions based on a literature review (Chapter 2). Second, building on this knowledge, I present the Smart Nutrient Retention Networks (SNRNs) concept as a new management approach to improve water quality and nutrient conservation in networks of inland waters through water quality management (Objective 1). A core aspect is the spatial feedback loop between nutrient loading, ecosystem state and nutrient retention in chains of lakes. Chapter 2 concludes with an overview of existing models that could help to develop SNRN management strategies, analyzing whether simple models already exist that include mechanisms of nutrient retention, lake ecosystem state and management options in lakes (Objective 2). Such models could serve as building block to model networks of inland waters up to a basin-scale.

Next, I explored ecological *theories* to develop relatively simple lake models to support the development of SNRNs (Objective 2) (Chapter 3 and 4). Such models should capture patterns of nutrient retention in relation to regime shifts (i.e., alternative stable states) or more gradual replacements between macrophyte- and phytoplankton-dominated states in shallow lakes. First, I applied *theoretical* insights and the knowledge integrated in the existing GPLake model (Chang et al. 2019), by developing a conceptual and mathematical model of equilibrium macrophyte and phytoplankton densities: GPLake-M (Chapter 3). Here the mechanisms underlaying alternative stable states of macrophyte and phytoplankton are explained through the critical turbidity concept. This model includes alternative stable states and nutrient retention and therefore provides a first step towards modeling of connected lakes. Thereafter, I build on the GPLake-M model to, first, create an equilibrium and then, a dynamic model of nutrient retention in relation to ecosystem state: GPLake-R (Chapter 4). This versatile model can directly be used as a building block to model networks of lakes to support the development of SNRNs. For both models, I performed a pattern-oriented comparison against the relatively complex lake ecosystem model PCLake (Janse 1997).

Furthermore, I applied the extended PCLake+ model (Janssen et al. 2019a) in a scenario analysis of thousands of Chinese lakes to explore the effect of ecosystem state, nutrient retention and nutrient loading to downstream systems (Chapter 5). I focus on Chinese lakes because Asia is one of the global hotspots of N and P inputs to rivers and coastal systems (Seitzinger et al. 2005; Li et al. 2022), and water quality in lakes has been decreasing in the last decades (Qin et al. 2022). Here, I dive into TN:TP ratios under different scenarios of socio-economic development and climate change (Objective 3), since water quality management goes beyond the management of single nutrients (Zhou et al. 2014; Paerl et al. 2016) and climate change may exacerbate eutrophication (Moss et al. 2011; Xia et al. 2016). Therewith, Chapter 5 increases insight in the feedback mechanisms underlaying the SNRN concept and where Chinese water quality management could focus on to improve lake water quality in the future.

Lastly, I present a serious game approach in the form of a digital "Escape Room", called the "EscapeBLOOM" (Chapter 6). The purpose of this game is to increase understanding of concepts and results that arise from a modeling exercise (Objective 4). In the game, players have to find the historic management strategy that was applied in a real lake to combat algal blooms. During the game, players apply and interpret three mathematical models for hydrodynamics (i.e., GOTM (Burchard et al. 1999; Golub et al. 2022) rand ecological processes (i.e., GPLake (Chang et al. 2019) and PCLake (Janse 1997)) in water ecosystems. The EscapeBLOOM game was applied and evaluated on multiple occasions, and we assessed its contribution to perceived learning on lake models and water quality management concepts. The game is designed as a *tool* to aid the communication of environmental modeling cases and I envision that our approach can be applied, modified, or used as inspiration by others to use in their own environmental education activities.

1.6 Thesis outline

In short, Chapter 1 (this chapter) introduces the societal and scientific background, research objectives and approach (Fig. 1.1). Chapter 2 presents the SNRN concept that I developed as a novel management *perspective*, based on existing ecological knowledge. It concludes with an overview of existing nutrient retention models for inland waters and indicates which models and knowledge are lacking. From the insights from

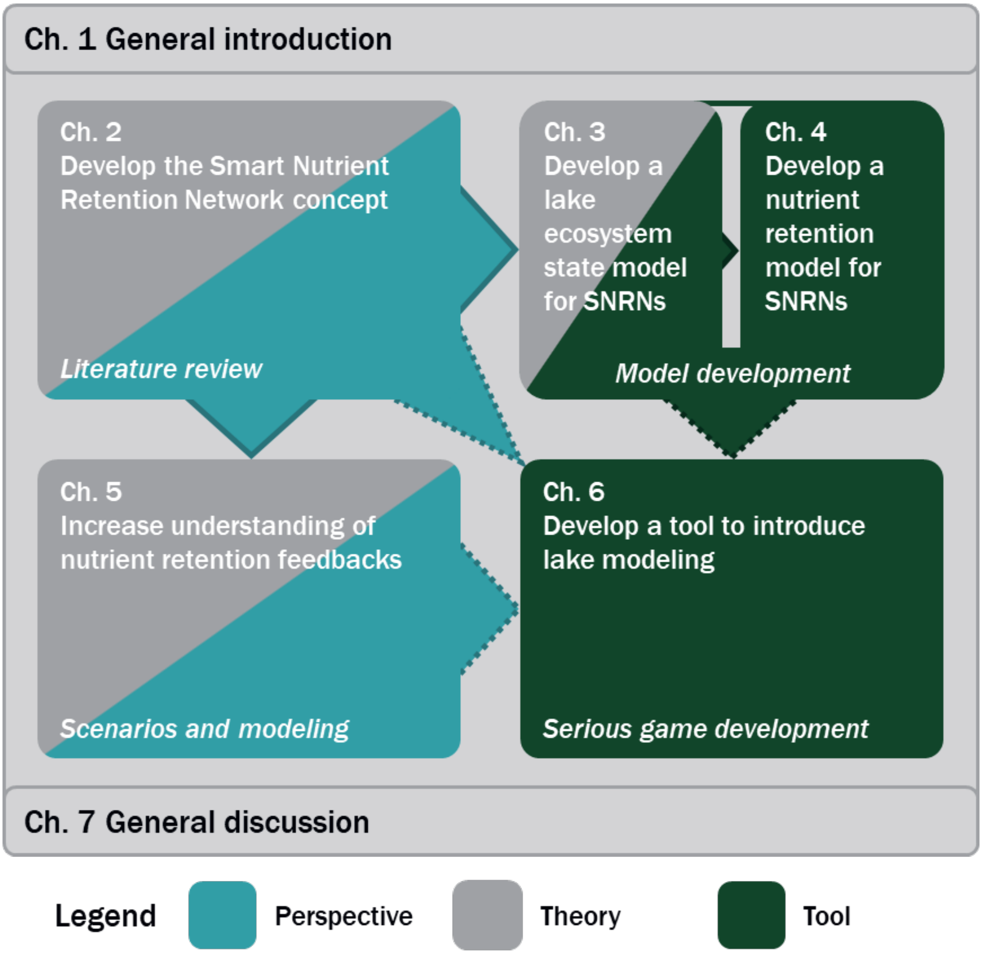
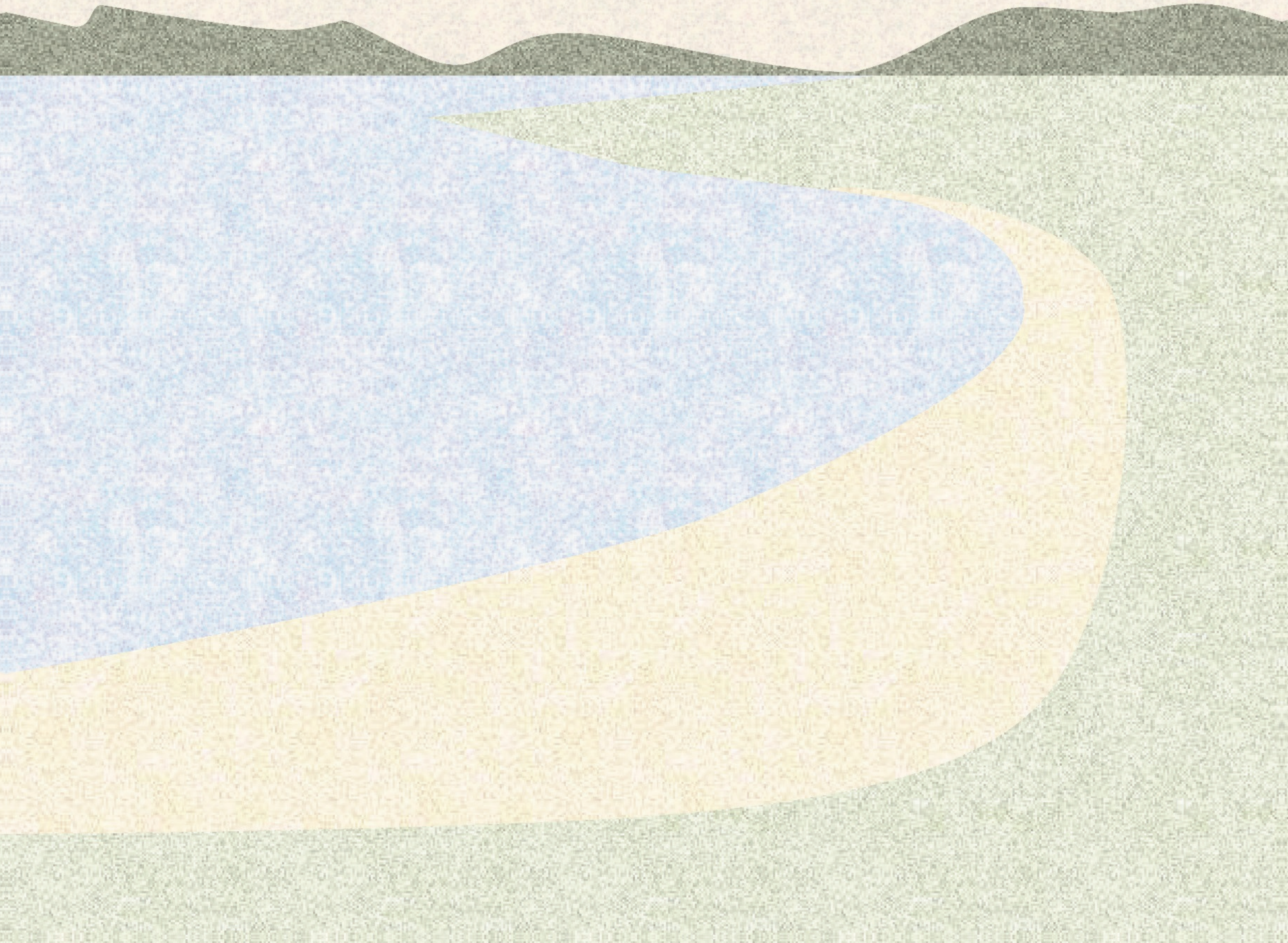


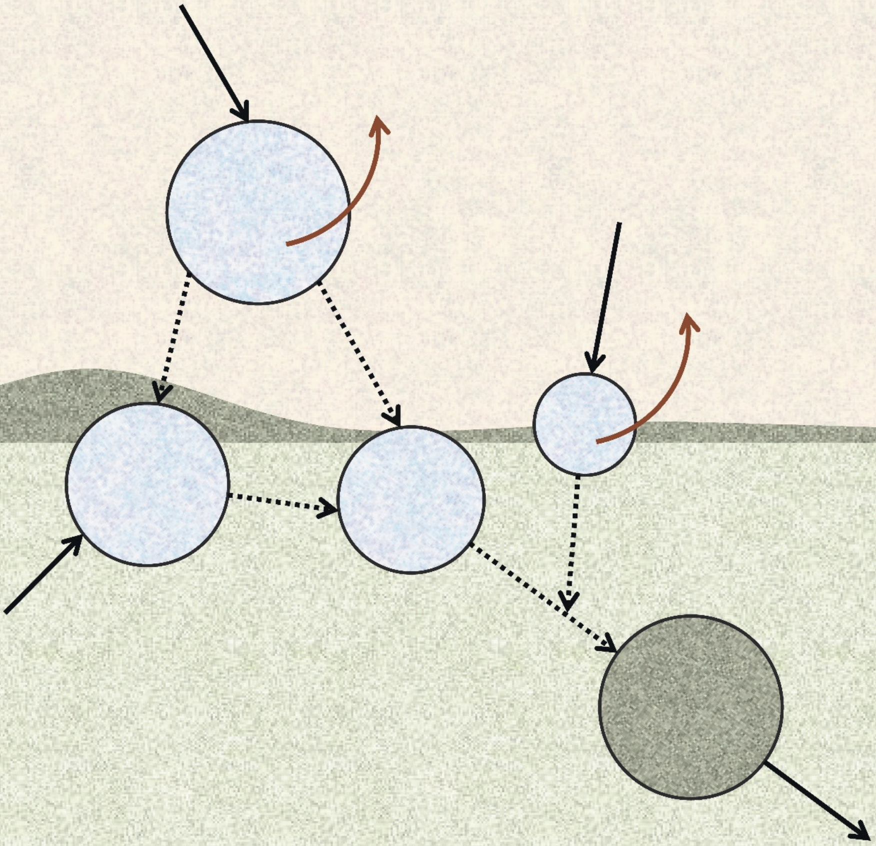
Figure 1.1. Overview of the interconnectedness of the chapters (Ch.) of this thesis with a summary of their research objective (text in boxes), approach (*italics*), and whether they aim to develop a perspective, theory or tool. Triangles represent connections in terms context (dashed) and content (closed).

Chapter 1, two research lines emerge aimed at: a) developing relatively simple models as *tools* to support the development of SNRNs (Chapter 3 and 4), and b) deepening *theoretical* insight in feedback mechanisms underlaying the SNRN concept in case studies to improve long-term water quality management (Chapter 5). First, Chapters 3 and 4 present the consecutive development of the GPLake-M and GPLake-R model *tools* based on ecological *theory*. Second, Chapter 5 consists of a scenario analysis of thousands of Chinese lakes to deepen *theoretical* insights and to inform water quality management *perspectives*. Thereafter, Chapter 6 takes a broader look at knowledge integration and application, bringing multiple scientific approaches together in a serious game: the “EscapeBLOOM”. This *tool* helps to communicate about modeling in relation to water quality management, which is an important aspect of the other chapters of this thesis. Finally, in Chapter 7, I integrally discuss the results and conclusions of Chapter 2-6.



Chapter 2

Smart Nutrient Retention Networks: a novel approach for nutrient conservation through water quality management



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Abstract

Nutrients are essential resources for food production but are used inefficiently, and thereby they pollute inland and coastal waters and are lost into the oceans. Nutrient conservation by retention and consecutive reuse would prevent nutrient losses to the atmosphere and downstream ecosystems. We present Smart Nutrient Retention Networks (SNRNs) as a novel management approach to achieve nutrient conservation across networks of connected waterbodies through strategic water quality management. To present the key features of SNRNs, we review existing knowledge of nutrient retention processes in inland waters, water quality management options for nutrient conservation, and nutrient retention models to develop SNRNs. We argue that successful nutrient conservation - even at a local level - through SNRN management strategies requires clearly formulated goals and catchment-wide system understanding. Waterbody characteristics such as hydraulic residence time, and the presence of macrophytes shape local nutrient retention with potential network-wide cascading effects of improved water quality and are therefore key targets of SNRN management strategies. Nutrient retention models that include the self-reinforcing feedback loop of ecological water quality, nutrient retention and nutrient loading in networks of inland waters in relation to management options can support the development of SNRNs. We conclude that SNRNs can contribute to sustainable use of nutrients in human food production.

2.1 Introduction

2.1.1 Societal challenge

"Fleets of vessels are dispatched, at great expense, to collect the dung of petrels and penguins at the South Pole, and the incalculable element of opulence which we have on hand, we send to the sea. All the human and animal manure which the world wastes, restored to the land instead of being cast into the water, would suffice to nourish the world." (Victor Hugo in "Les Misérables": Volume V - Jean Valjean, Second Book, 1862.)

Nutrients are essential resources for food production and socioeconomic development, but they pollute inland waters before they are washed to the sea. Currently, about 95 Tg of nitrogen (N) and 16 Tg of phosphorus (P) are applied annually as synthetic fertilizer worldwide (Beusen et al. 2016). Together with other anthropogenic and natural nutrient sources, this input leads to a global nutrient loading into inland waters of 64–253 Tg N and 9–30 Tg P per year (Smil 2000, Beusen et al. 2016, Yuan et al. 2018, Fig. 2.1), resulting in eutrophication problems such as harmful algal blooms (Heisler et al. 2008) and anoxia (Chislock et al. 2013). Nutrients eventually flow to the sea where they cause coastal eutrophication before being lost to the seabed or atmosphere (de Jonge et al. 2002). Thus, although the efficiency of obtaining nutrients has dramatically increased from guano mining in the time Victor Hugo wrote Les Misérables to mining finite deposits of mineral P and the Haber-Bosch process used to produce N today, the critical issue of losing these essential resources into the sea recognized a century and a half ago (Hugo 1862) persists.

2.1.2 Networks of inland waters

Individual waterbodies (e.g., reservoirs, lakes, rivers and wetlands) can form a network of inland waters, exchanging nutrients and other substances through hydrological connections (Teurlincx et al. 2019) and influence each other's chemical and ecological water quality (Tundisi et al. 1998, Carpenter and Lathrop 2014, Teurlincx et al. 2019). One waterbody can act as a net nutrient source or sink to downstream waterbodies (Zhang et al. 2012).

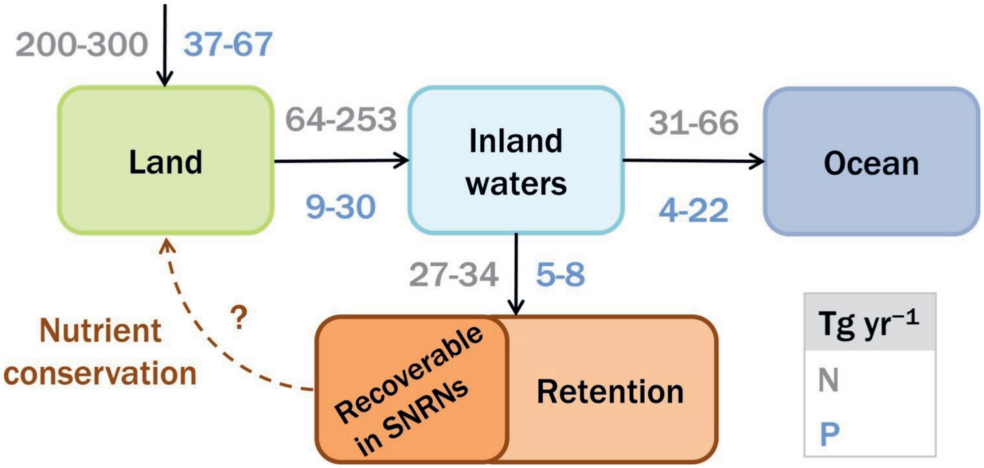

Figure 2.1. Global nitrogen (N; gray numbers) and phosphorus (P; blue numbers) flows in Tg per year (Smil 2000, Green et al. 2004, Van Drecht et al. 2005, Tysmans et al. 2013, Beusen et al. 2016). Nutrient inputs on land include natural and anthropogenic sources. Considerable amounts of these nutrients end up in inland waters. After entering inland waters, nutrients are retained within waterbodies or transported into the oceans. Note that these numbers represent estimates of global totals. Ratios between the different flows may differ strongly between individual river catchments (Tysmans et al. 2013). The question mark indicates an unknown fraction of retained nutrients that can be recovered in Smart Nutrient Retention Networks (SNRNs) to be reused on land for nutrient conservation.

Higher nutrient retention is associated with higher water quality (i.e., clear, submerged macrophyte dominated vs. turbid, phytoplankton dominated waters). Water flows through the network influence hydraulic residence times, which also determine nutrient retention (Van Gerven et al. 2017). When nutrient load reduction leads to an ecological regime shift from phytoplankton dominance to submerged macrophyte dominance in one waterbody, nutrient retention could increase locally, resulting in lower nutrient loading to connected waterbodies (discussed later; also see Supplementary material A). This feedback could cause cascading effects of improved water quality and offer opportunities to benefit from local interventions on a network scale. However, despite the recognized importance of hydrological connections on nutrient flows and retention, water quality is generally assessed for individual waterbodies, and only a few model studies address the potential cascading effects of ecological water quality and nutrient retention in connected inland waters (Hilt et al. 2011, Van Gerven et al. 2017).

2.1.3 A novel approach for nutrient conservation through water quality management

Our aim was to fill this gap in the explicit use of inland water networks in water quality management by presenting what we named "Smart Nutrient Retention Networks" (SNRNs), a novel management approach for nutrient conservation through water quality management (Fig. 2.2). Here, we define nutrient conservation as the prevention of nutrient losses to the atmosphere and downstream ecosystems by nutrient retention and consecutive nutrient reuse. Nutrient retention comprises natural internal retention within and natural losses from waterbodies, as well as harvesting by humans. Retained nutrients are only conserved if reused, for example, as organic fertilizer to mitigate synthetic fertilizer production and application. Contrary to traditional water quality management that focuses on nutrient pollution reduction and local remediating interventions (Paerl et al. 2016, Strokal et al. 2020), SNRNs employ the biogeochemical *nutrient retention* potential of networks of inland waters to deal with nutrient pollution and promote nutrient conservation. Thus, we focus on a type of nutrient reuse that is often ignored.

SNRNs aim to restore degraded inland waters, mitigate further ecological degradation, prevent nutrient losses into the ocean, and stimulate on-land reuse of nutrients harvested from inland waters (Fig. 2.2, bottom right panel), through smart combinations of catchment-specific interventions that account for cascading effects of improved water quality in connected waterbodies. Hence, in SNRNs the *network* of inland waters is managed in a *smart* way, where contextual adaptive management decisions are based on actual data and prior knowledge. This smart management includes manipulation of the system's hydrology and ecological states to enhance nutrient retention. Moreover, nutrients in SNRNs are retained and reused by, for example, harvesting macrophytes, sediment, or fish (Fig. 2.2, top right panel). Overall, SNRNs could mitigate socioeconomic impacts related to nutrient pollution, which encompass chemical and ecological water quality degradation and unsustainable nutrient resource management.

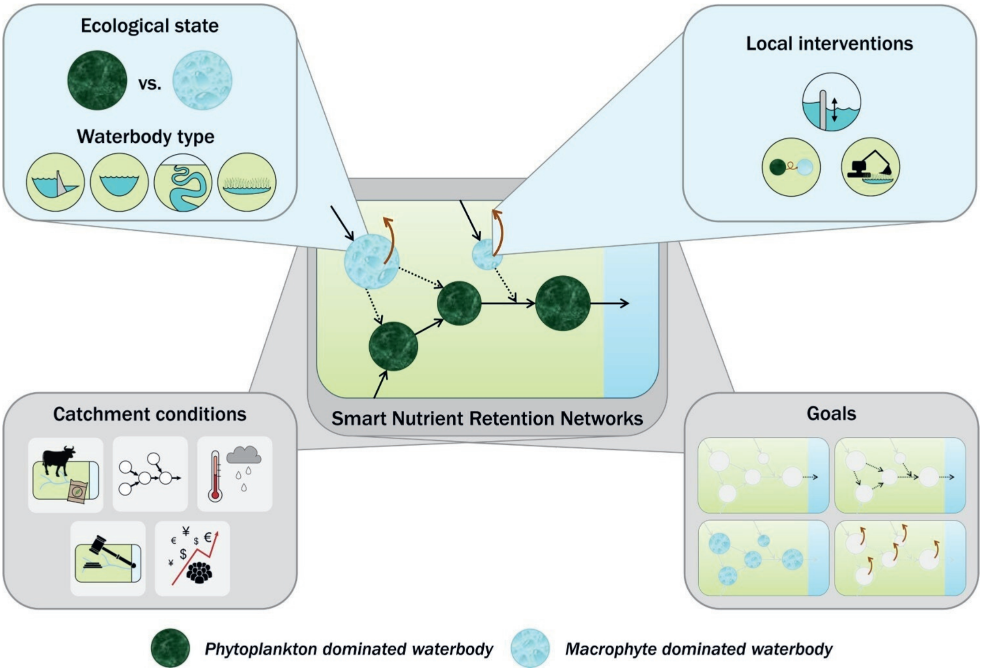

Figure 2.2. Smart Nutrient Retention Networks (middle panel) have multiple dimensions, that should be considered to achieve the goal(s) set for the network of inland waters: minimized nutrient loss to the oceans, maximized nutrient retention in inland waters, good ecological water quality, or maximized reuse of nutrients retained within the network (bottom right panel). At the level of individual waterbodies, the ecological state and waterbody type influence the potential for nutrient retention (top left panel). Local interventions can influence this nutrient retention potential, for example, by adjusting the hydrology, changing the ecological state, or harvesting and reusing nutrient retaining ecosystem components (top right panel). At the catchment level, conditions apply which are beyond the scope of local water managers: external nutrient loading, configuration of hydrological connections, climate change, catchment-level legislation, and socioeconomic conditions (bottom left panel).

In this paper, we explore current knowledge to develop SNRN management strategies. We specifically elaborate on (1) natural nutrient retention processes in individual waterbodies and networks of inland waters, (2) water quality management options for nutrient conservation, and (3) nutrient retention models. We focus on the northern temperate zone where strong human impacts on water systems (e.g., a legacy of intense nutrient enrichment) prevail, and regularly refer to examples from (sub)tropical regions where nutrient conservation is more common. Within the northern temperate zone, we expect that the principles of SNRNs can especially improve water quality and nutrient management in regions with highly modified and controlled water systems and many shallow lakes (with potential for macrophyte-dominated vs. phytoplankton-dominated states), such as lowland western Europe.

2.2 Nutrient retention processes in inland waters

In SNRNs, nutrient retention is maximized to benefit the whole catchment. The catchment covers the largest spatial scale of networks of inland waters, including connected waterbodies and the land draining into these waters. At the waterbody level, nutrients are either retained or flow freely with the water in dissolved or particulate forms such as detrital matter or phytoplankton (Teurlincx et al. 2019). Nutrient retention processes include (1) natural internal retention (e.g., long-term storage by sedimentation, burial of biomass, and P bound to mineral particles; Uhlmajnn and Horn 1992, Smolders et al. 2006, Finlay et al. 2013, Kong et al. 2019), (2) natural losses from the waterbody (e.g., denitrification and consumption by migrating waterfowl; Saunders and Kalff 2001, Doughty et al. 2016, Kong et al. 2019), or (3) harvesting by humans (e.g., in the form of macrophytes, sediment, or fish). Water management can influence nutrient retention pathways directly (e.g., harvesting by humans), and indirectly through ecosystem state management (e.g., increased denitrification by bank reshaping). In general, increases in nutrient retention processes could decrease the risk of harmful algal blooms. Some nutrient retention processes counteract nutrient conservation (e.g., N_2 degases by denitrification), which enhances water quality but constitutes a loss process.

2.2.1 Waterbody characteristics

The hydraulic residence time of a waterbody promotes denitrification and sedimentation because it increases sediment–water contact (Ahlgren et al. 1988, Jansson et al. 1994, Saunders and Kalff 2001, Brett and Benjamin 2008, de Klein and Koelmans 2011; Table 2.1). Waterbodies with a large volume and relatively low water discharge, such as large and dammed reservoirs, have long residence times (Maavara et al. 2015). In the meta-analysis by Saunders and Kalff (2001), rivers had the largest average water discharge rate, followed by lakes and wetlands, whereas total N (TN) retention was largest for wetlands, followed by lakes and rivers. Although the average TN retention differed per waterbody type, it was similar in all waterbody types when correcting for discharge rates (Saunders and Kalff 2001). Higher water residence times in wetlands may partly be due to dense macrophyte stands that reduce flow velocity and increase sedimentation (Petticrew and Kalff 1992, Benoy and Kalff 1999, Saunders and Kalff 2001). In streams, macrophytes may lower water velocity and provide shelter, stimulating sedimentation (Svendsen and Kronvang 1993, Schulz et al. 2003). The highest nutrient storage potential in rivers was found within and downstream of areas with macrophytes (Svendsen and Kronvang 1993, Schulz et al. 2003). Especially in summer, areas with macrophytes tend to retain more nutrients, but weed cutting and autumn storm flows counteract this temporary storage through resuspension (Svendsen and Kronvang 1993).

Additionally, stratification, relative nutrient processing rates, and the volume to surface area ratio of waterbodies influence the strength of nutrient retention processes (Table 2.1). Once a lake or reservoir stratifies and the hypolimnion becomes anoxic, it may act as a P source when the water column remixes or the outlet is at the bottom of a dam (Nürnberg 1984, Kõiv et al. 2011). The meta-analysis by Kõiv et al. (2011) of 54 reservoirs and lakes (0-6.6 m deep) showed that stratifying waterbodies are generally deeper, and their P retention capacity decreases with relative depth. This redox-dependent P retention in lake sediment also depends on nitrate, sulfate and particulate iron concentrations (Andersen 1982, Gächter and Müller 2003). Moreover, the balance, or even tradeoff, between biogeochemical nutrient processing rates and hydraulic residence time may determine net nutrient retention (Höhener and Gächter 1993, Powers et al. 2012, Schmadel et al. 2018), as described by the nutrient spiraling theory for individual streams (Newbold et al. 1981). For example, the combination of shorter hydraulic residence times, relatively invariant reaction times, and larger nutrient loadings during high-flow periods results in a lower N retention efficiency in rivers with higher streamflow variability (Ye et al. 2012). Additionally, direct P adsorption/desorption between water and sediment may be more important than sedimentation in shallow lakes with a relatively large sediment surface area to lake volume (Andersen 1997). Also, shallow wetlands with a large surface area likely retain N through denitrification, whereas those with a smaller surface area more likely retain P by sedimentation (Hansson et al. 2005).

Table 2.1. Illustrative examples of how waterbody type and system characteristics contribute to higher (+) or lower (−) N and P retention, focused on the northern temperate zone.

Waterbody type	System characteristics	N retention potential	P retention potential	Reference
Dammed reservoir	Hydraulic residence time	+	+	(Maavara et al. 2015; Vörösmarty et al. 2003)
	Stratification	+	-	(Beaulieu et al. 2014; Kõiv et al. 2011; Nürnberg 1984)
Lake	Hydraulic residence time	+	+	(Ahlgren et al. 1988; Brett and Benjamin 2008; Saunders and Kalff 2001)

	Stratification	+	-	(Beaulieu et al. 2014; Kõiv et al. 2011; Nürnberg 1984)
	Macrophyte/ phytoplankton dominance	+/-	+/-	(Hilt et al. 2017)
River	Hydraulic residence time	+	+	(de Klein and Koelmans 2011; Saunders and Kalff 2001)
	Size	+	+	(Wollheim et al. 2006)
	Low-flow zone presence (e.g., with macrophytes)	+	+	(Schulz et al. 2003a; Svendsen and Kronvang 1993)
	Streamflow variability	-	-	(Ye et al. 2012)
Wetland	Hydraulic residence time	+	+	(Jansson et al. 1994; Saunders and Kalff 2001)
	Volume to surface area ratio	-	+	(Hansson et al. 2005)
	Inundation time	+/-	+/-	(Powers et al. 2012; Sollie et al. 2008)
	Macrophyte stand density	+/-	+/-	(Barko and James 1998; Sollie et al. 2008)
	Vegetation type	+/-	+/-	(Søndergaard et al. 2001)

Moreover, the amount of retained N and P tends to increase with nutrient loading (Prairie 1989, Saunders and Kalff 2001, Kõiv et al. 2011, Wang et al. 2020). Saunders and Kalff (2001) found that N loading is an excellent statistical predictor for the magnitude of TN retention in wetlands and lakes. Thus for N retention, water discharge or hydraulic residence time and nutrient loading are important determining factors, although hydraulic residence time’s effect was strongest in the global lake dataset of Finlay et al. (2013). Further, P sedimentation in 4 lakes worldwide was found to correlate with P loading and in-lake P concentrations (Prairie 1989). The relation between N and P retention and nutrient loading differs seasonally, however (Hansson et al. 2005). Moreover, increased total P concentrations can increase N retention by stimulating phytoplankton production, settling, and decomposition, which decreases dissolved oxygen concentrations and thereby increases denitrification rates (Finlay et al. 2013). For example, Finlay et al. (2013) showed for a diverse and broadly representative set of lakes that N retention was >7 times higher in P-rich eutrophic lakes than in oligotrophic lakes, and similar trends were found by Donald et al. (2015) for 12 reservoirs in Canada. This dependency of nutrient retention on nutrient loading and seasonal variation may partly be explained by the ecological configuration of the ecosystem in the growing season, with limited retention in oligotrophic systems with little macrophyte growth, increased retention in mesotrophic systems with strong macrophyte growth, and either high or low retention in eutrophic systems, depending on submerged macrophyte or phytoplankton dominance, respectively.

Especially when biological processes are dominant, nutrient retention shows seasonal patterns along with temperature dependencies of process rates (Kadlec and Reddy 2001, de Klein and Koelmans 2011, Wang et al. 2020). At higher temperatures, process rates (e.g., of denitrification) generally increase but oxygen levels tend to drop (Kadlec and Reddy 2001, Jeppesen et al. 2009). Low oxygen levels may result in lower nutrient retention by reducing nitrification and denitrification (Jeppesen et al. 2009, Özen et al. 2010) and enhancing sediment P release (Jensen and Andersen 1992). For example, in Lake Chaohu (China) low summer P retention is due to increased sediment P release and low winter N retention is due to low rates of denitrification (Wang et al. 2020). Reduced nutrient retention under winter conditions can also be explained by nitrate accumulation under ice cover and nutrient release by senescing vegetation (White and Bayley

2001). Moreover, snow changes hydrological conditions as it accumulates and causes long and intense runoff as it melts (German et al. 2003). During snowmelt, this process results in lower nutrient retention efficiencies (German et al. 2003), probably because of shorter hydraulic residence times.

Furthermore, climatic conditions such as precipitation, temperature, and degree of seasonality (Lewis 1996) are important for nutrient retention. Especially in tropical river lakes, seasonal precipitation may strongly affect hydraulic residence time (Lewis 1996) and thereby nutrient retention. In drier climates, less nutrient loading by runoff results in lower in-lake nutrient concentrations (Jeppesen et al. 2009, 2011, Özen et al. 2010). By contrast, in warmer climates more evaporation results in higher in-lake nutrient concentrations and higher chances of harmful algal blooms (Jeppesen et al. 2009, 2011, Özen et al. 2010). Similarly, macrophyte cover and critical nutrient loading levels at which lakes turn from clear to turbid are expected to decrease with warming (Jeppesen et al. 2009, 2011, Özen et al. 2010), and therefore lower nutrient retention is expected at higher temperatures. The balance between the effects of altered hydraulic residence time, nutrient loading, evaporation, and ecological state will determine the effect of different climates on nutrient retention.

The hydrological configuration of networks of inland waters influences local and network-wide nutrient retention. In systems with connected waterbodies, water quality, nutrient concentrations, and nutrient retention may differ depending on surrounding landscape and position in the catchment (Miranda et al. 2008, Schmadel et al. 2018, Teurlincx et al. 2019). For example, in river networks, large rivers retain more N than small rivers because they more effectively retain N per mean length of stream order, and they receive nutrients that are not retained in smaller rivers or that bypass them on land and directly enter the larger river (Wollheim et al. 2006). In general, network-wide nutrient retention is higher with abundant retaining waterbodies, such as lakes (Huttunen et al. 2016; see

Supplementary material B for an example of chains of lakes modeled with PCLake). Additionally, N removal increases with pond roundness and connectivity between ponds and streams (Schmadel et al. 2018). Also, when wetlands and floodplains temporarily connect to rivers by inundation, additional nutrient retention or release may occur (Noe and Hupp 2007). The multi-pond system above Chaohu Lake (China) exemplifies how connected waterbodies can influence nutrient retention (Yin et al. 1993). The ponds retain water, sediment, and nutrients and are used for rice field irrigation, which enhances nutrient recycling and retention on land. In 1993, Yin et al. (1993) reported that from January to September overall, 99% and 98% of N and P loading was retained.

2.2.2 Macrophytes

An intricate balance of direct and indirect processes determines the net effect of macrophytes on nutrient retention (Fig. 2.3). Macrophytes directly contribute to nutrient retention by assimilation and consecutive burial of plant litter (Granéli and Solander 1988, Jansson et al. 1994, Clarke 2002, Kreiling et al. 2011), enhancing sedimentation and decreasing resuspension (Howard-Williams 1983, Clarke 2002, Zhu et al. 2015). Moreover, macrophytes indirectly contribute to nutrient retention by providing an attachment surface for nutrient consuming epiphytes and denitrifying bacteria (Howard-Williams and Allanson 1981, Weisner et al. 1994) and stimulating both P sorption and (coupled nitrification-)denitrification by sediment oxygenation (Risgaard-Petersen and Jensen 1997, Ottosen et al. 1999, Smolders et al. 2002, Kreiling et al. 2011, Vila-Costa et al. 2016). Macrophytes indirectly stimulate denitrification by (dissolved) organic carbon supply to the water or sediment and sediment nitrate penetration by root water uptake while inhibiting denitrification by competition for N and production and release of oxygen (Weisner et al. 1994). Moreover, shading by macrophytes may both stimulate and inhibit denitrification, because it decreases oxygen production by photosynthesis and lowers the water temperature, respectively (Weisner et al. 1994). Furthermore, the

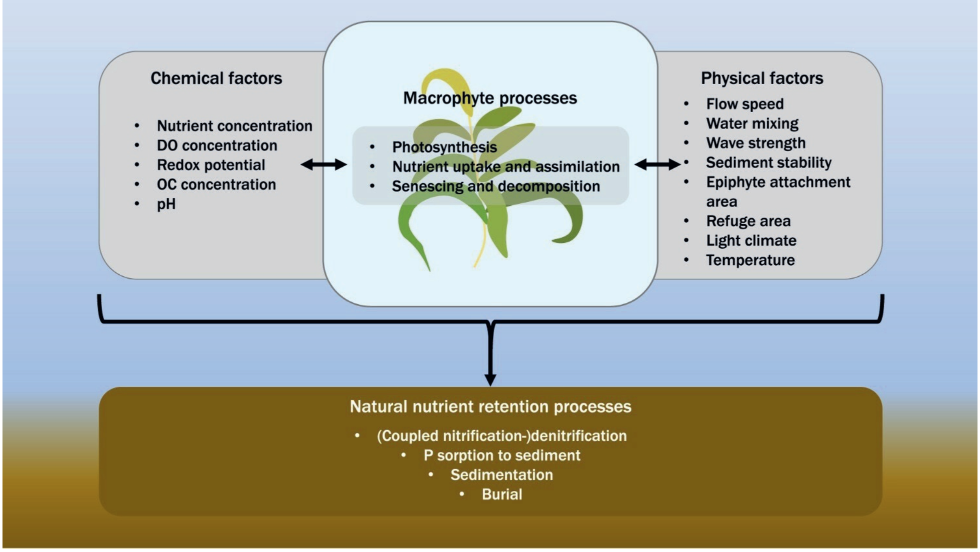

Figure 2.3. Macrophytes directly and indirectly influence natural nutrient retention processes (white text in brown box) through macrophyte processes (marked light blue). Nutrient uptake and assimilation followed by burial is the most direct route. Indirect influences are found through the effect of macrophytes on both chemical (e.g., dissolved oxygen [DO] and organic carbon [OC] concentration) and physical factors (marked gray). Note the importance of seasonality, nutrient form (particulate/dissolved), macrophyte functional group, and species for macrophyte and nutrient retention processes.

net effect of macrophytes on nutrient retention depends on the time scale of measurement and the nutrient form (Carpenter and Lodge 1986). For example, macrophytes accumulate nutrients during spring and summer but release nutrients during their senescence (Landers 1982). And in general, macrophyte stands contribute to net particulate P retention and net dissolved P release (Carpenter and Lodge 1986).

Macrophyte species and their functional groups may strongly influence their effect on nutrient retention. Larger vegetation types (e.g., helophytes) have more biomass and are therefore expected to contribute more to nutrient retention than low herbaceous vegetation (Sollie et al. 2008). Charophytes are more efficient nutrient sinks than vascular macrophytes because charophytes have lower decomposition rates and take up most of their nutrients from the water (vs. sediment) because of their larger shoot to root ratios (Kufel and Kufel 2002). Whether a macrophyte species is rooting and sessile or non-rooting and (similar to phytoplankton) flowing along with the water (Janssen et al. 2019b) is essential for their contribution to nutrient retention. Also, the functional group strongly influences denitrification rates. Especially, rooted macrophytes can increase denitrification by oxygenating the sediment, thereby enhancing coupled nitrification–denitrification (Risgaard-Petersen and Jensen 1997, Ottosen et al. 1999, Vila-Costa et al. 2016). Closed mats of floating macrophytes may increase denitrification and sediment P release through low dissolved oxygen concentrations (Veraart et al. 2011, Janssen et al. 2020). The net contribution to nutrient retention from other (e.g., submerged) macrophyte species is less evident (Søndergaard et al. 2001). In particular, dense macrophyte stands can seasonally cause a net sediment P release from low oxygen levels (e.g., during decomposition or by constrained water mixing) or increase pH due to high primary production (Søndergaard 1988, Frodge et al. 1991, Barko and James 1998).

Although outcomes among studies vary, they mostly show higher nutrient retention in macrophyte-dominated over phytoplankton-dominated shallow lakes (26 of 40 unique papers on nutrient retention in the review by Hilt et al. 2017). For example, from Veraart et al. (2011) we expect about 10 times more N retention in a vegetated over an unvegetated state (with 12 h light). The relative contribution of assimilation in macrophytes to overall nutrient retention also varies, with 8–77% for N and 12–73% for P (Reddy and De Busk 1985, Kreiling et al. 2011, Veraart et al. 2011, Wang et al. 2013). Vegetation also enhances nutrient retention in streams (Balestrini et al. 2018). Moreover, the nutrient retention capacity of macrophytes explains one of the self-reinforcing (i.e., mathematically positive) feedback loops that self-maintain macrophyte-dominated versus phytoplankton-dominated states in shallow lakes (Scheffer et al. 1993), demonstrated by the ecosystem model PCLake (Supplementary material A).

Feedback loops involving macrophytes as described by Scheffer et al. (1993) for individual waterbodies can also emerge in hydrological networks. For example, Gillis et al. (2014) showed that mangrove forests and seagrass beds retain nutrients, providing positive interactions with connected ecosystems (e.g., coral reefs) through reduced nutrient loadings. Such spatial effects of local nutrient retention by marine ecosystems could also be expected in networks of inland waters (Teurlincx et al. 2019) through a self-reinforcing feedback loop between nutrient loading, ecological water quality, and nutrient retention in networks of inland waters (Fig. 2.4). The underlying theory is that nutrient loading reduces water quality (i.e., increases the likelihood of phytoplankton dominance over macrophyte dominance and hence turbidity over clarity; Scheffer et al. 1993). Good water quality itself results in higher nutrient retention by the self-reinforcing feedback loop between macrophytes and water clarity within the waterbody. Finally, on the hydrological network level, the increased nutrient retention within the waterbody decreases nutrient loading to downstream waterbodies, where the feedback chain could repeat itself (i.e., has spatial cascading effects; Klose et al. 2020), resulting in a self-reinforcing feedback loop for the entire network of inland waters.

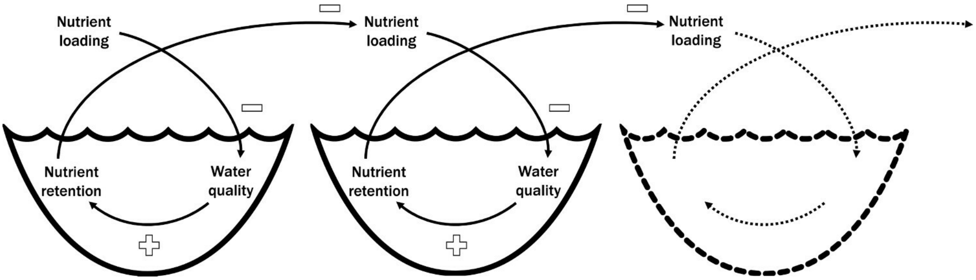

Figure 2.4. Schematic of the self-reinforcing (i.e., mathematically positive) feedback loop in networks of inland waters. Nutrient loading has a negative feedback on ecological water quality, water quality has a positive feedback on nutrient retention, and nutrient retention has a negative feedback on nutrient loading downstream, overall resulting in a self-reinforcing feedback loop that cascades down the network.

2.3 Water quality management options for nutrient conservation

2.3.1 Hydrological management

Hydrological management strategies to retain, harvest, and reuse more nutrients in and from inland waters can be applied with the ultimate goal to improve nutrient conservation in the entire catchment. Local changes in hydrology and nutrient retention affect downstream hydrology, ecology, and nutrient retention (Hilt et al. 2011, Jenny et al. 2014, Kondolf et al. 2014, Van Cappellen and Maavara 2016, Teurlincx et al. 2019, Maavara et al. 2020). Therefore, Hilt et al. (2011) and Teurlincx et al. (2019) argued for a hydrological network perspective and to tactically use local, upstream interventions. Local hydrological interventions may include water level and flow regulation by pumps, dams, and sluices and dechannelization (Vörösmarty 1997, Stanley and Doyle 2002, Li et al. 2013, Kong et al. 2017, Fraaije et al. 2019, Maavara et al. 2020). These measures alter the hydraulic residence time and risk of hypoxia (Jenny et al. 2014), thereby influencing nutrient retention in the waterbody (Wang et al. 2020). Also, waterbody types may be altered; for example, dam construction can convert river sections into dammed reservoirs and strongly increase P retention (Tundisi et al. 1998, Vörösmarty et al. 2003). In addition to waterbody-level interventions, management of the hydrological network structure may stimulate net nutrient retention, for example, by increasing lateral connections between rivers and vegetated lakes or wetlands (Mitsch et al. 2008, Kreiling et al. 2011, Newcomer Johnson et al. 2016). More natural reconstruction of hydrological networks may have mutual benefits; for example, increased nutrient retention and flood protection are expected after (re)construction of waterways and flooding areas in the Dutch “Room for the River” and “Living with Water” projects (Van Gerven et al. 2009).

2.3.2 Macrophyte-focused management

Stimulation and preservation of macrophytes (Hilt et al. 2006) may enhance nutrient retention and ecological water quality (e.g., according to the

European Water Framework Directive). However, macrophytes may cause problems for drinking water and hydropower production and block waterways for boating (Tundisi et al. 1998, Hilt et al. 2006). Yet, the public perception on macrophyte establishment, in for example urban streams, is generally positive or neutral (Larned et al. 2006). Moreover, macrophyte-stimulating interventions may have multiple benefits, such as enhancing biodiversity, recreational value, fish spawning areas, and nutrient retention. At present, the benefits of paludiculture (i.e., wet agriculture/forestry on rewetted peatlands) are being explored (Vroom et al. 2018). Moreover, more vegetated water systems are being promoted or developed to support biodiversity, such as thousands of kilometers of nature-friendly banks in the Netherlands (ter Veld 2014). For lakes specifically, diverse management options to promote macrophyte dominance over phytoplankton dominance exist: flushing with cleaner water, nutrient load reductions beyond the lower critical nutrient load, and biomanipulation by fish removal (Janse et al. 2008, Bernes et al. 2015, Janssen et al. 2019b). Here, we highlight 2 more examples of macrophyte-focused management that can be applied for nutrient conservation: constructed wetlands and an engineering project for macrophyte harvesting and reuse.

2.3.2.1 Constructed wetlands

Constructed wetlands are wet systems created with macrophytes (and sediment), mostly used to treat wastewater. For example, reed filters in a stream bypass purify and store water at the estate of Lankheet (the Netherlands; Mulder and Querner 2008), and in (sub)tropical regions, common water hyacinth (*Eichhornia crassipes*) and water lettuce (*Pistia stratiotes*) are used to bioremediate multiple wastewater types (Reddy and D’angelo 1990, Kutty et al. 2009, Lu et al. 2010, Akinbile and Yusoff 2012). Howard-Williams (1985) extensively reviewed N and P retention in wetlands and the early developments of constructed wetlands, and Wu et al. (2015) comprehensively reviewed constructed wetland application and recent developments on their sustainable design. The nutrient retention effectiveness of constructed wetlands tends to decrease over time, especially for P (Mitsch et al. 2014), possibly explained by saturation of the soil and accumulation of detritus and plant biomass (Mitsch et al. 2012). To counteract saturation and accumulation effects and to maintain effectiveness of the constructed wetlands, these nutrient-retaining components should be harvested and used as a (nutrient) source elsewhere, thereby enhancing nutrient conservation (e.g., see Reddy and D'angelo 1990). For example, the new "bio-cascade water purification" approach applies knowledge of biogeochemical processes in soil, water, and macrophytes to prevent saturation effects in connected water basins and to conserve nutrients by harvesting helophytes and floating macrophytes (Kwakernaak et al. 2015). However, to meet increasingly strict water quality standards, research and development is still required for appropriate plant harvest and reuse strategies in constructed wetlands (Wu et al. 2015).

2.3.2.2 Harvesting

More nutrients could be reused by mowing macrophytes (Kuiper et al. 2017), dredging sediment, or fishing. Think of using reed as a building material (Köbbing et al. 2013), lake-dredged materials and decayed or processed water hyacinths as soil amendments (Sigua 2009, Aremu et al. 2012, Masto et al. 2013), or fish as a food source (Edwards et al. 1997, McIntyre et al. 2016, Kim et al. 2019). Such harvests are currently occurring but rarely considered for nutrient conservation or to combat eutrophication problems. For example, Tang and Xie (2000) considered fish catches, like water outflow, a nutrient outflow. Nevertheless, fishing conserved 3–4% and 10% of the N and P loading, respectively. We noted one example of macrophyte harvesting to purposefully remove nutrients from a natural waterbody: an ecological engineering project in subtropical Lake Caohai (China; Wang et al. 2013). Here, seedlings of common water hyacinth were planted in constructed enclosures, harvested after growth, and processed into biogas and organic fertilizer. This process removed 76% of the inflowing TN, with 65% of the overall retained N in the form of macrophyte biomass. Wang et al. (2013) concluded that "large scale utilization of *E. crassipes* for removal of N in the eutrophic lake [Caohai] is practicable," thus the potential for nutrient conservation exists. However, harvesting should be applied with care to avoid drastic ecosystem disruptions (Van Zuidam and Peeters 2012, Kuiper et al. 2017) and the loss of indirect contributions of macrophytes to nutrient retention. Moreover, risks of contaminating food chains should be carefully assessed before reusing macrophytes and dredged materials (Beyer and Stafford 1993, Aremu et al. 2012).

2.3.3 Catchment-level nutrient management

Most water quality management measures are applied to individual waterbodies but would become more effective if embedded in catchment-wide management strategies, considering potentially cascading effects of improved water quality in networks of inland waters (Fig. 2.4). At the catchment level, additional measures can be taken by, for example, regional or (inter)national governing authorities (Fig. 2.2). These measures can target external nutrient loading (i.e., nutrients from diffuse and point sources in the catchment, which may eventually reach target waterbodies) and hydrological connections. These issues may be addressed by landscape-level legislation and enforcement (e.g., fertilizer application limits and wastewater treatment standards) or catchment level-management (e.g., changing hydrological network structure by (re)constructing waterways and adjusting macrophyte mowing schemes) but are beyond the scope of local water managers. Moreover, nutrient loading and retention are influenced by socioeconomic and climatic changes, for example land use change, population and economic growth, increasing temperatures, and changes in precipitation and runoff (Strokal et al. 2016). These (inter)national and global challenges require adjustments at even larger scales.

2.4 Nutrient retention models

SNRN management strategies can be designed with the help of nutrient retention models available at various spatial scales (Supplementary material C). Nutrient retention models simulating individual waterbodies are often process-based (i.e., employing process rates and mechanistic insights to estimate nutrient retention; Van Gerven et al. 2009). For example, PCLake(+) (Janse 2005, Janssen et al. 2019a), PCDitch (Janse and Van Puijenbroek 1997, Janse 2005), and the GLOBIO-Wetlands model (under development; Janse et al. 2019) are process-based models from which nutrient retention processes and balances can be derived (Kong et al. 2019). These models include feedback loops between ecological states and nutrient retention and have been used to explore water quality management options (Janssen et al. 2019b). An example of a partly process-based model to analyze the effect of interventions on water quality is the Dutch KRW-Verkenner (Water Framework Directive Explorer). Users can themselves assign nutrient retention fractions of waterbodies, guided by meta-models for lowland streams, shallow lakes, and rivers that are statistically derived from the mechanistic process-based model AquaVenus (de Klein 2008, Van Gerven et al. 2009). Although some of the meta-models include the effect of macrophytes on nutrient retention, they do not include feedback loops between nutrient loading, ecological water quality, and nutrient retention (Van Gerven et al. 2009). Wetland models most explicitly cover the effect of macrophytes on nutrient retention and are usually more specific, for example, focusing on either N or P, or on a specific wetland type and location (Mitsch and Reeder 1991, Van Dam et al. 2007). Most of these and other waterbody-level nutrient retention models include macrophyte and/or phytoplankton presence (Supplementary material C).

On the hydrological network level (i.e., global or catchment scale in Supplementary material C), nutrient retention is often expressed as a fraction of the nutrient flow into the system that is retained and derived by statistical relationships to one or multiple waterbody characteristics. For example, the global model WorldQual derives P retention in waterbodies as a function for the whole catchment depending on hydraulic residence time (Fink et al. 2018). In other global models, the nutrient retention fraction is, in addition to hydraulic residence time, based on denitrification and sedimentation rates (Harrison et al. 2009, Beusen et al. 2016). GlobalNEWS includes denitrification in rivers as a function of water depth and travel time (Seitzinger et al. 2002), nutrient removal by water abstraction for irrigation and other human consumptive water use, and retention in dammed reservoirs as a function of hydraulic residence time and depth (Mayorga et al. 2010). The MARINA model builds on the latter global model but is specified for Chinese river catchments, with multiple subcatchments and channel section-specific nutrient retention (Strokal et al. 2016). In addition to the retention processes in GlobalNEWS, MARINA includes dissolved inorganic P retention in rivers by, for example, sedimentation and accumulation (Strokal et al. 2016). All these and other large-scale nutrient retention models exclude management options for individual waterbodies and generally disregard the effect of ecological state (Supplementary material C).

To support the development of SNRNs, a model should include management options and the self-reinforcing feedback loop of ecological water quality, nutrient retention, and nutrient loading in networks of inland waters. Hence, existing nutrient retention models for individual waterbodies seem more promising than large-scale models. Especially, global-scale models strongly simplify nutrient retention, which may be justified because they are intended to identify global pollution hotspots and long-term water quality trends, whereas local-scale models are more often designed to assess management options (Tang et al. 2019). Large-scale models disregard alternative ecological states of lakes, which might be explained by their focus on rivers, and neither explicitly consider biogeochemical nutrient retention processes other than denitrification. Most local-scale models are more detailed and process-based, but also have their limitations for modeling nutrient retention management at catchment-scale. For example, these models do not focus on nutrient retention, or they focus only on specific nutrients or waterbody types (Supplementary material C). The advantage of detailed, process-based models for SNRN management strategy development is that they more often include management options, primary producers, and potentially include feedback loops between ecological states and nutrient retention. By their mechanistic basis, these more process-based local-scale models can serve as a building block to consider cascading effects on a hydrological network scale; alternatively, their insights can be applied in large-scale models.

2.5 Toward Smart Nutrient Retention Network management strategies

The specific design of any SNRN management strategy depends on the configuration and state of the targeted network of inland waters, including its local waterbody types and their ecological states, and availability and efficacy of local intervention options (Fig. 2.2). Moreover, successful nutrient conservation through the implementation of SNRN management strategies requires an understanding of catchment conditions and clearly formulated goals (Fig. 2.2). Catchment conditions include biogeochemical and social system properties such as external nutrient loading, hydrological connections, climate change, catchment-level legislation, and socioeconomic conditions. Tailoring case-specific goals and strategies to such cross-sectoral catchment conditions is beyond the scope of water managers alone and requires partnerships of stakeholders and involvement of larger scale governing authorities (see catchment-level nutrient management discussion earlier).

Formulation of clear goals before implementation is a key task for responsible managers and stakeholders. It is crucial that the manager is aware of potential local and regional tradeoffs of interventions and between goals. For example, interventions may have contrary effects on N and P retention, denitrification can enhance water quality but counteract nutrient conservation, and increased flushing may locally improve water quality while deteriorating downstream ecosystems through increased nutrient loading. To avoid unforeseen tradeoffs, more complete and quantitative empirical studies must be conducted on the effect of macrophytes on nutrient retention at the level of networks of inland waters. Empirical examples and studies of effective, efficient, and safe nutrient harvesting and reuse can inform the further development of SNRNs, specifically to manage the risk of undesired changes in ecological state and nutrient retention potential. Ideally, the impact of SNRN management strategies on processes and goals aside from nutrient retention and conservation should be considered, as advocated by integrated water resource management approaches (Al-Jawad et al. 2019). For example, greenhouse gas emissions (Deemer et al. 2016, Chen et al. 2019), biodiversity loss (Dudgeon 2000, Hansson et al. 2005), and sediment starvation (Kondolf et al. 2014) should be considered.

SNRN management strategies can be designed conceptually, based on expert knowledge, or with the help of simulation models. Simulation models can provide outcomes of multiple scenarios for quantitative comparison but integrated models must be developed to include (1) applications to networks of inland waters; (2) feedback between ecological states, nutrient retention, and nutrient loading; and (3) nutrient retention management options. Networks of inland waters could be modeled using a node-link schematization, building on existing waterbody models, as suggested by Teurlincx et al. (2019). When a wide range of management options is available, such models could be run with optimization algorithms to determine the optimal solution (Al-Jawad et al. 2019, Strokal et al. 2020). While time-consuming and challenging, using an optimization approach could result in novel solutions to water management problems that might not be found intuitively.

Developing complex nutrient retention network models could drive significant improvements in network-level water management for nutrient conservation. Nonetheless, these developments are not necessary for water managers to start to include the core principles of SNRNs. SNRN principles could, for instance, be applied to the “River Basin Management Plans” required by the European Water Framework Directive (Griffiths 2002). Beyond Europe, considering nutrient retention in networks of inland waters may support sustainable water quality and nutrient management.

Human food production was long dependent on, and limited by, nutrient recycling by manure application on agricultural lands. With the onset of the industrial age, feeding a growing world population became increasingly dependent on unsustainable fertilization techniques that exploit mineral P deposits and marginally renewable geological stocks of fossil fuels for N fixation. Maintaining, and ensuring for all, the high living standards that result from such unsustainable agricultural practices, but within the means of the planet, is today’s greatest challenge (Raworth 2012). Smart Nutrient Retention Networks can be one component of a sustainable and just future as they are designed around biogeochemical nutrient cycling processes and contribute directly to at least 3 UN Sustainable Development Goals (SDGs): zero hunger (SDG 2), clean water and sanitation (SDG 6), and responsible consumption and production (SDG 12) (United Nations 2015).

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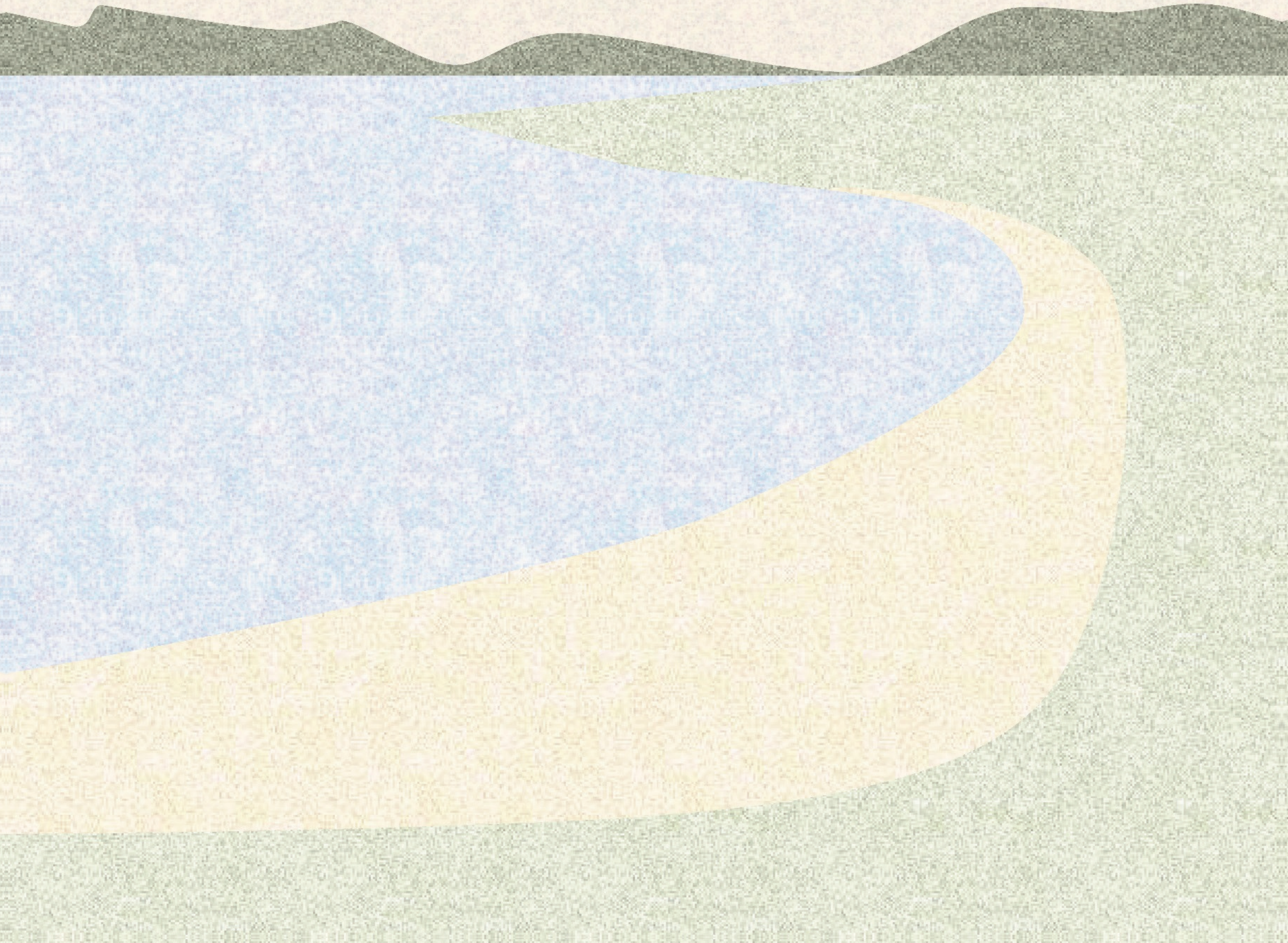
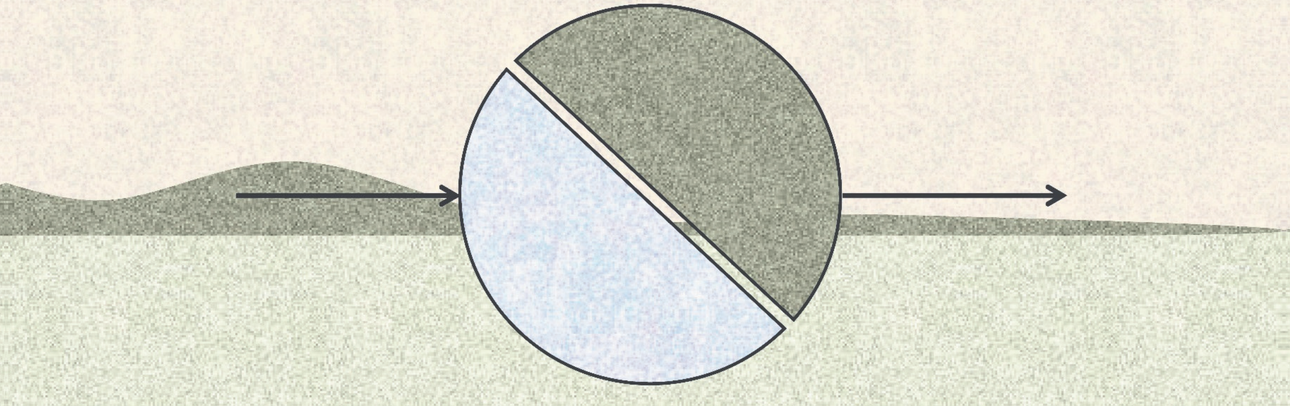


Chapter 3

Regime shifts in shallow lakes explained by critical turbidity



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Abstract

Worldwide, water quality managers target a clear, macrophyte-dominated state over a turbid, phytoplankton-dominated state in shallow lakes. The competition mechanisms underlying these ecological states were explored in the 1990s, but the concept of critical turbidity seems neglected in contemporary water quality models. In particular, a simple mechanistic model of alternative stable states in shallow lakes accounting for resource competition mechanisms and critical turbidity is lacking. To this end, we combined Scheffer's theory on critical turbidity with insights from nutrient and light competition theory founded by Tilman, Huisman and Weissing. This resulted in a novel graphical and mathematical model, GPLake-M, that is relatively simple and mechanistically understandable and yet captures the essential mechanisms leading to alternative stable states in shallow lakes. The process-based PCLake model was used to parameterize the model parameters and to test GPLake-M using a pattern-oriented strategy. GPLake-M's application range and position in the model spectrum are discussed. We believe that our results support the fundamental understanding of regime shifts in shallow lakes and provide a starting point for further mechanistic and management-focused explorations and model development. Furthermore, the concept of critical turbidity and the relation between light-limited submerged macrophytes and nutrient-limited phytoplankton might provide a new focus for empirical aquatic ecological research and water quality monitoring programs.

3.1 Introduction

Worldwide, harmful algal blooms are threatening aquatic ecosystems and the services they provide, like drinking water and food provision and many cultural services such as recreation (Rodrigues 2015; Hilt et al. 2017; Chang et al. 2020). This threat is rising by increased nutrient inputs (i.e., through urbanization and agricultural intensification) and is aggravated by climate change (Moss et al. 2011). Harmful algae belong to the bigger group of phytoplankton that competes with macrophytes for nutrients and light. In water quality management, turbid, phytoplankton dominated waters are often related to water quality problems whereas clear waters with submerged macrophytes (from now on "macrophytes") are associated with good water quality. Especially in shallow lakes, macrophyte abundance has declined dramatically (Körner 2002). For example, in north-east Germany in 1950 about 30% of 300 investigated lakes had lost their macrophytes, and by the 90s 55-85% out of 100 lakes had low macrophyte abundance (<5% macrophyte coverage) (Körner 2002). Although last decades macrophytes showed some recovery, the average Dutch surface water quality for macrophytes is still bad to moderate according to the European Water Framework Directive (CLO 2018).

Water quality management is complicated by potential hysteresis and corresponding regime shifts (Smith and Schindler 2009; Cuddington et al. 2013). Regime shifts are sudden shifts in the ecosystem state. In this study we focus on shifts between a clear, macrophyte-dominated and a turbid, phytoplankton-dominated state and vice versa, as observed in temperate shallow lakes (Scheffer et al. 1993). Hysteresis means that two different equilibrium states (i.e., alternative stable states) are possible at identical stressor levels, depending on the initial (i.e., historic) state (May 1977). In shallow lakes, either macrophytes or phytoplankton can dominate in the hysteretic range, depending on whether the lake was initially clear or turbid, respectively (Jeppesen et al. 1990; Scheffer 1990; Janse 1997). This also implies that there are two critical stressor levels at which regime shift can occur, but the direction of change differs per critical stressor level (black arrows in Fig. 3.1). In lakes, this is associated with a relatively high and low critical nutrient loading. At the high critical nutrient loading, regime shifts from macrophyte to phytoplankton dominance can occur and at the low critical nutrient loading, macrophytes may start to dominate over phytoplankton (Janse et al. 2010). Because of this, a larger reduction in nutrient loading is needed to reverse a shift from macrophyte to phytoplankton dominance than the increase in nutrient loading that caused that shift. Models can help to estimate under which conditions regime shifts will occur in a variety of lakes and can thereby support water quality management. In particular, models grounded in ecological theory are valuable when extrapolation is required, as is the case for many lakes with limited data and within the context of global change (Cuddington et al. 2013).

3.1.1 State of the art and knowledge gap

The competition mechanisms underlying regime shifts between macrophyte versus phytoplankton dominance in shallow lakes were explored in the 1990s (Scheffer 1990; Scheffer et al. 1993) but the concept of critical turbidity (Fig. 3.1) seems neglected in mechanistic water quality models. Both macrophytes and phytoplankton use nutrients and light as major resources, but also influence the availability of these resources (Titus et al. 1975; Healey and Hendzel 1980; Spence 1982; Huisman and Weissing 1995; van Gerven et al. 2015). These feedback loops are described in the seminal work of Scheffer et al. (1993), showing that macrophytes compete with phytoplankton by nutrients and phytoplankton compete with macrophytes through light. The resulting alternative stable states were visualized in a graphical model with critical turbidity as an explanatory concept and captured in a “minimal” mathematical model that simplifies the ecological competition mechanisms (Scheffer 1990). Later, the mechanistic lake ecosystem model PCLake was developed to describe regime shifts in shallow lakes, based on many ecosystem processes (Janse 1997). With this

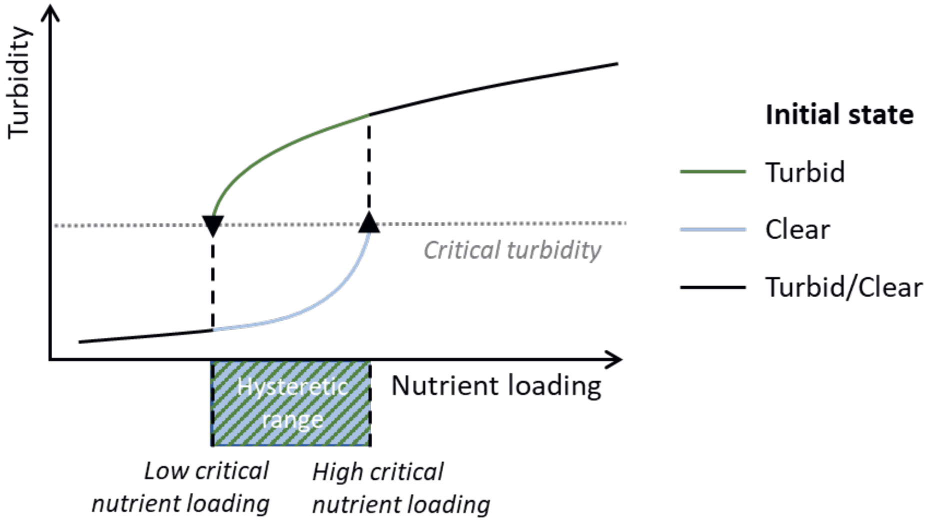


Figure 3.1. Schematic of alternative stable states in shallow lakes with nutrient loading as a stressor (x-axis). In the hysteretic range between the low and high critical nutrient loading the equilibrium ecosystem state (y-axis) depends on the initial ecosystem state (i.e., historically turbid phytoplankton-dominated, dark green line versus clear macrophyte-dominated, light blue line). Regime shifts to the clear or turbid equilibrium state (black arrows) can occur by oligotrophication at the low critical nutrient loading and eutrophication at the high critical nutrient loading, respectively. These critical nutrient loading levels correspond with the critical turbidity (gray dashed line) being the turbidity at which regime shifts occur.

increasing model complexity and the focus on critical nutrient loadings as model output, underlying mechanisms of competition for nutrients, and especially for light, have become hidden at first sight.

We lack a mathematically simple, mechanistic model of alternative stable states in shallow lakes, admitting there are multiple resource competition theories and models on nutrient and light limitation of primary producers to build on. Tilman's (1982) seminal work on resource competition mechanistically explained the outcomes of species competition for homogeneously distributed resources like nutrients. Huisman and Weissing (1994) extended this theory to competition for light as a heterogeneous resource for phytoplankton. However, these resource competition theories are inherently unsuitable to model the alternative stable states as described by Scheffer (1990; 1993) when using parameters complying with empirical knowledge (Supplementary material A). Yet, van Gerven et al. (2015) applied the theory of Huisman and Weissing (1994; 1995) in a layered macrophyte model where a floating layer causes light extinction above a submerged layer. Such a layered approach could also be suitable to mechanistically simulate phytoplankton suspended in the water column above submerged rooting macrophytes (Supplementary material B). Later, Chang et al. (2019a) combined these resource competition theories with knowledge from empirical and process-based approaches in the Generalically Parameterized model of Lake eutrophication (GPLake). This relatively simple model captures the amount of phytoplankton at equilibrium during summer in relation to nutrient loading for a nutrient-limited and light-limited phase by a Slope and Plateau parameter, respectively.

3.1.2 A novel model of alternative stables states

Here we present a novel, relatively simple, and mechanistically understandable model that describes alternative stable states in shallow lakes: GPLake-M. We aimed for a mathematically simple model that captures patterns of regime shifts between macrophyte- and phytoplankton-dominated states and gives a first estimate of the amount of macrophytes and phytoplankton, depending on the incoming nutrient loading. We focus on submerged macrophytes and phytoplankton because they play an important role in water quality assessments, yet similar mechanisms may apply to competition between submerged macrophytes and floating macrophytes or periphyton (Phillips et al. 1978; Scheffer et al. 2003). Furthermore, the model should comply with the graphical alternative stable states model of Scheffer (1990) with critical turbidity explaining regime shifts and include nutrients and light as major resources for competition (Tilman 1982; Huisman and Weissing 1994; 1995). During the model development we embraced the core principle of the GPLake model to link knowledge from empirical, theoretical and process-based approaches (Chang et al. 2019). The resulting GPLake-M model helps to estimate alternative stable states in shallow lakes whilst accounting for resource competition mechanisms and critical turbidity.

3.2 Methods

We build on the models and theories of Scheffer (1990), Tilman (1982), and Huisman and Weissing (1994; 1995) to develop one conceptual, graphical model for alternative stable states in shallow lakes: GPLake-M. Here M refers to macrophytes, which were not included in GPLake before. We specifically combined knowledge from empirical and theoretical literature on 1) the relation between light-limited macrophytes and nutrient-limited phytoplankton and 2) critical turbidity as a mechanism behind regime shifts. Next, a mathematical implementation of the graphical GPLake-M model was developed. Bifurcation analyses were performed with the process-based PCLake model to support the conceptual development and parameterization of GPLake-M. By this, knowledge from empirical, theoretical and process-based approaches are combined in the GPLake-M model. Lastly, GPLake-M and PCLake output were compared using a pattern-oriented strategy (Grimm et al. 2005) through bifurcation analyses. An R-file with the GPLake-M model code used for this comparison is provided (File 1).

3.2.1 Bifurcation analysis with PCLake

We selected the PCLake model as a reference to support the development of GPLake-M because it is empirically validated for shallow lakes and based on a detailed mechanistic understanding of lake ecology. Moreover, its major purpose is the same as for GPLake-M: to study regime shifts in shallow lakes (Janse, 2005). PCLake was developed, parameterized and empirically validated for 43 shallow European lakes (Janse et al. 2010). The model has been applied to explore climate change effects (Mooij et al. 2007), macrophyte mowing schemes (Kuiper et al. 2017) and implications of spatial hydrological and nutrient loading for ecological water quality (Janssen et al. 2019b). The extended version of PCLake+ is applicable for deep lakes (Janssen et al. 2019b) and includes floating and denitrifying cyanobacteria (Chang et al. 2020). Furthermore, the PCLake models have been applied to different climates (Coppens et al. 2020) and lake types (Janse et al. 2008; Janssen et al. 2017), and most recently to 9 lake types, representing 19.000 Chinese lakes (Janssen et al. 2021). Whereas PCLake is expanding in application range and complexity, we aimed for broad applicability whilst maintaining simplicity in the GPLake-M model. Because of our focus on regime shifts in shallow lakes, we used the bifurcation analysis function of the original PCLake model (File 2).

In a bifurcation analysis, equilibrium outcomes of a state parameter are determined over a range of stressor levels and, in the case of alternative stable states, for deviating initial states (Fig. 3.1). Here, PCLake output for summer averaged primary producer nutrient content was plotted against nutrient loading for initial clear and turbid states. Per functional group, these plots contain two nutrient-response curves: one for eutrophication (i.e., initial clear state) and one for oligotrophication (i.e., initial turbid state). First, the limiting factors for macrophytes and phytoplankton during hysteresis and the relation between them were assessed from these curves (Supplementary material C). Second, the critical extinction coefficient ($Ext_{crit,}$ -) at which regime shifts occur was determined by plotting extinction coefficient aExtTot (-) as a state parameter on the y-axis (Supplementary material D). Moreover, the nutrient-response curves were used to parameterize Slope and Plateau parameters that describe the relationship between the amount of primary producer and nutrient loading under nutrient and light limitation, respectively (Supplementary material E). Thirdly, patterns between GPLake-M and PCLake output were compared with a focus on 1) the scaling of the Slope and Plateau with hydraulic residence time and lake depth, 2) the value of the Plateau, and 3) the position of regime shifts on the nutrient loading axis. This pattern-oriented modeling strategy may help to find an optimal level of model complexity that falls in the "Medawar Zone" where model complexity is high enough to advance science but low enough to allow for understanding and practical applicability (Loehle 1990; Grimm et al. 2005).

The bifurcation analyses were run using the standard "bifurcation analysis function" in the PCLake model interface for a "standard lake" representing an 'average Dutch lake' (Table 3.1, set 1 in bold) (Janse 2005). A simulation period of 50 years was applied, at which the system is assumed to have reached equilibrium (Janse et al. 2008). During the parameterization and pattern-oriented model comparison, PCLake was also run for larger ranges of depth z (m) and hydrological loading Qin (mm d^{-1}) (sets 2-11 in Table 3.1). Either z or hydraulic residence time τ (d) was varied, whilst keeping the other parameters constant. The hydraulic residence time τ was estimated as z (with unit conversion to mm) divided by Qin. Whilst running GPLake-M for pattern-oriented output comparison, we assumed that nutrient loading is only caused by inflowing water and used a mass balance with nutrient retention in line with Vollenweider's normalized nutrient loading (see Supplementary material F and G, including an explanation of the addition of time scaling parameter s to ensure unit correctness).

3.3 Results

3.3.1 A graphical model of alternative stable states: GPLake-M

The GPLake-M model describes the amount of macrophytes and phytoplankton for a 1) nutrient-limited, 2) light-limited, and 3) zero-biomass phase. The order of these three phases and when a switch from one phase to the other occurs differ for macrophytes and phytoplankton, as well as for the initial ecological state (i.e., clear macrophyte-dominated versus turbid phytoplankton-dominated). These results are presented in a graphical model with four curves to describe alternative stable states in shallow lakes (Fig. 3.2).

Table 3.1. Sets of lake characteristics used as input in PCLake (depth z and hydrological loading Qin) and GPLake-M (depth z and hydraulic residence time τ), with the "standard lake" settings in bold. Blue and green shading indicates sets varying τ and z, respectively.

Set	z (m)	Qin (mm d^{-1})	τ (d)
1	**2**	**20**	**100**
2	2	40	50
3	2	16	125
4	2	13.3	150
5	2	5.5	364
6	1	10	100
7	1.5	15	100
8	2.5	25	100
9	3.5	35	100
10	4	40	100
11	5	50	100

3.3.1.1 The four curves of GPLake-M

The GPLake-M eutrophication curves show what happens when nutrient loading increases, starting from a clear macrophyte-dominated state (light lines and bars in Fig. 3.2). Rooted macrophytes take up nutrients from the sediment and water column (Granéli and Solander 1988), leaving less nutrients available for phytoplankton. Thereby, macrophytes suppress the

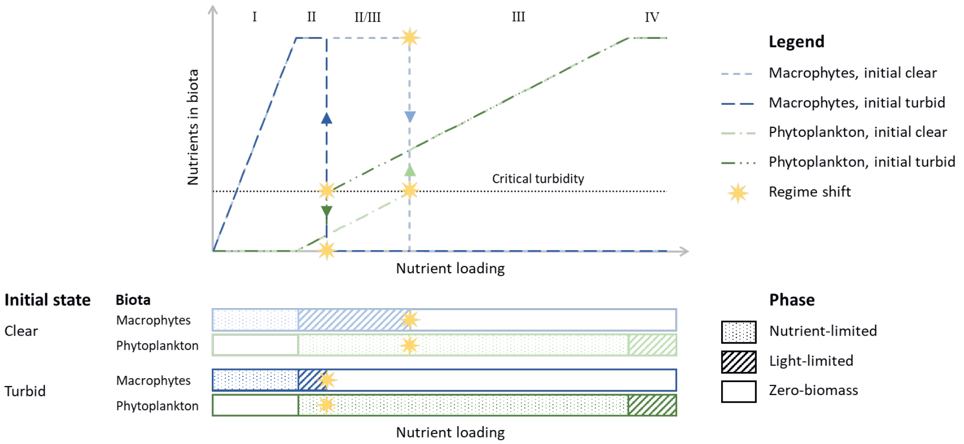


Figure 3.2. Graphical GPLake-M model showing the four nutrient-response curves for macrophytes with an initial clear state (light blue) and initial turbid state (dark blue), and phytoplankton with an initial clear state (light green) and initial turbid state (dark green). The critical turbidity (black dashed line) indicates the phytoplankton nutrient content at which regime shifts (yellow star) occur. Other changes in the shape of the nutrient-response curves correspond to switches between the nutrient-limited, light-limited and zero-biomass phases (bars at the bottom). The model consists of four equilibria sets that correspond with the unique combinations of limitation phases of macrophytes and phytoplankton (bars at the bottom): I) nutrient-limited macrophytes and zero-biomass phytoplankton, II) light-limited macrophytes and nutrient-limited phytoplankton, III) zero-biomass macrophytes and nutrient-limited phytoplankton, and IV) zero-biomass macrophytes and light-limited phytoplankton. Please see section 3.1.1 and 3.2.2 for a detailed description of the four curves and the mathematical description of the equilibria sets, respectively.

occurrence of phytoplankton and maintain a good light climate for their survival. At low nutrient loadings, this results in nutrient-limited macrophytes that outcompete phytoplankton. With increasing nutrient loading the amount of macrophytes increases until they become light-limited by self-shading. Once macrophytes reach the light-limited phase, un-retained nutrients are available for phytoplankton. Increasing amounts of available nutrients can now support phytoplankton growth (i.e., switching from zero-biomass to nutrient limitation). When the amount of phytoplankton reaches the critical turbidity, phytoplankton can outcompete the macrophytes through competition for light and a regime shift can occur. In a shallow, flat-bottomed lake this implies that macrophytes switch to the zero-biomass phase (Scheffer 1990). Without macrophytes, the phytoplankton have access to all the nutrients; the phytoplankton first are nutrient-limited and their amount increases with nutrient loading, once they become light-limited by self-shading they reach the light-limited phase (Wetzel 1988). Without macrophytes, phytoplankton follow the function of GPLake (Chang et al. 2019), which largely resembles the GPLake-M oligotrophication curve for phytoplankton.

The GPLake-M oligotrophication curves display the effect of nutrient load reduction, starting from a turbid phytoplankton-dominated state (dark lines and bars in Fig. 3.2). With oligotrophication, phytoplankton go from the light-limited into the nutrient-limited phase. In the nutrient-limited phase, the amount of phytoplankton decreases with nutrient load reduction. When the amount of phytoplankton drops below the critical turbidity, they can no longer suppress macrophytes through light limitation and a regime shift occurs (i.e., macrophytes switch from zero-biomass to light-limited phase). Now macrophytes suppress phytoplankton by reducing nutrient availability. When nutrient loading keeps decreasing beyond this regime shift, phytoplankton first continue to follow the same lower nutrient limitation curve as the phytoplankton eutrophication curve. Once the macrophytes become nutrient-limited and deplete all available nutrients, the phytoplankton will be outcompeted and reach the zero-biomass phase.

Two essential aspects of GPLake-M will be explained in more detail; 1) the relation between light-limited macrophytes and nutrient-limited phytoplankton in the hysteretic range, and 2) the critical turbidity that was first introduced by Scheffer (1990) to explain regime shifts.

3.3.1.2 The relation between light-limited macrophytes and nutrient-limited phytoplankton

The main mechanism to explain alternative stable states in shallow lakes is that macrophytes compete with phytoplankton for nutrients and phytoplankton compete with macrophytes for light (Scheffer et al. 1993). In multiple ways, macrophytes are the weaker competitors for light. First, by being suspended in the water column, phytoplankton will consume some of the light before it reaches the submerged rooting vegetation below them (Duarte 1995), as is the case for layered macrophyte communities (van Gerven et al. 2015). Second, phytoplankton use light more efficiently than macrophytes because of more efficient exposure of chlorophyll to light and higher chlorophyll concentrations (Sand-Jensen and Borum 1991). Therefore, macrophyte light requirement is larger than phytoplankton light requirement and macrophytes are light-limited sooner than phytoplankton. Accordingly, in GPLake-M the nutrient loading at which macrophytes switch from nutrient to light limitation will always be lower than that of phytoplankton (Fig. 3.2). For both species, the switch from nutrient to light limitation can be explained by increased self-shading with increased nutrient loading. Once macrophytes are light-limited, their growth and nutrient uptake will be limited despite increasing nutrient loading. This implies that some free nutrients will be available for phytoplankton growth in the presence of macrophytes. Indeed, low amounts of phytoplankton were found in most of the 18 studied Dutch clear shallow lakes when macrophyte coverage is >25% (Meijer et al. 1999). In GPLake-M this is reflected in the nutrient-limited phase of the initially clear phytoplankton curve up to the point where phytoplankton outcompete macrophytes by crossing the critical turbidity (light green line in Fig. 3.2). The same pattern is visible in PCLake output (Supplementary material C).

3.3.1.3 Critical turbidity as the mechanism behind regime shifts

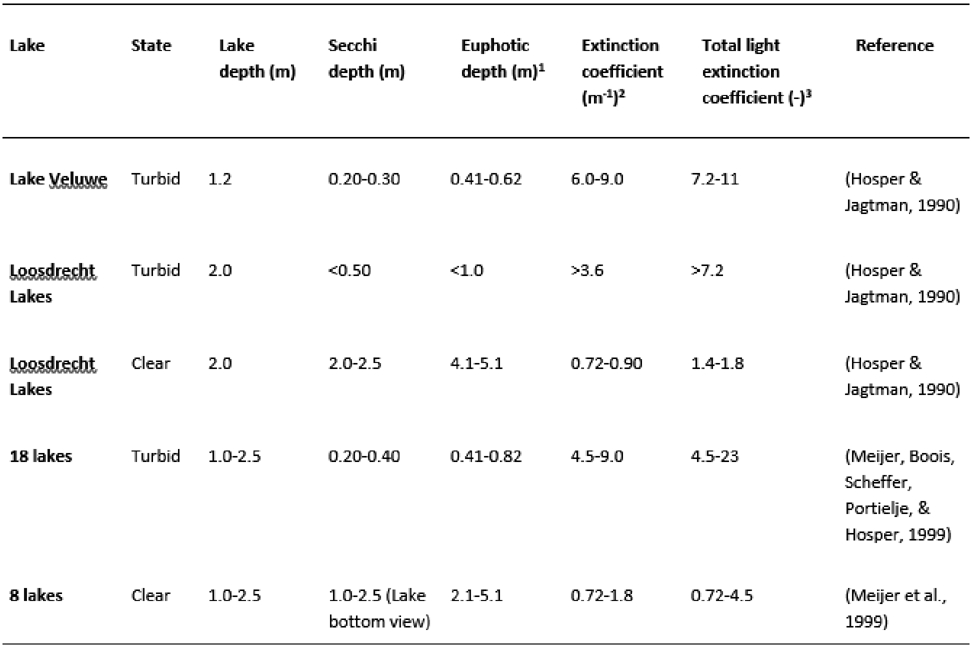
Critical turbidity can be understood from the total light extinction coefficient in Lambert Beer’s law, which was used in the light limitation model of Huisman and Weissing (1994) and is recognizable in PCLake output for a range of lake depths and hydrological loadings (Supplementary material D). Attenuated light is unavailable for macrophytes, therefore turbidity can limit macrophyte growth. The critical turbidity represents the total light extinction which disables macrophyte occurrence. The critical turbidity may help to explain the maximum colonization depth of submerged vegetation (sensu Middelboe and Markager (1997)) in lakes of varying depths. Here we assume that phytoplankton is the major source of light extinction, as was the case in Lake Wingra (Wisconsin, USA) in the mid-1970s (Jones et al. 1983). As such, it is an indicator of the high critical nutrient loading where phytoplankton outcompete macrophytes. Also, it can explain the low critical nutrient load. This is the nutrient loading where the turbidity, hence phytoplankton levels, will drop below the critical turbidity. At this point, macrophytes will receive sufficient light to establish themselves and they can outcompete phytoplankton by competition for nutrients. Thus, the light limitation-based concept of critical turbidity can mechanically explain both regime shifts. In GPLake-M the critical turbidity is expressed in areal phytoplankton P content (horizontal dotted line in Fig. 3.2).

The critical turbidity should be lower than turbidity levels that occur under phytoplankton dominance, and higher than the levels at which macrophytes can persist. Preferably the total light extinction coefficient is used as a measure of critical turbidity because it combines the depth-specific turbidity (i.e., extinction coefficient) and lake depth, which together determine how much light reaches the lake bottom to support macrophyte germination and growth (Penning et al. 2013). Nevertheless, the more commonly measured Secchi depth as a measure of transparency (i.e., reciprocal of turbidity) can be used to derive (total light) extinction coefficients (Table 3.2) (Wofsy 1983; Huisman and Weissing 1994).

In 20 turbid Dutch shallow lakes, Secchi depths between 20 and 50 cm were measured (Hosper and Jagtman 1990; Meijer et al. 1999) (Table 3.2). This is in line with a study of 100 northeast German lakes, where no or very few submerged macrophytes were found in lakes with a mean Secchi depth of 57 cm (Körner 2002). In 8 of the 20 Dutch lakes, biomanipulation by fish removal succeeded to achieve lake bottom views where macrophytes could grow (Meijer et al. 1999). The transparency levels of these 8 lakes (1.0-2.5

m) correspond with extinction coefficients of 0.72-1.8 m^{-1} and total light extinction coefficients of 0.72-4.5 (Table 3.2). Similarly, Penning et al. (2013) argue that macrophytes can potentially germinate at a total light extinction coefficient of <3.2. The Secchi depths of the 20 turbid lakes correspond with extinction coefficients of 3.6-9.0 m^{-1} and total light extinction coefficients of 4.5-23 (Table 3.2). Based on these Dutch lakes, the extinction coefficient for the critical turbidity is expected to lie between 1.80 and 3.6 m^{-1}. Following Phillips et al. (1978), this translates into a euphotic depth of 1.0-2.0 m. For an average Dutch lake of 2.0 m, this would imply a Secchi depth of 0.40-1.0 m and a critical total light extinction coefficient of 3.6-7.2.

Table 3.2. Overview of lake depth, Secchi depth, euphotic depth and (total light) extinction coefficients from studies on 20 unique shallow Dutch lakes, for a turbid and clear state if available.



Lake	State	Lake depth (m)	Secchi depth (m)	Euphotic depth (m)^1	Extinction coefficient (m^{-1})^2	Total light extinction coefficient (-)^3	Reference
Lake Veluwe	Turbid	1.2	0.20-0.30	0.41-0.62	6.0-9.0	7.2-11	(Hosper & Jagtman, 1990)
Loosdrecht Lakes	Turbid	2.0	<0.50	<1.0	>3.6	>7.2	(Hosper & Jagtman, 1990)
Loosdrecht Lakes	Clear	2.0	2.0-2.5	4.1-5.1	0.72-0.90	1.4-1.8	(Hosper & Jagtman, 1990)
18 lakes	Turbid	1.0-2.5	0.20-0.40	0.41-0.82	4.5-9.0	4.5-23	(Meijer, Boois, Scheffer, Portielje, & Hosper, 1999)
8 lakes	Clear	1.0-2.5	1.0-2.5 (Lake bottom view)	2.1-5.1	0.72-1.8	0.72-4.5	(Meijer et al., 1999)

[1] Calculated based on Phillips et al. (1978): Euphotic depth is 3.7 divided by extinction coefficient; [2] Calculated based on Wofsy (1983): Extinction coefficient is 1.8 divided by Secchi depth; [3] Calculated based on Huisman and Weissing (1994): Total light extinction coefficient is extinction coefficient times lake depth

3.3.2 A mathematical GPLake-M model

A mathematical implementation of the graphical GPLake-M model (see MS Excel tool in File 3) was developed in an approach similar to that of GPLake (Chang et al. 2019). GPLake estimates the maximum amount of phytoplankton biomass during summer (W^*, mg chl-*a* m^{-3}) per inflowing resource concentration (R_{in}, mg m^{-3}) during nutrient and light limitation (see Supplementary material H for the mathematical derivation based on the model by Huisman and Weissing (1994; 1995)). It follows Liebig's law of the minimum, meaning that either nutrients or light are limiting. This results in a nutrient-response curve with a sloping phase during nutrient limitation and a constant biomass plateau during light limitation (Chang et al. 2019). The first parameterization of GPLake focused on phosphorus (P) as a major limiting nutrient (Chang et al. 2019), later the model was applied for colimitation by P and nitrogen as well (Chang et al. 2022). In GPLake-M both, the amount of phytoplankton and macrophytes at equilibrium, are described by a Slope (days) during nutrient limitation and a Plateau (g m^{-2}) during light limitation. Where GPLake expresses the amount of primary producer in biomass concentration (i.e., chl-*a* per volume), GPLake-M uses areal nutrient content of phytoplankton (i.e., amount of nutrients per surface area) to enhance unity between macrophytes and phytoplankton. From here on we will focus on P as a specific form of nutrient "R" in GPLake-M, because P often is the major limiting nutrient in freshwater ecosystems (Vollenweider and Kerekes 1982; Hecky and Kilham 1988; Håkanson et al. 2007).

3.3.2.1 New model parameters

Compared to GPLake, GPLake-M only needs two new parameters to capture regime shifts between phytoplankton and macrophytes: Critical turbidity (Pcrit) and macrophyte Slope ($Slope_{macr}$). Pcrit is used to mechanistically describe the regime shifts. In GPLake-M, Pcrit is parameterized as a critical phytoplankton P content of 0.073 g P m^{-2}, derived from an average critical extinction coefficient of 6.4 from PCLake output (Supplementary material

Table 3.3. GPLake-M symbols with unit and description.

Symbol	Unit	Description	Category
Pcrit	g P m^{-2}	Critical P content of phytoplankton (i.e., a measure of critical turbidity)	Biological parameter
Pi	g P m^{-2}	Areal P content of species i macrophytes (macr) or phytoplankton (phyt)	Output variable
Pload	g P m^{-2} d^{-1}	Areal P loading	Input variable
$Slope_i$	d	Areal P content of species i over areal P loading at equilibrium during nutrient-limited phase	Biological parameter
$Plateau_i$	g P m^{-2}	Areal P content of species i at equilibrium during light-limited phase	Biological parameter

D). This value falls in the empirical range expected for Dutch shallow lakes (see 3.1.3). $Slope_{macr}$ is required to express the amount of macrophytes during nutrient limitation, similar to the Slope for phytoplankton in GPLake. A standard lake in PCLake was used to parameterize the Slope during nutrient limitation and the Plateau during light limitation using GPLake-M units. For macrophytes a constant $Slope_{macr}$ of 237 d, and for phytoplankton a $Slope_{phyt}$ of 47.3 d was found (Supplementary material E). Depending on one's need, the $Slope_{phyt}$ can be applied as a constant or variable (see Supplementary material D and section 3.3). For the light-limited phase, a modeling experiment with PCLake showed that the Plateaus of macrophytes and phytoplankton are similar over a range of lake depths (1-5 m) and hydrological loadings (uQin, 5.5-40 mm d^{-1}; covering a residence time range of 50-364 d) (Supplementary material C). Therefore, no additional macrophyte Plateau parameter value ($Plateau_{macr}$) was required. Here we parameterized the Plateau as 0.259 g P m^{-2} (Supplementary material E). An overview of the major symbols and units from GPLake-M is provided in Table 3.3.

3.3.2.2 Model equilibria

The macrophyte and phytoplankton equilibrium curves of GPLake-M (with * denoting equilibrium) are divided into four sets, based on combinations of the possible limitation-phases of macrophytes and phytoplankton in the graphical model (Roman numbers in Fig. 3.2):

Set I: Nutrient-limited macrophytes - Zero-biomass phytoplankton:

$$Pmacr^* = Slope_{macr} \times Pload \qquad \text{Eq. (3.1a)}$$

$$Pphyt^* = 0 \qquad \text{Eq. (3.1b)}$$

Set II: Light-limited macrophytes - Nutrient-limited phytoplankton:

$$Pmacr^* = Plateau_{macr} \qquad \text{Eq.(3.2a)}$$

$$Pphyt^* = Slope_{phyt} \times (Pload - \frac{Plateau_{macr}}{Slope_{macr}}) \qquad \text{Eq.(3.2b)}$$

Set III: Zero-biomass macrophytes - Nutrient-limited phytoplankton:

$$Pmacr^* = 0 \qquad \text{Eq.(3.3a)}$$

$$Pphyt^* = Slope_{phyt} \times Pload \qquad \text{Eq.(3.3b)}$$

Set IV: Zero-biomass macrophytes - Light-limited phytoplankton:

$$Pmacr^* = 0 \qquad \text{Eq.(3.4a)}$$

$$Pphyt^* = Plateau_{phyt} \qquad \text{Eq.(3.4b)}$$

The P loading at which a transition between these sets occur are defined by four switch points:

$$I \longleftrightarrow II = \frac{Plateau_{macr}}{Slope_{macr}} \qquad \text{Eq. (3.5a)}$$

$$II \rightarrow III = \frac{Plateau_{macr}}{Slope_{macr}} + \frac{Pcrit}{Slope_{phyt}} \qquad \text{Eq. (3.5b)}$$

$$II \leftarrow III = \frac{Pcrit}{Slope_{phyt}} \qquad \text{Eq. (3.5c)}$$

$$III \leftarrow\rightarrow IV = \frac{Plateau_{phyt}}{Slope_{phyt}} \qquad \text{Eq. (3.5d)}$$

When switches points $\mathrm{II} \rightarrow \mathrm{III}$ and $\mathrm{II} \leftarrow \mathrm{III}$ differ, hysteresis occurs.

Here Pcrit, Slopes and Plateaus were parameterized based on PCLake output. These parameters can also be mechanistically understood and described by the equilibrium solutions of a basic set of differential equations (Supplementary material I).

3.3.3 Pattern-oriented comparison

We performed a pattern-oriented comparison of GPLake-M and PCLake output for a range of hydraulic residence times τ (d) and depths z (m) (sets 1-5, 7, 8, 10 and 11 in Table 3.1). For GPLake-M, here we assumed the scenario of Vollenweider-type nutrient retention with s is 81 d, derived from a parameterized $\mathrm{Slope_{phyt}}$ of 47.3 and a $\mathrm{D_{in}}$ of 0.01 in GPLake-M (Supplementary material F and G). In this scenario, GPLake-M captures the main patterns from PCLake considering 1) scaling, 2) Plateau values, and 3) regime shifts (Fig. 3.3-3.6). 1) In the nutrient-limited phase, $\mathrm{Slope_{phyt}}$ of both models increase with τ (Fig. 3.3). Although the areal P contents sometimes deviate slightly between the two models, the Slopes of macrophytes and phytoplankton of both models resemble each other well for the tested range of τ and z (Fig. 3.3-3.6). In GPLake-M the Plateau does not scale with τ and z, whereas it does in PCLake. Nevertheless, $\mathrm{Plateau_{phyt}}$ of GPLake-M roughly corresponds with the peak and leveling off of the phytoplankton P content from PCLake for τ 100-364 d and z 1.5 and 2 m (Fig. 3.3). Moreover, $\mathrm{Plateau_{macr}}$ from GPLake-M falls within the PCLake macrophyte P content peak at the hysteric phase for the tested range of τ (Fig. 3.5) and z 1.5-2.5 m (Fig. 3.6). At larger depths, GPLake-M somewhat overestimates the Plateaus relative to PCLake (Fig. 3.4 and 3.6). 3) The nutrient loadings at which the regime shifts occur are comparable among both models for all tested τ's (Fig. 3.3 and 3.5). However, beyond the range of z 2-2.5 m these results deviate between both models, since GPLake-M is independent of z and PCLake is not (Fig. 3.4 and 3.6).

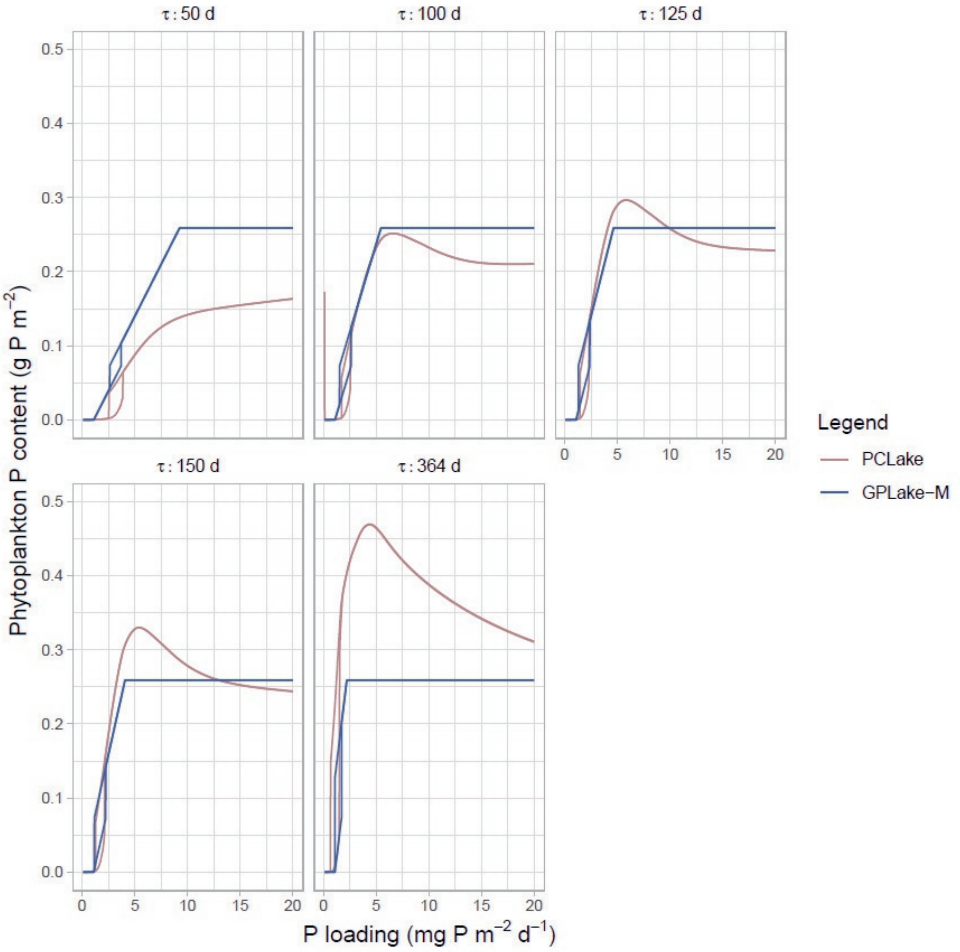


Figure 3.3. Comparison of GPLake-M (blue) and PCLake (red) phytoplankton P content per residence time (τ: 50-364 d) for depth 2m (set 1-5, Table 3.1), assuming the scenario in GPLake-M of Vollenweider-type nutrient retention. For a range of τ values, the models resemble each other in terms of Slope, P content at the Plateau, and critical nutrient loadings.

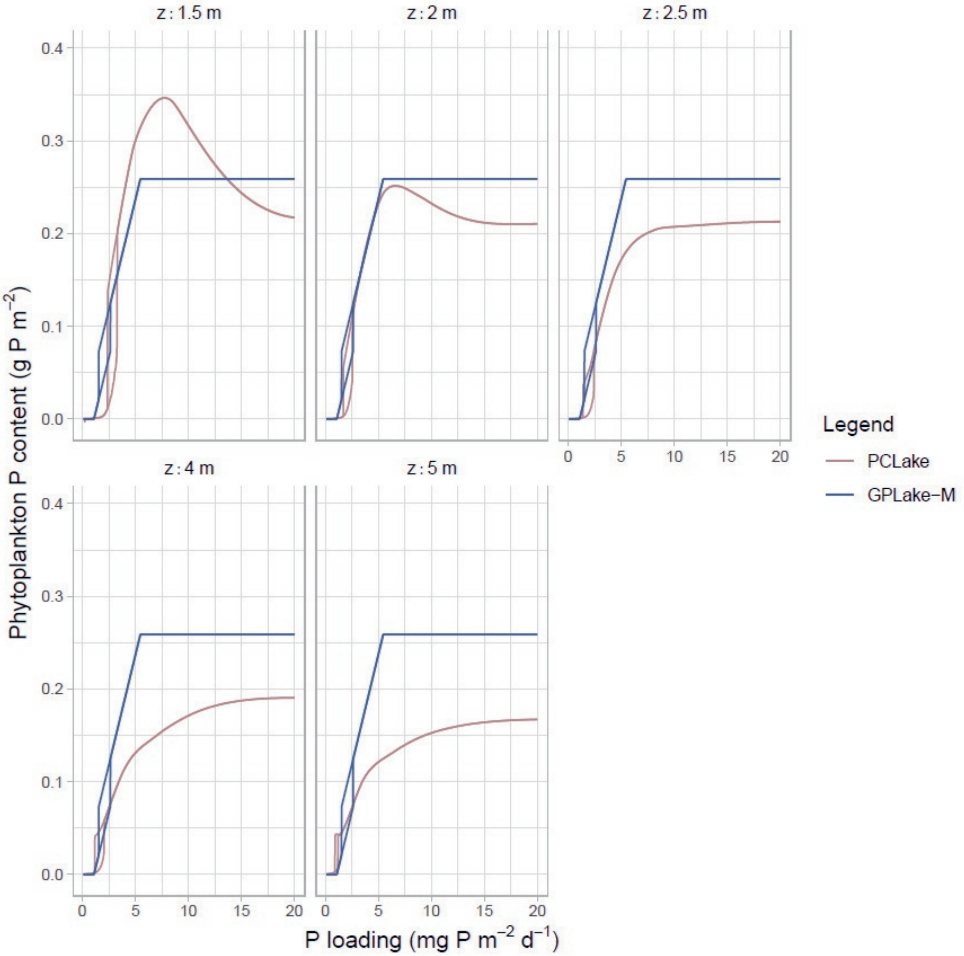


Figure 3.4. Comparison of GPLake-M (blue) and PCLake (red) phytoplankton P content per depth (z: 1.5-5 m) with a constant hydraulic residence time of 100 d (set 1, 7, 8, 10 and 11, Table 3.1), assuming the scenario in GPLake-M of Vollenweider-type nutrient retention. For a range of z values, the models resemble each other in terms of Slope. The models differ in the relation between z and critical nutrient loadings, and z and P content at the Plateau.

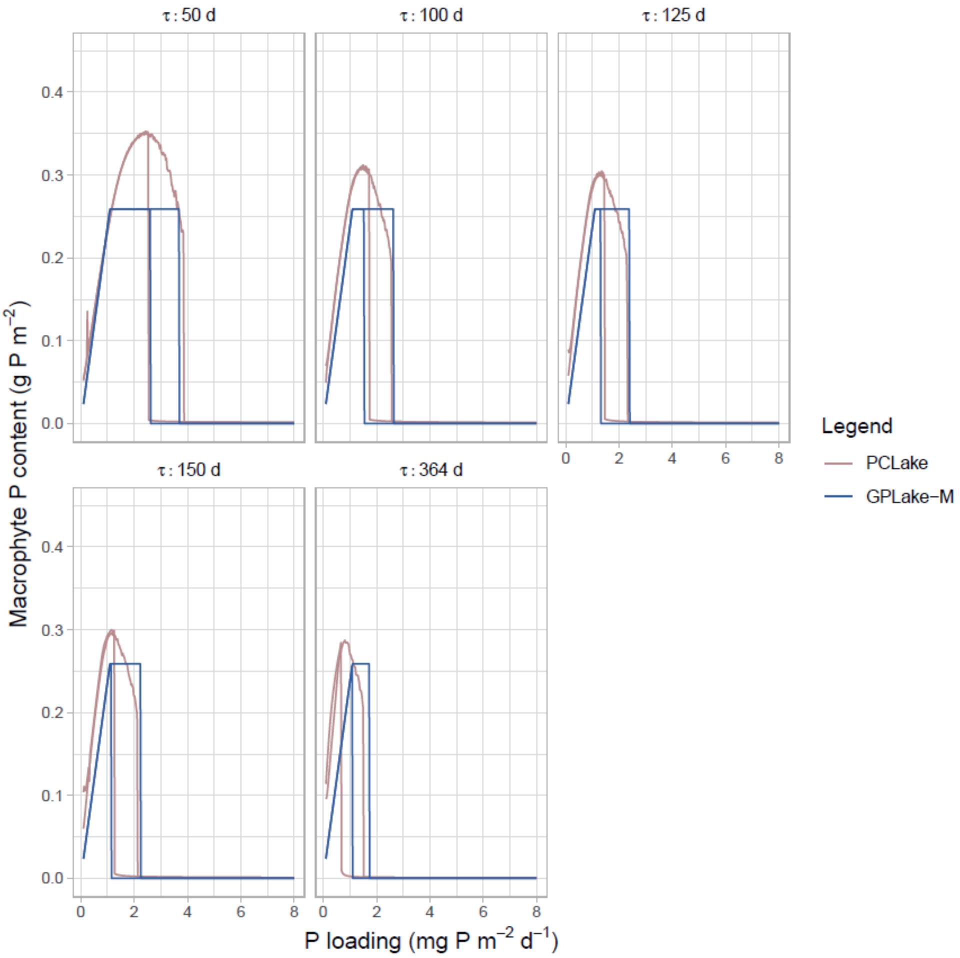


Figure 3.5. Comparison of GPLake-M (blue) and PCLake (red) macrophyte P content per residence time (τ: 50-364 d) for depth 2m (set 1-5, Table 3.1), assuming the scenario in GPLake-M of Vollenweider-type nutrient retention. For a range of τ values, the models resemble each other in terms of Slope, P content at the Plateau, and critical nutrient loadings.

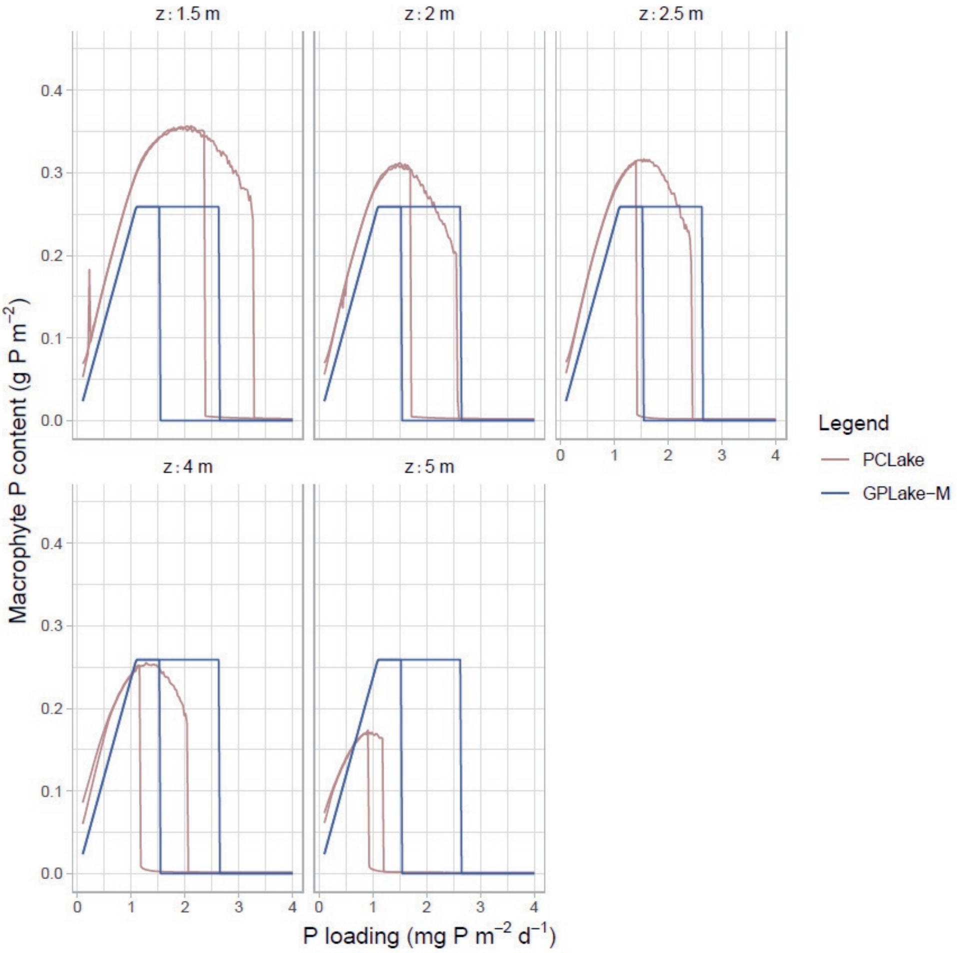


Figure 3.6. Comparison of GPLake-M (blue) and PCLake (red) macrophyte P content per depth (z: 1.5-5 m) with a constant hydraulic residence time of 100 d (set 1, 7, 8, 10 and 11, Table 3.1), assuming the scenario in GPLake-M of Vollenweider-type nutrient retention. For a range of z values, the models resemble each other in terms of Slope. The models differ in the relation between z and critical nutrient loadings, and z and P content at the Plateau.

3.3.4 Application of GPLake-M

The application of GPLake-M requires the initial state, current P loading, hydraulic residence time and depth of the system as input parameters. We added an MS Excel tool of GPLake-M as Supplementary material (File 3) to showcase the application of GPLake-M to estimate alternative stable states in shallow lakes whilst accounting for resource competition mechanisms and critical turbidity. After entering the input parameters, GPLake-M directly shows the estimated amount of macrophytes and phytoplankton, and the equilibrium set for the studied lake. A graph visualizes the output of GPLake-M, including the critical nutrient loadings and ecosystem state at the current P loading. In this tool, we provide a detailed example of the application of GPLake-M for a hypothetical lake of 2 m depth and a hydraulic residence time of 100 days, using the scenario of Vollenweider-type nutrient retention. We set the initial state as clear and the current nutrient load as 2 mg P m^{-2} day^{-1}, resulting in equilibrium set II of GPLake-M.

3.4 Discussion

3.4.1 The position of GPLake-M in the model-spectrum

GPLake-M is a mechanistically interpretable model that captures regime shifts between macrophyte- and phytoplankton-dominated states through Scheffer's (1990) concept of critical turbidity. It is a relatively simple model, consisting of only a few equations and parameters with empirical meaning, by combining knowledge from empirical, theoretical and process-based approaches. Like GPLake, GPLake-M can help to get a first insight into the potential ecological conditions of a lake and directions for solutions (e.g., decreasing the nutrient loading or managing lake characteristics) (Chang et al. 2019), for example in global assessments. More specifically, with GPLake-M users can estimate whether alternative stable states will occur in shallow lakes and whether light or nutrients are limiting. By this, GPLake-M helps to understand the dynamics underlying regime shifts in shallow lakes. Please see section 3.4.3 for more details on which value the model may have for different users.

The relative simplicity of GPLake-M stands in contrast with more complex models. There are many technically complex models of primary producers. For example, the WEED (Titus et al. 1975), HYDRIL and MILFO (Best et al. 2001) and AquaVenus (de Klein 2008) models help to predict the amount of macrophytes for a lake, rivers, and streams, respectively. These models are more complex than GPLake-M by, for example, including depth distribution of macrophyte biomass (Titus et al. 1975), specified phenologies (Best et al. 2001) or multiple nutrient forms (de Klein 2008). Besides, empirical models might be more complex than GPLake-M in terms of explaining variables (e.g., showing the importance of total nitrogen to total P ratio, temperature and salinity for cyanobacteria (Håkanson et al. 2007)). Models that combine macrophytes and phytoplankton are rarer and even more complex. For example, a model integration of the Yuqiao Reservoir Water Quality Model with the macrophyte submodel M-SAVM (Zhang et al. 2016) also includes total suspended solids and distinguishes macrophyte shoots and roots. And the ecosystem model PCLake(+) includes many more ecological processes, for example, related to zooplankton and fish (Janse, 2005; Janssen 2019). In some cases, the inclusion of the food-web may be essential to capture nutrient-response curves as observed in the field (Poikane et al. 2022), nevertheless GPLake-M captures the main patterns from the ecosystem model PCLake.

GPLake-M fits into the niche of relatively simple and mechanistically understandable models. Within this niche other models for alternative stable states exist with layered communities of macrophytes (van Gerven et al. 2015), and benthic and pelagic algae (Jäger and Diehl 2014). These two models specify background extinction and water column depth for submerged or pelagic species. Moreover, Jäger and Diehl (2014) distinguish between uptake from a sediment and water nutrient pool. This makes the dynamics of these models more complex than the GPLake-M model presented here. Additionally, Phillips et al. (1978) hypothesized that phytoplankton can cause macrophyte decline by shading in a macrophyte-periphyton-phytoplankton system and this was modeled by Hilt et al. (2018). An essential commonality between GPLake-M and these alternative stable state models and hypothesis is that they all include the effect of light consumption by one primary producer on the availability of light for the other primary producer. With GPLake-M we demonstrate that this is the core mechanism to describe and understand the alternative stable states of macrophyte and phytoplankton dominance in shallow lakes. Additional model complexity (e.g., including the food-web) may increase the feeling of ecological realism and help to fine-tune model outcomes, but is less essential and may be beyond the Medawar zone for model complexity depending on the research question.

3.4.2 Limitations of GPLake-M

In this study GPLake-M is parameterized for lakes with τ 100 and z 2 m and it matches reasonably well with PCLake over a range of τ (50-364 d) and z (1.5-5 m). Therefore, GPLake-M applies to a range of shallow lakes. Beyond the tested range, model performance is expected to decrease because of a larger divergence from the standard lake for which GPLake-M is currently parameterized. The application range of the model may be extended by examining the coupling strength of nutrient and water flows of the systems and thereby choosing the most relevant scaling scenario (Supplementary material F). However, for deep lakes different modeling approaches may be required because other mechanisms such as stratification (Janssen et al. 2019a) may be more relevant for water quality managers. Still, the presented GPLake-M model captures the main patterns from PCLake for temperate shallow lakes, which is sufficient for the model to be used as an educational tool, a building block to model hydrological networks and an agenda- setter (see section 3.4.3). In the future, the model can also be calibrated using larger datasets with multiple data types (i.e., field, lab and model). Moreover, building-up a library of Slope and Plateau parameter values for a range of lake characteristics (e.g., sediment type or climate) could help to extend the application range of GPLake-M. Because the model is relatively simple but potentially widely applicable, it is expected to be especially valuable in cases where many lakes need to be assessed (e.g., global scale) or when limited data and knowledge is available. In such cases, the generic insight from GPLake-M may help to advance knowledge and give first directions for water quality management.

3.4.2.1 Slopes and Plateaus

For additional parameterization of Slopes and Plateaus one should note that the definition of nutrient- and light-limited phases in datasets is arbitrary and therefore a range of Slope and Plateau values can be obtained. Moreover, assumptions on nutrient retention dynamics and how nutrient and water flows are coupled or decoupled will influence how the Slope scales with model parameters like τ (Supplementary material F). Also, $\text{Plateau}_{\text{macr}}$ can be parameterized separately and directly applied in GPLake-M, releasing the assumption that the macrophyte Plateau equals the phytoplankton Plateau. This might be relevant when applying GPLake-M beyond the range of lake characteristics that this assumption was tested for (z 1-5 m and Qin 5.5-40 mm d^{-1}, covering a τ range of 50-364 d; Supplementary material C). Thus, when reparametrizing Slopes and Plateaus for a different range of lake characteristics, it is recommended to reconsider these assumptions and to reassess new model output against a representative sample.

The current GPLake-M macrophyte Plateau of 0.259 g P m^{-2} falls well within the mean summer values for submerged macrophytes of 0.105-0.372 g P m^{-2} reported by Blindow (1992) and the phytoplankton Plateau of 0.259 g P m^{-2} is close to the 0.28 P m^{-2} of algae in the Dutch “Bergse plassen” (Jaarsma et al. 2008). Studies reporting areal P contents of phytoplankton are limited, probably because phytoplankton abundance is commonly measured per volume and in biomass or chl-*a* units rather than P content. In GPLake-M areal P contents are used to enhance the comparison between macrophytes and phytoplankton. For this we performed a unit conversion in PCLake to go from volumetric to areal phytoplankton P content (equation C.1 in Supplementary material C). A similar unit conversion of measured volumetric phytoplankton P contents would allow more thorough empirical validation of the phytoplankton Plateau. However, this is complicated by the lack of case-specific data on phytoplankton P content to chl-*a* ratio in existing field studies focused on chl-*a* levels (e.g., in Hosper and Jagtman (1990) and Meijer et al. (1999)).

3.4.2.2 Critical turbidity

Critical extinction was derived from PCLake output and converted to critical P content as a measure of critical turbidity that directly relates to phytoplankton P content. The critical turbidity can also be empirically measured, for example as a critical extinction level. However, results may deviate between studies by differences in macrophyte species for their critical extinction (Middelboe and Markager 1997; Best et al. 2001), the season of measurement (Jones et al. 1983), and definition of critical extinction. For example, a short-lived clear-water phase with extinction coefficients of 1-2.5 m^{-1} during the critical period for plant growth, facilitated a strong increase in submerged macrophyte occurrence in the shallow prairie lake Lake Christina (Minnesota, USA) (Hanson and Butler 1990). Similarly, Best et al. (2001) reported that macrophytes can just persist at an extinction coefficient of 2 m^{-1} in eutrophic fen lakes in a temperate climate. A modeling study for Lake Wingra (Madison, Wisconsin, USA) (Titus et al. 1975) and a Japanese field study (Takamura et al. 2003) show that macrophytes cannot grow at extinction coefficients of 2.5-6 m^{-1}. Compared to these studies, the extinction coefficient of 3.2 m^{-1} used for GPLake-M is relatively high. This may be explained by broader definitions of critical turbidity under field conditions, for example, including light scattering and sorption by sediment (Van Duin et al. 2001; Zhang et al. 2006) and epiphytes (Phillips et al. 1978; Jones et al. 1983), and energy storage to maintain macrophyte populations (Sand-Jensen and Borum 1991). For conceptual simplicity, in GPLake-M we focused on turbidity by phytoplankton, in line with Scheffer (1990). The parameterization is based on outcomes from PCLake that are rather robust, as they are applicable for a range of depths (0.5-5 m) and hydrological loadings (5.5-40 mm d^{-1}) (Supplementary material D). More complex GPLake-M equilibrium solutions that include the effect of background turbidity can be derived from the underlying differential equations (Supplementary material I).

3.4.3 Societal and scientific relevance of GPLake-M

3.4.3.1 GPLake-M as an educational tool and building block

Our results support a fundamental understanding of regime shifts in shallow lakes and provide a starting point for further mechanistic and management-focused explorations and model development. First of all, theoreticians might be interested in the relationship between Scheffer (1990) critical turbidity as the key mechanism underlying alternative stable states in shallow lakes and the fundamental theory of nutrient and light competition by Tilman (1982), and Huisman and Weissing (1994; 1995), respectively (Supplementary material A). For managers, GPLake-M provides a first estimate of a lake's ecological state and can be used to explore management options that influence lake characteristics (e.g., z and τ) or nutrient loading. Additionally, the mechanistic mini-model can be modified and expanded by students and modelers, without getting lost in numerous parameters and processes. For example, by working with GPLake-M students can explore the mechanisms of regime shifts through critical turbidity, instead of being faced with the indirect effect of nutrient loading that is derived from many processes captured in complex ecosystem models. Because of its mechanistic basis and the inclusion of nutrient retention in the mass balance equations, GPLake-M can be used as a building block to explore regime shifts in hydrological networks up to a basin-scale (Tang et al. 2019) as proposed for the development of Smart Nutrient Retention Networks (van Wijk et al. 2021). Additionally, it can be extended with components of interest, for example, zooplankton, sediment, temperature effects or harvesting of macrophytes. We expect such extensions would not affect the core mechanisms of GPLake-M and would only cause some shifts in the model curves. When diving into the mass balance equations underlying the equilibrium equations of GPLake-M

(Supplementary material F), also the effect of (de)coupling of water and nutrient flows can be explored.

3.4.3.2 GPLake-M as an agenda-setter

The concept of critical turbidity and the relation between light-limited macrophytes and nutrient-limited phytoplankton might provide a new focus for empirical aquatic ecological research and water quality monitoring programs. For empirical aquatic ecologists, it might be interesting to focus their research on key parameters of GPLake-M and the assumptions underlying the model. For example, critical turbidity can be empirically measured under controlled lab or field conditions by mesocosm or exclosure experiments on light requirements for macrophytes to survive in summer or to germinate and establish themselves in spring (e.g., the shading experiment by van Dijk and Vierssen (1991)). Such measurements for a range of lake characteristics and environmental conditions can help to calibrate GPLake-M for broader datasets to increase its application range. Similarly, empirical studies can help building-up a library of Slope and Plateau parameter values for a range of lake characteristics and test the assumption that the macrophyte and phytoplankton Plateaus are equal. Furthermore, our results may give water quality managers directions for measurements in monitoring programs. The concept of critical turbidity shows that it might be useful to measure light climate as a direct driver of regime shifts instead of nutrient levels. The light climate is easier to measure (e.g., by Secchi disk) than the nutrient balance of a whole lake system. It also offers opportunities for high-frequency lake monitoring, for example, by common photosynthetically active radiation sensors with options for automated cleaning (McBride and Rose 2018). This approach may help to detect the early rise of phytoplankton (i.e., turbidity) when macrophytes are light-limited, before the regime shift to phytoplankton dominance occurs. If confirmed by more empirical studies, this may provide an early warning signal for impending regime shifts to phytoplankton dominance.

3.5 Conclusion

We presented a novel approach to describe regime shifts in shallow lakes that is rooted in resource competition theory and the concept of critical turbidity. This approach has multiple levels of complexity that can be explored and applied depending on one's wishes and needs. The main results are the graphical (Fig. 3.2) and mathematical (section 3.3.2.2) GPLake-M model describing regime shifts in temperate shallow lakes by critical turbidity. The mathematical model gives the macrophyte and phytoplankton equilibria depending on the limiting factors and can easily be applied by the MS Excel Tool of GPLake-M (section 3.3.4). We also supplied the ordinary differential equations underlying these equilibria (Supplementary material I) and a generalized mass balance equation that can be applied to various (nutrient retention) scenarios (Supplementary material F).

We believe that GPLake-M is relatively simple and mechanistically understandable and can help to advance our understanding and the management of regime shifts in temperate shallow lakes. The model captures the main patterns from the lake ecosystem model PCLake. Moreover, based on just four lake characteristics, GPLake-M can practically help to estimate whether alternative stable states occur and whether light or nutrients are limiting. By applying the concept of critical turbidity, it advocates a stronger focus on light conditions in empirical aquatic ecological research and water quality monitoring programs. We foresee an educational role of GPLake-M to raise a new generation of water quality managers with an understanding of ecological mechanisms underlaying alternative stable states in shallow lakes. This understanding will help to make informed decisions to protect and restore lake ecosystems and the services they provide, like drinking water provision and recreation.

Acknowledgments

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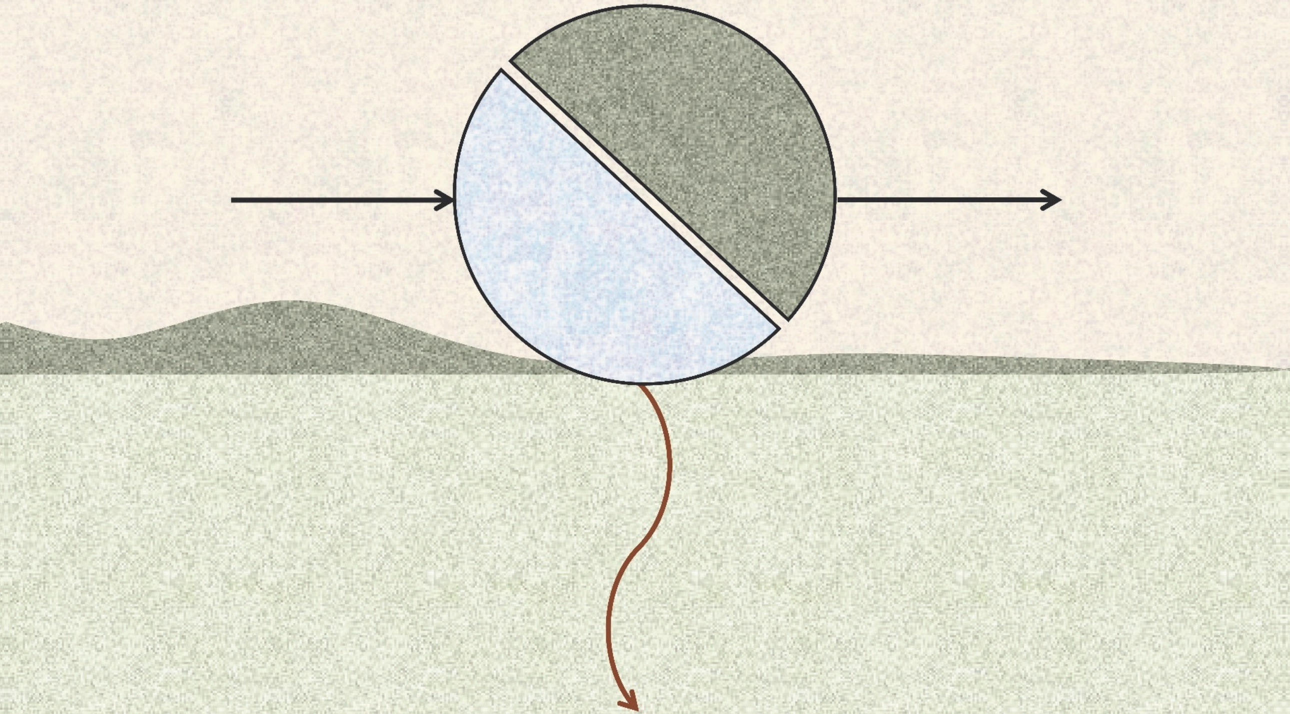
Chapter 4

A versatile process-based model of nutrient retention in relation to ecosystem state in shallow lakes: GPLake-R



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Abstract

Nutrient pollution of surface waters contributes to eutrophication problems and constitutes a loss of valuable resources for human food production. Nutrient retention in lakes prevents part of this loss and downstream pollution, and depends on the ecosystem state. This dependency of a waterbody's nutrient retention capacity on ecosystem state is one of the key aspects of Smart Nutrient Retention Networks, with macrophyte-dominated lakes having higher phosphorus retention than phytoplankton-dominated lakes. To support the development of such nutrient retention focused management strategies, we aimed to develop a simple and versatile dynamic model of nutrient retention in relation to ecosystem state in shallow lakes that combines insights from resource competition theory. Here, we present the GPLake-R model, with the "GP" standing for "generically parameterized" and “R” standing for “retention”. Like GPLake-M, GPLake-R describes equilibrium macrophyte and phytoplankton abundance in shallow lakes in response to nutrient loading, but with the added ecologically relevant options for co-limitation of nutrients and light in macrophytes and phytoplankton and coexistence of macrophytes and phytoplankton around critical nutrient loadings. As an outcome, GPLake-R gives a single equation for phosphorus retention in relation to ecosystem state that captures the hysteretic pattern from the more complex PCLake model. Finally, we provide the differential equations that lead to these equilibrium outcomes. We believe that the GPLake-R model can be used to develop a model tool to support water quality management strategies for networks of surface waters.

4.1 Introduction

Nutrient losses into hydrological networks have multiple drawbacks, ranging from the degradation of surface water quality to the loss of nutrients as valuable resources for human food production once they are washed out into the seas and oceans. Lentic waters - such as lakes and reservoirs - experience eutrophication but at the same time prevent the loss of nutrients, especially phosphorus (P), to downstream systems by biogeochemical nutrient retention (Maranger et al. 2018). Recently, the Smart Nutrient Retention Networks concept, focused on nutrient retention in hydrological networks, was proposed as an approach to contribute to the conservation of nutrients by water quality improvement (van Wijk et al. 2021). One core principle in this approach is that the nutrient retention capacity of a waterbody depends on its ecosystem state and the ecosystem state on the nutrient loading (Rast and Lee 1978; Ahlgren et al. 1988; Hilt et al. 2017; van Wijk et al. 2021). In this study, we focus on the higher nutrient retention in the submerged macrophyte- over the phytoplankton-dominated ecological state of shallow lakes (Hilt et al. 2017).

4.1.1 Models of nutrient retention in relation to ecosystem state

Aquatic nutrient retention models are valuable tools to support the development of Smart Nutrient Retention Network management strategies if they include the feedback between nutrient loading, ecosystem state, and nutrient retention. Most contemporary large-scale models lack detail on the level of nutrient retention processes in relation to ecosystem state, and local-scale models tend to be too focused on a specific case (van Wijk et al. 2021). As a result, there are only a few models that include the mechanisms underlying these feedback (e.g., PCLake (Janse 1997)), but it is complicated and time consuming to apply them to networks of connected waterbodies. On the other hand, a simple spatially explicit model of regime shifts in shallow lakes exists but this model is not based on nutrient mass balances and does not explicitly include nutrient retention (Hilt et al. 2011). Therefore, we here aimed to develop a relatively simple and versatile dynamic model of nutrient retention under submerged macrophyte versus phytoplankton dominance in shallow lakes that also adheres to the principle of mass conservation and combines insights from resource competition theory.

In the 1990s, the alternative stable states of either macrophyte or phytoplankton dominance in shallow lakes and the underlying mechanisms were described by a feedback diagram (Scheffer et al. 1993). Thereafter, Janse (1997) developed the PCLake model to mechanistically simulate the rapid shifts (i.e., regime shifts) between these ecosystem states, and the critical nutrient loadings at which these shifts occur. This model also embodies the hysteretic range in which the equilibrium ecosystem state depends on the initial ecosystem state (i.e., clear, macrophyte-dominated or turbid, phytoplankton-dominated) (Janse 1997). More recently, the patterns from the PCLake model and empirical observations (Jeppesen et al. 1990; Scheffer et al. 1993) were captured by the relatively simple and mechanistically understandable GPLake-M model (van Wijk et al. 2023). This model combines insights from theory by Scheffer et al. (1993), Tilman (1982), and Huisman and Weissing (1994; 1995) to estimate the equilibrium ecosystem state in temperate shallow lakes on basis of the concept of critical turbidity (van Wijk et al. 2023).

However, the GPLake-M model is not yet suitable to apply to networks of shallow lakes because the model does not yet calculate nutrient retention. Moreover, GPLake-M lacks some aspects of ecological competition with consequences for nutrient retention. First, the use of a minimum function (following Liebig’s Law of the minimum) for the transition between nutrient and light limitation of each primary producer in GPLake-M results in abrupt transitions from nutrient to light limitation and ignores potential co-limitation of these resources (Huisman and Weissing 1995; Burson et al. 2018). Second, while in line with theory on catastrophic regime shifts in ecological systems (Scheffer et al. 2001), the abrupt transitions between macrophytes and phytoplankton in GPLake-M at critical nutrient loadings do not align with a potentially more gradual replacement of macrophytes by phytoplankton according to ecological resource competition theory (Huisman and Weissing 1995; Supplementary material A and B in van Wijk et al. 2023). In addition to their ecological relevance, implementing the option for co-limitation and coexistence would lead to a continuous and differentiable version of GPLake-M that would technically ease application on the lake network scale. Such an improved model to simulate nutrient retention and transport in relation to ecosystem state could be a building block for the future development of Smart Nutrient Retention Networks, in particular if a full dynamic network version would be available.

4.1.2 GPLake-R

Here we present the GPLake-R model, with "GP" standing for "generically parameterized" (Chang et al. 2019; 2022) and “R” standing for “retention”. As explained above, we build on the GPLake-M model (van Wijk et al. 2023) that consists of equations for macrophytes and phytoplankton in four equilibria sets representing the shift from nutrient to light limitation in macrophytes and phytoplankton and the regime shifts between macrophyte and phytoplankton dominance during eutrophication and oligotrophication (see equations 1-5 in van Wijk et al. 2023). In GPLake-R we generalized this into equations for macrophyte and phytoplankton equilibrium abundance in response to nutrient loading that allows for co-limitation of light and nutrients in macrophytes and phytoplankton, and coexistence of macrophytes and phytoplankton around critical nutrient loadings whilst maintaining the model parameters and parameterization from GPLake-M. Moreover, in GPLake-R we give equations for the free phosphorus (P) concentration in the water and P retention that are implicit to GPLake-M. Furthermore, we provide differential equations underlying the equilibrium equations for macrophyte and phytoplankton abundance resulting in a simple and versatile dynamic model of nutrient retention in shallow lakes and networks thereof.

In this paper, we present the GPLake-R model. First, we describe how the model was developed, parameterized, and applied in a pattern-oriented model comparison. Next, we provide the equilibrium equations of GPLake-R (including nutrient retention), and the differential equations that dynamically lead to these equilibrium outcomes. We present the pattern-oriented comparison of GPLake-R against the more complex and well established shallow lake ecosystem model PCLake (Janse 1997). Finally, we discuss the ecological relevance of including co-limitation and coexistence in GPLake-R and give an outlook for the potential of GPLake-R to support the development of Smart Nutrient Retention Networks.

4.2 Methods

First, we developed a new notation for the equations of GPLake-M. Thereafter, we made the nutrient retention that is implicit to GPLake-M explicit by rewriting the Slope parameters of macrophytes and phytoplankton as defined in GPLake-M (van Wijk et al. 2023) in terms of retention rates of macrophytes (R_{macr}) and phytoplankton (R_{phyt}), and the hydrodynamic dilution rate (D). Next, we developed a mathematical function that could describe co-limitation during the transition from nutrient limitation to light limitation with increasing nutrient load. Furthermore, we implemented the possibility of coexistence between macrophytes and phytoplankton around critical nutrient loadings. This enabled us to formulate a single equation for nutrient retention depending on nutrient loading and initial ecosystem state. Finally, starting from this equilibrium version of GPLake-R, we also developed a dynamical and a network version of GPLake-R. Here we introduce the parameterization of GPLake-R based on GPLake-M, and the pattern-oriented comparison between the GPLake-R and PCLake models.

4.2.1 Model parameterization

To parameterize GPLake-R (Table 4.1), the GPLake-M summer averaged Plateau values (M_i) of 259 mg P m^{-2} and critical turbidity Pcrit of 73 mg P m^{-2} were used (van Wijk et al. 2023). Assuming the retention rate of macrophytes to be independent of the dilution rate, the value of the macrophyte nutrient retention rate (R_{macr},d^{-1}) was derived from the GPLake-M macrophyte Slope (S_{macr}) of 237 d (van Wijk et al. 2023) as follows:

$$R_{macr} = \frac{1}{S_{macr}} \Rightarrow S_{macr} = \frac{1}{R_{macr}} \qquad \text{Eq. (4.1)}$$

In contrast to this, the dilution dependent phytoplankton nutrient retention rate (R_{phyt}, d^{-1}) was derived by assuming Vollenweider-type nutrient retention with a time scaling parameter s of 81 d, as defined by van Wijk et al. (2023):

$$R_{phyt} = \frac{\sqrt{s\,D}}{s} \qquad \text{Eq. (4.2)}$$

and then used to calculate the phytoplankton Slope (S_{phyt}, d) as a function of the dilution rate (D, d^{-1}) by:

$$S_{phyt} = \frac{1}{R_{phyt}+D} = \frac{1}{\frac{\sqrt{s\,D}}{s}+D} \qquad \text{Eq. (4.3)}$$

Please note that the nutrient retention rates R_{macr} and R_{phyt} were presented as parameters $Dmacr_{ret}$ and $Dphyt_{ret}$ in GPLake-M, respectively (see Supplementary material F and G in van Wijk et al. 2023).

Table 4.1. GPLake-R parameter settings with unit and description, each copied or derived from the parameters of GPLake-M.

Parameter	Value	Unit	Description
Pcrit	73	mg P m^{-2}	Critical turbidity
R_{macr}	0.00422	d^{-1}	Macrophyte nutrient retention rate (denoted as $Dmacr_{ret}$ in GPLake-M)
R_{phyt}	0.0111	d^{-1}	Phytoplankton nutrient retention rate at a dilution rate of D = 0.01 (denoted as $Dphyt_{ret}$ in GPLake-M, see also Equation 4.2 and Table 4.2)
s	81	d	Time scaling parameter for Vollenweider-type nutrient rate of phytoplankton
S_{macr}	237	d	Areal P content of macrophytes over areal P loading at equilibrium during nutrient-limited phase (denoted as $Slope_{macr}$ in GPLake-M)
S_{phyt}	47.4	d	Areal P content of phytoplankton over areal P loading at equilibrium during nutrient-limited phase at a dilution rate of D = 0.01 (denoted as $Slope_{phyt}$ in GPLake-M, see also Equation 4.3 and Table 4.2)
M_{macr}	259	mg P m^{-2}	Areal P content of macrophytes at equilibrium during light-limited phase (denoted as $Plateau_{macr}$ in GPLake-M)
M_{phyt}	259	mg P m^{-2}	Areal P content of phytoplankton at equilibrium during light-limited phase (denoted as $Plateau_{phyt}$ in GPLake-M)

4.2.2 Pattern-oriented model comparison

We tested the GPLake-R model equilibria against PCLake on the level of P retention fraction by bifurcation analysis. In the bifurcation analysis, equilibrium outcomes of P retention fractions were determined over a range of P loading and for initial clear and turbid ecosystem states. We used summer averaged model output from PCLake after running the model for 30 years to approach equilibrium because the parameters of GPLake-M were also derived from summer averages. As a starting point we used a "standard lake" representing an "average Dutch lake" (Janse 2005) of 2 m depth with a dilution rate D of 0.01 d^{-1} (i.e., a hydraulic residence time of 100 days), whilst assuming a point loading of nutrients, which is decoupled from the hydrological inflow. Next, we conducted a pattern-oriented model comparison with PCLake for multiple dilution scenarios (Table 4.2). For this, D was estimated as hydrological loading Qin (mm d^{-1}) divided by water depth z (with unit conversion to mm). In this comparison we focused on the critical nutrient loadings at which regime shifts occur and the height of the bifurcation graphs at varying dilution rates. Furthermore, we defined two measures of P retention. First, the areal retention rate Pret (mg P m^{-2} d^{-1}) is a measure of absolute or net nutrient retention, which here is the difference between the Pload and the outflow of P (Pout, wPoutflTot in PCLake, in mg P m^{-3} d^{-1}) corrected for lake depth z (m):

$$Pret = Pload - z\,Pout \qquad \text{Eq. (4.4)}$$

Second, the P retention fraction fPret (-) is the areal P retention rate Pret (mg P m^{-2} d^{-1}) over the areal P loading to the lake Pload (mg P m^{-2} d^{-1}):

$$fPret = \frac{Pret}{Pload} \qquad \text{Eq. (4.5)}$$

We used fPret for the pattern-oriented model comparison and the areal retention rate returns in the mass balance equations of GPLake-R (section 3.3 and 3.4).

Table 4.2. Sets of lake characteristics used as input in PCLake (depth z and hydrological loading Qin) and GPLake-R (depth z, dilution rate D or its reciprocal hydraulic residence time τ, R_{phyt}, and S_{phyt}) with the "standard lake" settings in bold.

Set	z (m)	Qin (mm d^{-1})	D (d^{-1})	τ (d)	R_{phyt} (d^{-1})	S_{phyt} (d)
1	**2**	**20**	**0.010**	**100**	**0.0111**	**47.37**
2	2	40	0.020	50	0.0157	28.00
3	2	13.3	0.0067	150	0.0091	63.51

4.3 Results

We first present our results for the development of the equilibrium version of GPLake-R. This equilibrium version aims to be a versatile and backward compatible implementation of GPLake-M that makes retention explicit and allows for co-limitation of nutrients and light for macrophytes and phytoplankton and coexistence of macrophytes and phytoplankton around the critical P loadings during eutrophication and oligotrophication. Thereafter, we present our results for the development of a dynamic version of GPLake. Finally, we report on the pattern-oriented comparison between the retention of nutrients calculated with GPLake-R with the complex ecosystem model for shallow lakes PCLake.

4.3.1 GPLake-R equilibrium equations

Here we first present the GPLake-R model in the form of equilibrium equations. We formulated an alternative mathematical notation of the original GPLake-M model (van Wijk et al. 2023) as a first step towards the development of GPLake-R (Supplementary material A). Specifically, we reorganized the model into equations for each of the four GPLake-M equilibrium curves (one for macrophytes and one for phytoplankton for the initial clear state and a second pair for the initial turbid state) instead of per equilibrium set as was done in van Wijk et al. (2023). We then combined these equations for the initial clear and turbid state into one equation for the equilibrium abundance of macrophytes and one for the equilibrium abundance of phytoplankton (Supplementary material A). Thereafter, we rewrote the model in terms of retention rates of macrophytes and phytoplankton instead of Slopes as defined in GPLake-M (Supplementary material B). To keep the mass balance simple, here we focused on shallow lakes with a point loading of nutrients, which is decoupled from the hydrological inflow. Still, alternative mathematical notations can be formulated based on the generalized mass balance equations presented for GPLake-M (see Supplementary material F in van Wijk et al. 2023).

Next, we implemented co-limitation of nutrients and light in macrophytes and phytoplankton using a single and versatile "intlog" function that has the original GPLake-M Slope and Plateau as its (approximate) asymptote (Supplementary material C). Thereafter, coexistence of macrophytes and phytoplankton around the critical nutrient loadings was implemented by linking the phase in which macrophytes dominate with the phase in which phytoplankton dominates for each initial state with a continuous Hill function (Supplementary material D). Both the intlog and the Hill function have an auxiliary parameter, named n_{intlog} and n_{Hill}, respectively. Additionally, we formulated a single equation for nutrient retention depending on nutrient loading and initial ecosystem state. Finally, starting from this equilibrium version of GPLake-R, we also developed a dynamical version of GPLake-R (Supplementary material E) and a network implementation thereof (Supplementary material F).

With the equilibrium version of GPLake-R, the areal retention rate at equilibrium ($Pret^*$ in mg P m^{-2} d^{-1}) can be calculated by a single equation, and through the principle of mass-conservation the amount of nutrients flowing out along the water discharge at equilibrium (Pdil* in mg P m^{-2} d^{-1}) can be derived:

$$Pret^* = R_{macr}Pmacr^* + R_{phyt}Pphyt^* \tag{4.6a}$$

$$Pdil^* = D\ Pphyt^* + z\ D\ Pwater^* \tag{4.6b}$$

$$Pload - Pret^* - Pdil^* = 0 \tag{4.6c}$$

With Pphyt* (mg P m^{-2}), Pmacr* (mg P m^{-2}) and Pwater* (mg P m^{-3}) being the areal phytoplankton and macrophyte P content, and the P concentration in the water at equilibrium, respectively.

Moreover, based on the equilibrium state equations, also one GPLake-R equation for the nutrient retention fraction at equilibrium fPret* (-) can be formulated:

$$fPret^* = \frac{Pret^*}{Pload} = \frac{R_{macr}Pmacr^* + R_{phyt}Pphyt^*}{Pload} \tag{4.7}$$

4.3.2 GPLake-R differential equations

We also developed a dynamic version of GPLake-R (Supplementary material E) that leads to the equilibrium solutions of GPLake-R (Supplementary material D). The differential equations for macrophytes and phytoplankton consist of proportional growth and loss terms. The proportional macrophyte loss rate equals the macrophyte retention rate while the phytoplankton loss rate covers both the process of retention and dilution. The proportional growth rate of macrophytes and phytoplankton covers both nutrient limitation through a Monod term and density dependence through a logistic term. The latter term is based on the GPLake-R equilibrium density at the actual nutrient loading and the actual ecosystem state. By using the actual ecosystem state in the dynamical version of GPLake-R, the binary parameter representing the initial ecosystem state of the equilibrium version of GPLake-R is eliminated. The differential equation for water includes the P loading as a gain term and uptake by macrophytes and phytoplankton and dilution by the outflowing water as loss terms.

Finally, the mass-balanced differential equations lead to single equations of the areal P retention rate at time t ($Pret_t$ in mg P m^{-2} d^{-1}) and the amount of P flowing out along with the water discharge at time t ($Pdil_t$ in mg P m^{-2} d^{-1}), similar to those for the equilibrium condition:

$$Pret_t = R_{macr}Pmacr_t + R_{phyt}Pphyt_t \qquad \text{Eq. (4.8a)}$$

$$Pdil_t = D\ Pphyt_t + z\ D\ Pwater_t \qquad \text{Eq. (4.8b)}$$

4.3.3 Pattern-oriented model comparison of nutrient retention in GPLake-R and PCLake

For multiple dilution scenarios, GPLake-R (using n_{intlog} = 3 and n_{Hill} = 30) and PCLake produced similar patterns of P retention fraction in response to P loading (Fig. 4.1). Both models show hysteretic regime shifts in the P retention fraction, indicating distinctly higher nutrient retention efficiencies at low P loading and lower nutrient retention efficiencies at high P loading. This reflects the higher nutrient retention efficiency of macrophyte- versus phytoplankton-dominated states in both lakes, with the position of the regime shifts being the critical nutrient loadings of the lake. The critical nutrient loadings increase with dilution rate (i.e., reciprocal of hydraulic residence time in Table 4.2) and their values correspond between both models. However, in this example, the effect of dilution rate on P retention fraction is somewhat stronger in GPLake-R than in PCLake (especially for the phytoplankton-dominated state with low P retention fractions) (Fig. 4.1). The resulting height of the P retention fraction load-response curve and its sensitivity to the dilution rate can be further modified in GPLake-R by adjusting the n_{intlog} parameter for co-limitation (Supplementary material C). This also affects the position of the lower critical nutrient loading (i.e., shifts from phytoplankton to macrophyte dominance). Finally, by adjusting the coexistence parameter n_{Hill}, the graduality of the transition from the macrophyte- to the phytoplankton-dominated state, and vice versa, can be controlled (Supplementary material D).

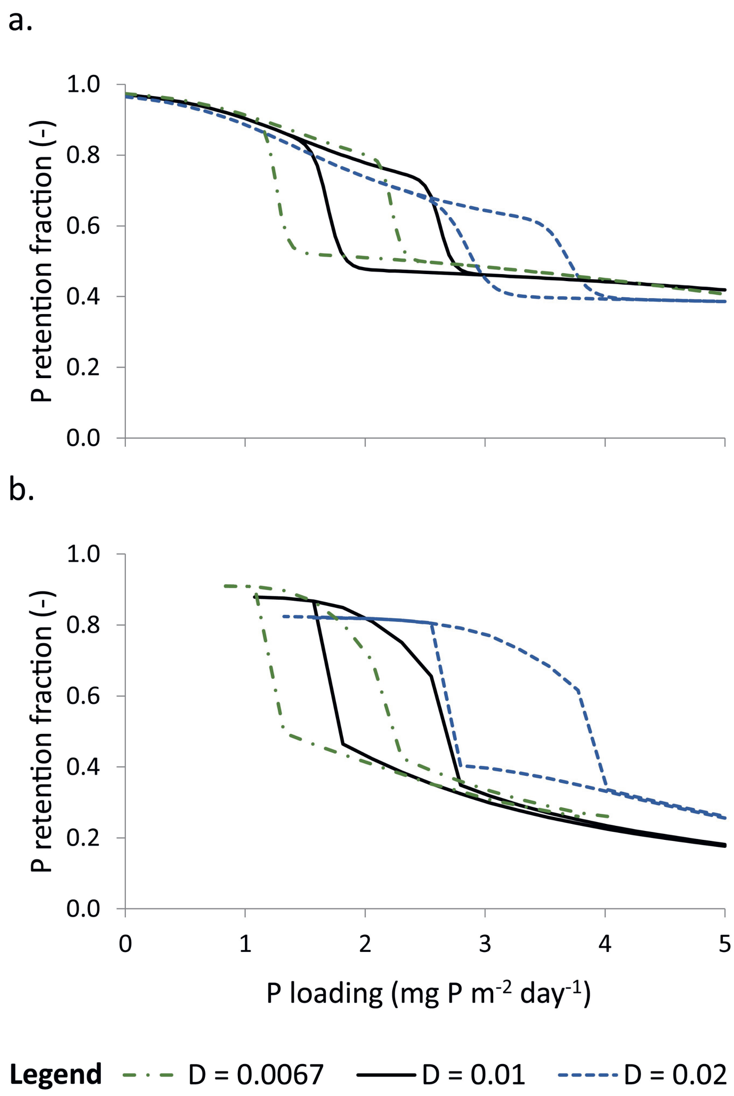

Figure 4.1. Pattern-oriented comparison of summer averaged P retention fraction (-) for a) GPLake-R against b) PCLake for multiple dilution scenarios. GPLake-R was run using the intlog function with n_{intlog} = 3 and the Hill function with n_{Hill} = 30. See section 4.2.1 and Table 4.1-4.2 for more details on parameter values.

4.4 Discussion

We developed GPLake-R as the first simple process-based and mass-balanced model of nutrient retention under regime shifts in temperate shallow lakes we know of. GPLake-R includes the feedback between ecosystem state, nutrient retention, and nutrient loading and it behaves similar to the more complex PCLake model for various dilution rates. Process-based models that combine insights from ecological theory — such as GPLake-R — are in particular extrapolatable to novel conditions (e.g., other lake characteristics) and can be applied to analyze management scenarios under global change (Cuddington et al. 2013). Here, we first explain the ecological relevance of including co-limitation of nutrients and light in macrophytes and phytoplankton, and of including coexistence of macrophytes and phytoplankton around critical nutrient loadings in GPLake-R. Thereafter, we review the parameterization of the novel n_{intlog} and n_{Hill} parameters of GPLake-R. Lastly, we discuss how the versatile GPLake-R model can support the development of Smart Nutrient Retention Network management strategies.

4.4.1 Ecological relevance of co-limitation and coexistence in GPLake-R

By means of the newly developed intlog function of GPLake-R, one can now choose whether to simulate single-resource limitation or co-limitation of nutrients and light in macrophytes and phytoplankton. Single-resource limitation is backward compatible with GPLake-M which treats nutrients and light according to Liebig's Law of the minimum as perfectly essential resources (cf., Tilman 1980) resulting in a sharp transition between nutrient and light limitation of the primary producer due to self-shading (van Wijk et al. 2023). However, a more gradual flattening-off of the curves with P loading due to co-limitation of nutrients and light might be more realistic based on the physiological interdependence of these resources in primary producers. Interacting effects of nutrients and light would be expected because light is needed to produce energy for nutrient acquisition (i.e., through photosynthesis), and nutrients are essential for the photosynthetic machinery (Huisman and Weissing 1995). For example, under nutrient-sufficient conditions, the effect of co-limitation is observed through increasing cell nutrient requirements and chlorophyll-*a* levels of phytoplankton when light levels decrease (Rhee and Gotham 1981). Additionally, under P-limited conditions, co-limitation effects on the competitive strength for P and altered cell P contents were demonstrated for a cyanobacterium under near-light-limiting conditions (Riegman and Mur 1985).

Besides offering freedom in the extent of co-limitation of nutrients and light, GPLake-R also allows for coexistence between macrophytes and phytoplankton around the critical nutrient loadings. Such coexistence can be understood from Tilman's (1982) seminal resource competition theory and Huisman and Weissing's (1994; 1995) theoretical models of phytoplankton under nutrient- and light limitation. When using empirically relevant parameter settings for the competitive strength for nutrients and light of submerged macrophytes and phytoplankton, these theories predict their coexistence around the critical nutrient loadings (see Supplementary material A in van Wijk et al. 2023) and are therefore at odds with theory on regime shifts that predict an abrupt replacement between macrophytes and phytoplankton (Scheffer et al. 1993). For the above mentioned empirical characteristics of macrophytes and phytoplankton, the outcome of their competition differs when systems are a) vertically mixed (i.e., Huisman and Weissing (1994; 1995)) or b) when phytoplankton are positioned above macrophytes in the water column (i.e., following van Gerven et al. (2015)). These individual vertical organizations themselves cannot produce patterns of regime shifts in shallow lakes (see Supplementary material A and B in van Wijk et al., (2023)), but do so by combining them in GPLake-R. For the parametrization of the model of Huisman and Weissing (1994; 1995) that we studied, GPLake-R resembles the coexistence for vertical organization a) and b), during eutrophication and oligotrophication, respectively (Supplementary material G). This shows that GPLake-R is in fact a model of alternative stable states of coexistence of macrophytes and phytoplankton as opposed to the classical view on alternative stable states being monocultures of either macrophytes or phytoplankton

(Supplementary material G). Finally, combining co-limitation and coexistence in GPLake-R results in bifurcation plots that resemble plots of alternative stable states in shallow lakes, but with more gradual load-response curves at the transition from nutrient to light limitation, and between macrophyte and phytoplankton dominance (e.g., Fig. 4.2).

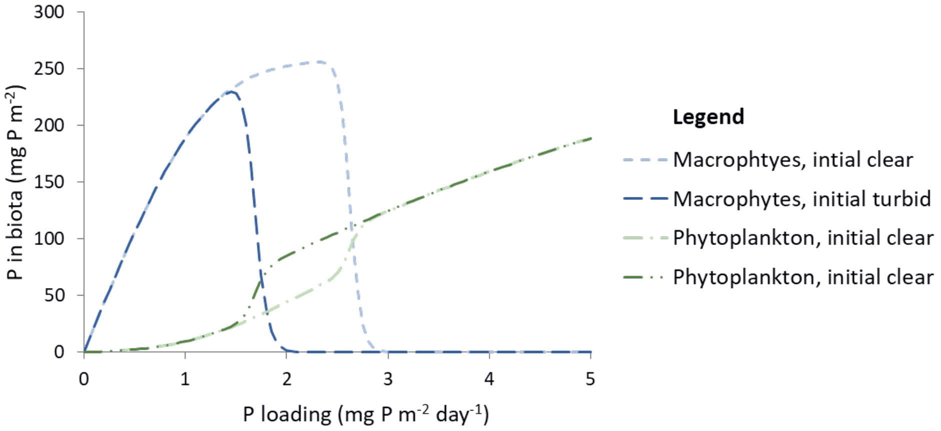

Figure 4.2. Bifurcation plot of GPLake-R that shows a gradual but hysteretic response of equilibrium ecosystem state (i.e., P in biota) to P loading, with co-limitation for nutrients and light in macrophytes and phytoplankton, and coexistence of macrophytes and phytoplankton around the critical nutrient loadings. In this example, the intlog function with n_{intlog} = 3 and the Hill function with n_{Hill} = 30 was used that resulted from the pattern-oriented comparison of GPLake-R and PCLake.

4.4.2 Estimating the n_{intlog} and n_{Hill} parameters of GPLake-R

One of the design principles of the GPLake suite of models (Chang et al. 2019; 2022; van Wijk et al. 2023) is that they aim to be parameterized based on empirical data, theoretical considerations, and model output. GPLake-R has only two additional parameters, n_{intlog} and n_{Hill}, compared to GPLake-M and for the majority of parameters of GPLake-R we can therefore rely on the parametrization of GPLake-M (van Wijk et al. 2023). However, for n_{intlog}, that captures the abruptness in the transition from nutrient limitation to light limitation in macrophytes and phytoplankton, and for n_{Hill} that captures the abruptness of the replacement of macrophytes by phytoplankton and vice versa, we found little data that would allow us to set empirically based values. A comparison of four potential load-response curves and different values of parameter n_{intlog} against field data from Vollenweider (Jones and Lee 1986), resulted in comparable R^2 values and therefore provided no guidance on which load-response curve to use in GPLake-R (Supplementary material I). Since regime shifts between clear and turbid ecosystem states are beyond the scope of the Vollenweider data set, it does not provide information on parameter n_{Hill}. Alternatively, the comparison between GPLake-R and the theoretical Huisman-Weissing model (Supplementary material G) resulted in estimates of n_{intlog} = 14 for macrophytes, n_{intlog} = 8 for phytoplankton, $n_{Hill,clear}$ = 2.5, and $n_{Hill,turbid}$ = 15 using Pcrit = 50. Still, these n_{intlog} values depend on the parameter settings of the Huisman-Weissing model that determine the R^* of macrophytes and phytoplankton, which in themselves are not well connected to empirical data. Also, the n_{Hill} values might be characteristic of the current parameterization of the Huisman-Weissing model but are neither empirically tested. To complement this, the pattern-oriented comparison between GPLake-R and PCLake gave good results for n_{intlog} = 3 and n_{Hill} = 30 (see section 4.3.3 and Fig. 4.1). In conclusion, we proved that the GPLake-R model is versatile as can capture the patterns of the Vollenweider field data, the theoretical Huisman-Weissing model, and the process-based PCLake model, but we currently lack an empirical basis to generically parameterize n_{intlog} and n_{Hill}. We argue that the latter has only a limited impact on the power of GPLake-R to calculate nutrient retention because this primarily depends on the parameters established during the development of GPLake-M (van Wijk et al. 2023).

4.4.3 The potential of GPLake-R for Smart Nutrient Retention Networks

GPLake-R can be used in several ways to explore Smart Nutrient Retention Network management options. One of the nutrient retention management options in Smart Nutrient Retention Networks is the local management of ecosystem state (van Wijk et al. 2021). With the GPLake-R model one can relatively simply estimate the lake ecosystem state and the associated nutrient retention fraction at equilibrium given the initial ecosystem state and actual nutrient loading (e.g., using an MS Excel tool). Therefore, the model can be used to explore lake ecosystem state management options for individual lakes, for example, by testing the effect of changed dilution rate and nutrient loading on the equilibrium ecosystem state. Moreover, the model is mass-balanced, which is essential when using models as a building block to reliably simulate nutrient flows in networks of lakes. Accordingly, GPLake-R can be used to quickly explore the potential ecosystem states of connected lakes at equilibrium. When applied in the context of Smart Nutrient Retention Networks, one can easily adjust the initial state of one or multiple lakes to test the potential long-term effect of local lake management on the water quality of other lakes in the network.

Additionally, hydrological management options such as water level and flow regulation, and altering hydrological connections between waterbodies, belong to the management options for Smart Nutrient Retention Networks (van Wijk et al. 2021). Because of the temporal variability of hydrological flows, it may be essential to model lakes over time to test and plan for hydrological interventions. The differential equations of the process-based GPLake-R model (section 4.3.3) can be used to simulate such systems dynamically and to explore timing of management options (e.g., using an R script). Moreover, for the development of Smart Nutrient Retention Networks, it is relevant to know when a lake’s ecosystem state is expected to change and how nutrient retention changes along, as regime shifts may not only cascade down a hydrological network over space but also in time (Hilt et al. 2011). The dynamic GPLake-R model can also be used to explore this on a network scale.

4.5 Conclusion

We developed and presented the GPLake-R model as the first simple dynamic model of nutrient retention under regime shifts in shallow lakes.

GPLake-R is versatile through the novel options to simulate co-limitation of nutrients and light in macrophytes and phytoplankton, and coexistence of macrophytes and phytoplankton around critical nutrient loadings. Moreover, the model can be applied to estimate the lake ecosystem state and the associated nutrient retention fraction at equilibrium given the initial ecosystem state and actual nutrient loading. Additionally, one can use the differential equations of GPLake-R for more detailed applications in time and space. GPLake-R captures the hysteretic nutrient retention pattern from the more complex PCLake model, with macrophyte-dominated lakes having higher P retention than phytoplankton-dominated lakes. We believe that the simple, process-based and mass-balanced GPLake-R model is a major step in the development of a model tool to support development of Smart Nutrient Retention Networks because it includes the feedback between ecosystem state, nutrient retention, and nutrient loading.

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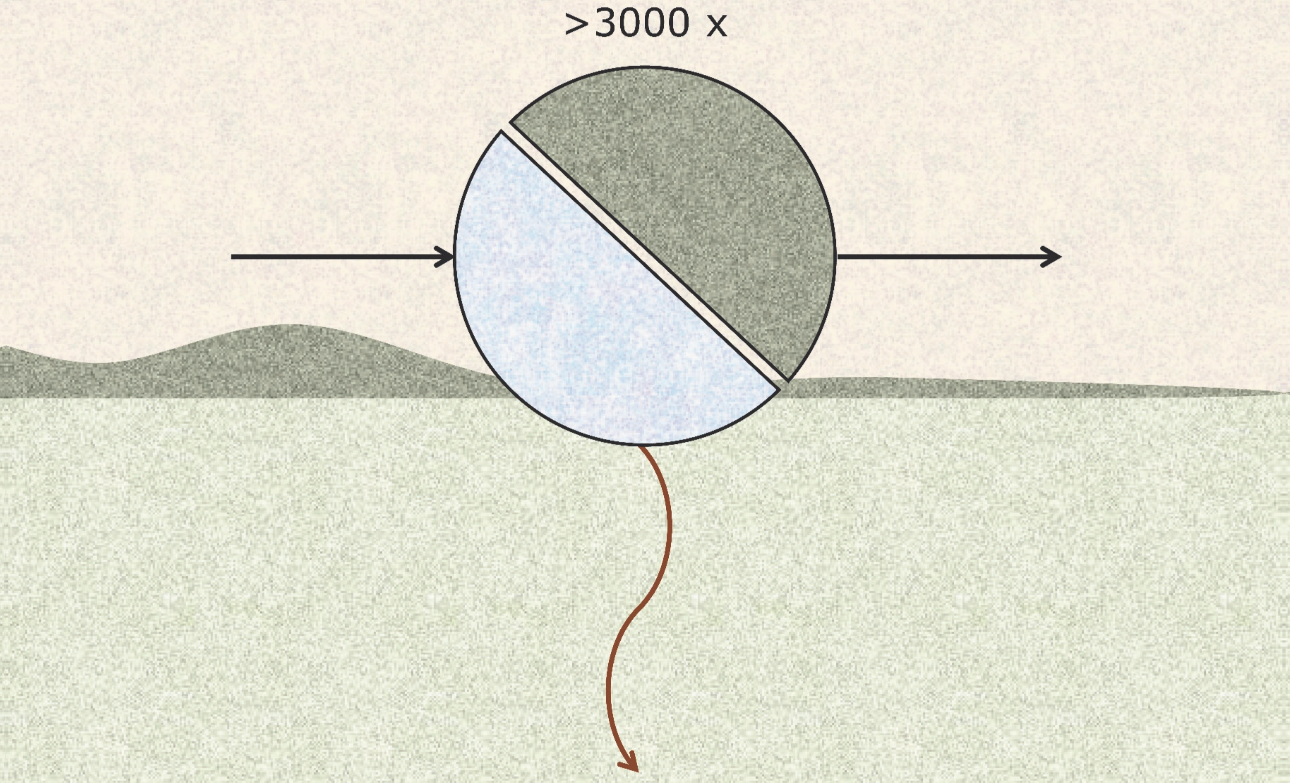
Chapter 5

How nutrient retention and TN:TP ratios depend on ecosystem state in thousands of Chinese lakes



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Abstract

Worldwide, anthropogenic activities threaten surface water quality by aggravating eutrophication and increasing total nitrogen to total phosphorus (TN:TP) ratios. In hydrologically connected systems, water quality management may benefit from in-ecosystem nutrient retention by preventing nutrient transport to downstream systems. However, nutrient retention may also alter TN:TP ratios with unforeseen consequences for downstream water quality. Here, we aim to increase understanding of how nutrient retention may influence nutrient transport to downstream systems to improve long-term water quality management strategies. We analyzed lake ecosystem state, in-lake nutrient retention, and nutrient transport (ratios) to downstream systems by 2050 under a low climate change and sustainability-, and a high climate change and economy-focused scenario for 3482 Chinese lakes using the lake ecosystem model PCLake+. In both 2050 scenarios, the effect of nutrient input reduction outweighs that of temperature rise, resulting in more lakes with good ecological water quality (i.e., macrophyte-dominated) than in 2012. Generally, the sustainability-focused scenario shows a more promising future for water quality than the economy-focused scenario. Nevertheless, most lakes remain phytoplankton-dominated. The shift to more macrophyte-dominated lakes in 2050 is accompanied by higher nutrient retention fractions and less nutrient transport to downstream waterbodies. In-lake nutrient retention also alters the water's TN:TP ratio, depending on the inflow TN:TP ratio and the ecosystem state. In 2050 higher TN:TP ratios are expected in the outflows of lakes than in 2012, especially for the sustainability-focused scenario. However, the impact of this on downstream ecosystems also depends on actual nutrient loadings and on the limiting nutrient in the receiving system. We conclude that nutrient input reductions, improved water quality, higher in-lake nutrient retention fractions, and lower nutrient transport to downstream waterbodies go hand in hand. Therefore, water quality management could benefit even more from nutrient pollution reduction than one would expect at first sight.

5.1 Introduction

Globally, nutrient inputs and retention have increased over the 20th century, as well as nutrient transport to the oceans (Bouwman et al. 2005; Beusen et al. 2016). Nutrient pollution threatens water quality and is expected to continue to increase by anthropogenic changes such as human population growth, urbanization, agricultural intensification, and climate change (Bouwman et al. 2005; Seitzinger et al. 2010; Wang et al. 2020). Excess nutrients promote turbid, phytoplankton-dominated waters which may be toxic (Codd et al. 2005) and provide fewer ecosystem services compared to lakes with clear water (Janssen et al. 2020). Furthermore, climate change aggravates eutrophication effects (Moss et al. 2011) through rising temperatures that favor the growth of cyanobacteria over other primary producers such as other phytoplankton species (Paerl and Huisman 2008; 2009) and submerged macrophytes (Mooij et al. 2007). Thus, with ongoing socio-economic developments and climate change, the risks of eutrophication are expected to rise. Nevertheless, water quality managers may be able to benefit from (natural) nutrient retention processes to partly prevent nutrient transport to downstream systems (van Gerven et al. 2017; Teurlincx et al. 2019) and lessen downstream eutrophication (van Wijk et al. 2021).

Limnological research increasingly considers multiple waterbodies within landscapes, including nutrient retention as an important and vulnerable regulating ecosystem service (Kling et al. 2000; Heino et al. 2021). Catchment-scale studies tend to primarily focus on nutrient retention on land and transport by rivers (e.g., Bouwman et al. (2005)). However, especially lentic systems — such as lakes — play an important role in nutrient retention in watersheds (Finlay et al. 2013; Maavara et al. 2015; Cheng and Basu 2017; Liu et al. 2018; Schmadel et al. 2018). Recently, the importance of the feedback between nutrient loading, ecosystem state, and nutrient retention was highlighted in the context of such connected waterbodies (van Wijk et al. 2021). This is especially relevant for shallow lakes which may experience different ecosystem states (e.g. phytoplankton or macrophyte dominance) (Scheffer et al. 1993; Smith and Schindler 2009). Since nutrient retention fractions are generally higher in clear, macrophyte-dominated than turbid, phytoplankton-dominated waters, the ecosystem state does not only depend on nutrient inputs into the waterbody but also influences nutrient transport to downstream systems (van Wijk et al. 2021). Yet, research on this spatial feedback theory is limited.

Furthermore, total nitrogen to total phosphorus (TN:TP) ratios have generally increased by changes in relative nutrient inputs and retention in waterbodies which may affect water quality (Jeppesen et al. 2005; Finlay et al. 2013; Glibert et al. 2018). As appeared in the 1970-80’s, ecological water quality (i.e., ecosystem state) strongly depends on phosphorus levels (Nicholls and Dillon 1978; Vollenweider and Kerekes 1982; Ahlgren et al. 1988). More recently, the co-limitation effects of P and N (Paerl et al. 2016) and the importance of TN:TP ratio (Guildford and Hecky 2000) have been put to the fore. More effective reduction of the point than diffuse nutrient sources, and (consequently) more effective P than N reduction, has led to increases in TN:TP ratios, for example, in the Ruhr River catchment (Westphal et al. 2020). Additionally, the higher removal efficiency of P than N in improved municipal wastewater treatment contributes to higher TN:TP ratios (Tong et al. 2020). Some argue that such higher TN:TP ratios are associated with oligotrophic lakes (Downing and McCauley 1992) and less toxic phytoplankton blooms in several hydrological systems (Chen et al. 2013; Harris et al. 2016). Others point to higher risks of algal blooms in coastal zones (Wu et al. 2022), and higher chlorophyll-*a* concentrations (Smith 1982) and toxin contents in phytoplankton (van de Waal et al. 2014) with increased TN:TP ratios. Additionally, higher TN:TP ratios are associated with decreased drinking water quality and reduced lake food-web biodiversity (Wu et al. 2022). Nevertheless, only a few studies assessed the relative retention of N and P in waterbodies and its implication for TN:TP ratios of loading to downstream systems (e.g., Grantz et al. (2014) and Liu et al. (2018)).

Here we use the lake ecosystem model PCLake+ (Janssen et al. 2019a) to explore how water quality, in-lake nutrient retention, and nutrient transport to downstream systems may develop in the future. We aim to increase understanding of how nutrient retention may influence nutrient transport to downstream systems to improve long-term water quality management strategies. Our study considers TN and TP loading, and their ratios, since all are important for ecological water quality. We explore two scenarios of socio-economic development and climate change for 2050 and compare them to the situation in 2012. We focus on Chinese lakes because Asia is one of the global hotspots of N and P inputs to rivers and coastal systems (Seitzinger et al. 2005; Li et al. 2022). For example, in the East China Sea downstream of the Yangtze River, the frequency and area of harmful algal blooms have increased together with TN:TP ratios between 1950 and 2007 (Li et al. 2014). Furthermore, despite water quality improvements in Chinese rivers, water quality, and ecological condition in most Yangtze River lakes decreased between 2008 and 2018 in the study by Qin et al. (2022). Where other studies have focused on nutrient inputs to Chinese rivers and coastal eutrophication (Strokal et al. 2016; Wang et al. 2020), we, therefore, focus on the water quality of lakes and their influence on nutrient transport to downstream systems through nutrient retention. Our scenario analysis for 3482 Chinese lakes illustrates how model analyses may help to focus management efforts to minimize adverse nutrient impacts and to protect surface water quality for future generations.

5.2 Methods

We used PCLake+ (Janssen et al. 2019a) to calculate lake water quality (definition in Supplementary material A), nutrient retention, and TN:TP ratios of water outflows for a baseline and two scenarios. PCLake+ is a lake ecosystem model to simulate water quality based on ecological interactions and covers a wide range of freshwater lakes differing in stratification regime and climate-related processes (Janssen et al. 2019a). We extended PCLake+ with equations for the hydrological transport of nutrients out of the lake and net in-lake nutrient retention (section 5.2.3). The model was applied to 3482 unique lakes in the five largest river basins in China with varying depths (0.7-205.4 m), surface area (0.1-254 km^2), and climate zones (temperate to tropical). To prevent model runtime errors, this selection excludes cases with unrealistic water balances (i.e., water flows =<0), permanent ice cover, or without nutrient loading. Groundwater flows (i.e., seepage and infiltration) were assumed to be negligible and each selected lake has a water in- and outlet, which eases the net nutrient retention calculation. Moreover, we checked that each lake had N and P retention fractions between 0 and 1, to assume they had reached equilibrium with their inflowing nutrient loading. Model input for each lake consisted of average lake depth, fetch, and latitude from a dataset earlier published and used with PCLake+ (Janssen et al. 2021). Furthermore, the sediment characteristics of each lake were derived using the approach of Janssen et al. (2021b), and surface water inflows were derived from the HydroLAKES (Messager et al. 2016) and ISIMIP (Inter-Sectoral Impact Model Intercomparison Project) databases (Golub et al. 2022) (Fig. B.1 in Supplementary material B). This data was supplemented with data on climate and nutrient loading (Supplementary material C) from the climate change and socio-economic development scenarios, respectively (section 5.2.1 and 5.2.2).

For each lake, we ran PCLake+ for a range of TP loadings for 2012 and the climate scenarios to derive nutrient response curves. The nutrient response curves present the potential annual average parameter values for the specific lake and climate scenario, depending on the nutrient loading, and — in the case of alternative stable states (as explained in Supplementary material A) — the initial ecosystem state. To this end, each lake was forced from an initial clear to a more turbid state and back by, respectively, increasing (eutrophication) and decreasing (oligotrophication) the TP loading. We estimated a minimum and maximum ecologically relevant TP loading per lake from a typical range of chlorophyll-*a* concentrations (1.6 to 160 μg chl-*a* l^{-1}) using the lake eutrophication model GPLake-S. To ensure that the nutrient loadings of the socio-economic development scenarios were also captured, we widened the range of the found TP loadings to the extent that the actual 2012 and 2050 loadings fall within the simulation range. Each lake run was initiated with a 30-year spin up from the default initial clear state. Next, the core runs were started with the lake-specific minimum TP loading, slowly increasing the load over a 300-year run toward the maximum TP loading (eutrophication). Consecutively, the run was continued for another 300 years in reverse order; from the maximum to the minimum TP loading (oligotrophication). The long run was deliberately chosen to minimize the effect of the response time of lakes to the changes in loadings on the calculated annual average water quality, nutrient retention, and nutrient outflow parameters (cf., legacy effect (Cuddington 2011)). From the resulting nutrient response curves, scenario-specific output parameter values were derived for initial clear and turbid states, being the intercept of the parameter value at the nutrient loading of the corresponding socio-economic development scenario (using the approx interpolation function in R). Furthermore, TN:TP mass ratios were calculated.

We analyzed future trends for two scenarios for the year 2050: the sustainability-focused and economy-focused scenario. The sustainability-focused scenario uses Representative Concentration Pathway (RCP) 2.6 as climate change scenario (van Vuuren et al. 2011) in combination with shared socio-economic pathway (SSP) 1 for China developed by Wang et al (2017; 2020). The economy-focused scenario is based on RCP8.5 and SSP5. By this, the sustainability-focused scenario projects some temperature rise and a strong decrease in nutrient loadings whereas economy-focused scenario has a larger temperature rise and more modest decrease in nutrient loadings (see section 5.2.1 and 5.2.2 for more details). In our analysis we distinguish initial and equilibrium ecosystems states. Initial ecosystem state (clear or turbid) is an input parameter of PCLake+, whereas the equilibrium ecosystem state (macrophyte or phytoplankton dominance) is an output (see Supplementary material A for more details).

5.2.1 Climate change scenarios

We applied the RCP2.6 and RCP8.5 as climate change scenarios for the sustainability-focused and economy-focused scenarios, respectively. RCP2.6 (i.e., 2.6 W m^{-2} radiative forcing in 2100) is the lowest of the intermediate radiative forcing scenarios, including the use of bio-energy and carbon capture and storage, and requiring rigorous climate policies to limit emissions (van Vuuren et al. 2011). In contrast, RCP8.5 (i.e., 8.5 W m^{-2} radiative forcing in 2100) is a highly energy-intensive scenario with high population growth, a lower rate of technology development, and no climate policy (van Vuuren et al. 2011). The radiative forcing per 2050 RCP scenario was interpreted according to the ISIMIP2b approach (Golub et al. 2022) to produce input parameters for the hydrological model VIC-LAKE (Hostetler and Bartlein 1990; Hostetler 1991; Bowling and Lettenmaier 2010). Typical climate years were defined from these VIC-LAKE simulations by taking the daily average over a 30-year period prior to the simulated year. For 2012, we used existing validated data (R^2_{adj} between 0.84-0.87) from VIC-LAKE simulations (Janssen et al. 2021). The resulting dataset of 365 values for each, the 2012 baseline, the sustainability- and economy-focused scenario, were used as climate input for PCLake+ (TableC.1 in Supplementary material C). The distribution patterns of the resulting lake epilimnion temperature kernel density curves are similar, but the lakes in the sustainability- and economy-focused scenario are on average 0.63 and 0.78 °C warmer than in 2012, respectively (Supplementary material D). The hydrological input parameters were kept constant in 2012 and the 2050 scenarios (Supplementary material B and C1).

5.2.2 Socio-economic development

Our 2050 scenarios for socio-economic development follow the SSP storylines and associated gridded data of N and P losses to rivers from agriculture and sewage for China developed by Wang et al (2017; 2020). We used SSP1 and SPP5 for the sustainability-focused and economy-focused 2050 scenario, respectively. We converted the N and P losses in 2012 and 2050 of these two scenarios to nutrient loadings to lakes based on the in-river retention equation from Behrendt and Opitz (2000) (equation B.1-6 and Fig. B.2 in Supplementary material B). The resulting dataset was used as input for PCLake+ in the form of TN and TP loadings and their ratio for 2012, the sustainability- and the economy-focused scenario. In SPP1, a dramatic (but gradual) shift towards sustainability is assumed with a strongly improved connection to and treatment of sewage, an increased low-meat diet preference, and a strong increase in nutrient recycling (e.g., manure recycling) in the food production system and agricultural productivity whilst minimizing overfertilization. As a result, nutrient loadings per lake generally decrease (on average 86% and 53% reduction for TP and TN, respectively) and TN:TP ratios increase compared to 2012 (Supplementary material D). In SSP5, steps towards sustainability are taken in a more conventional way assuming a priority for economic development and urbanization with a moderate improvement in connection to and treatment of sewage, an increased food demand, particularly for meat products, and a moderate increase in nutrient recycling in the food production system. In this scenario, TP loading slightly decreases whilst TN loading hardly changes compared to 2012, resulting in increased TN:TP ratios (Supplementary material D). The increase in TN:TP ratio relative to 2012 is on average three times larger for the sustainability- than the economy-focused scenario.

5.2.3 New equations in PCLake+

PCLake+ (Janssen et al. 2019b) was extended with equations for the hydrological transport of nutrients out of the lake and net in-lake nutrient retention. Nutrient outflow ($L_{out,i}$ for nutrient i; g nutrient m^{-2} lake d^{-1}; equation 5.1) is the transport of unretained (organic and inorganic) nutrients out of a lake along with the water discharge from the lake. This is the sum of the epilimnetic and hypolimnetic outflow nutrient concentrations ($[i]_{out,j}$ for nutrient i and water layer j; g nutrient m^{-3} d^{-1}), each multiplied by the depth of the respective water layer (z_j for water layer j; m; equation 5.1):

$$L_{out,i} = [i]_{out,epi} \times z_{epi} + [i]_{out,hyp} \times z_{hyp} \qquad \text{Eq. (5.1)}$$

Though, in practice this may be assumed to be dominated by epilimnetic outflow. In PCLake+, the nutrient loading into a lake is defined independent from the water inflow and represents the total external nutrient input into the lake ($L_{lake,i}$ for nutrient i; g nutrient m^{-2} lake d^{-1}; Equation B.6 in Supplementary material B) from, for example, atmospheric deposition directly into the lake, and diffuse and point sources accumulating in the water inflow. The difference between the nutrient outflow and the external nutrient input is the net nutrient retention. This absolute amount of nutrients is retained in the system (aR_i for nutrient i; g nutrient m^{-2} lake d^{-1}; equation 5.2), for example, by burial (i.e., permanently stored in the sediment) or denitrification (i.e., loss to the atmosphere).

$$aR_i = L_{lake,i} - L_{out,i} \qquad \text{Eq. (5.2)}$$

The nutrient retention fraction (R_i for nutrient i; unitless; equation 5.3) is derived by correcting for the external nutrient input as:

$$R_i = \frac{aR_i}{L_{lake,i}} \qquad \text{Eq. (5.3)}$$

Nutrient retention fractions of zero means that in total the nutrient outflow equals the external nutrient input, and a fraction of one means that the absolute nutrient retention equals the external nutrient input.

5.3 Scenario analysis results

5.3.1 In-lake water quality and nutrient retention

Our results for the 3482 lakes show a change in the distribution of macrophyte and phytoplankton levels between 2012 and 2050, depending on the initial state of the lakes (Fig. 5.1). We see a shift towards more lakes with high macrophyte and low phytoplankton levels, especially in the sustainability-focused scenario. In all simulations, the macrophyte levels are bimodally distributed (i.e., either high or low), with more lakes having low macrophyte levels when they are initially turbid (Fig. 5.1, left panels). These bimodal patterns are an indication of alternative stable states. When using the macrophyte to phytoplankton ratio of 1.75 g DW m^{-2} per mg chl-*a* m^{-3} as a threshold for the equilibrium ecosystem state (Supplementary material A), we find that only 18% of the lakes are macrophyte-dominated in the 2012 run (Table A.1. in Supplementary material A). This percentage increases somewhat towards 2050 in the economy-focused scenario (24%) and strongly in the sustainability-focused scenario (45%) (Table A.1. in Supplementary material A). Despite the increase in the number of macrophyte-dominated lakes in the 2050 scenarios, most lakes are found to be phytoplankton-dominated.

As for the equilibrium ecosystem state, in-lake nutrient retention values show a bimodal pattern (Fig. 5.2, top panels). Nutrient retention fractions are bimodal with mostly low (<0.5) or high (>0.75) values which correspond with phytoplankton- and macrophyte-dominated lakes, respectively (Fig. 5.2, middle and bottom panels). In the sustainability-focused scenario, the kernel density distribution of both N and P retention fractions shifts to higher values than in 2012 (Fig. 5.2, top panels). This corresponds with a larger share of lakes being macrophyte-dominated (Table A.1 in Supplementary material A). For the economy-focused scenario, a similar but weaker pattern occurs for P, but the N retention fraction distribution hardly shifts (Fig. 5.2, top panels). When focusing on phytoplankton-dominated lakes, the kernel density distribution shifts to

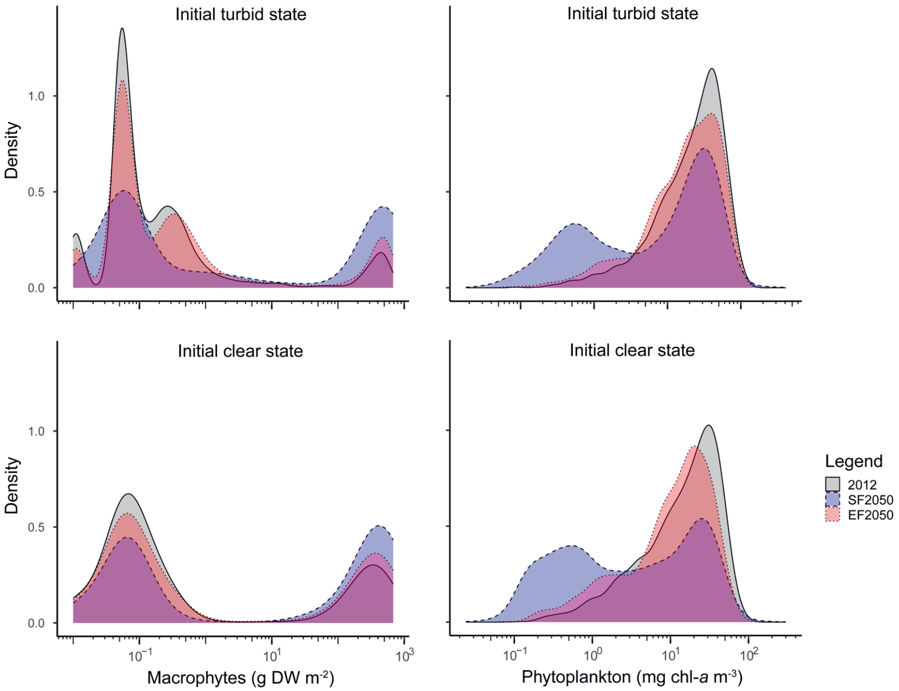

Figure 5.1. Kernel density plots of macrophyte (g DW m^{-2}) (left) and phytoplankton levels (mg chl-*a* m^{-3}) (right) per initial state (top turbid, bottom clear). Lines (gray filling) indicate 2012, dashes (blue filling) the sustainability-focused scenario (SF2050), and dots (red filling) the economy-focused scenario (EF2050).

slightly lower nutrient retention values in 2050 compared to 2012 (Fig. 5.2, middle panels). The nutrient retention fraction thus strongly differs among individual lakes and depends on the ecosystem state, with the largest increase from 2012 to 2050 being expected in the sustainability-focused scenario.

5.3.2 TN:TP ratios of lake outflows

For 2050, the scenarios show higher TN:TP ratios in the outflows of lakes than in 2012, especially for the sustainability-focused scenario. This correlates with the increasing TN:TP ratios of the inflow for 2012, and the sustainability- and economy-focused scenarios, respectively (Fig. 5.3). Notably, lakes with a low inflow TN:TP ratio (viz. <10) tend to have a lower

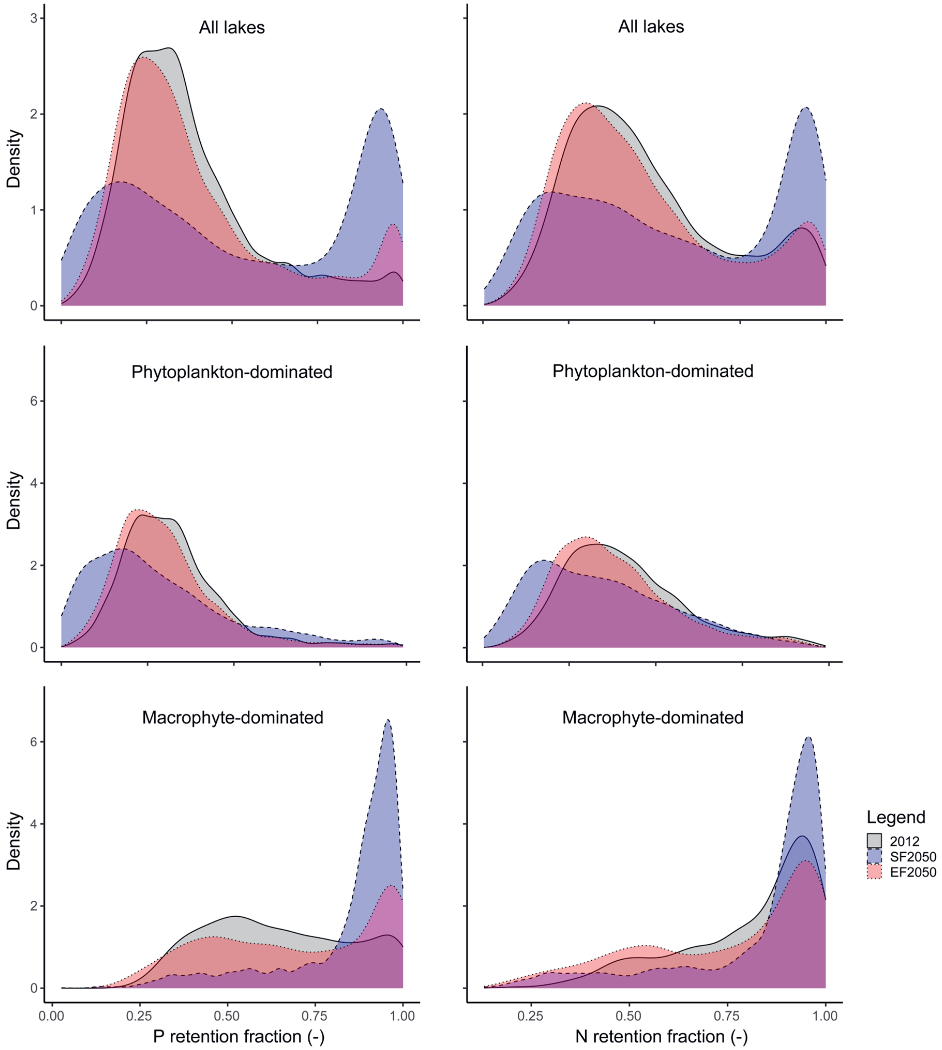

Figure 5.2. In-lake nutrient retention fraction kernel density plots for P (left) and N (right) for all lakes (top), and subsets of phytoplankton- (middle) and macrophyte-dominated lakes (bottom) based on the macrophyte to phytoplankton threshold ratio (Supplementary material A). Lines (gray filling) indicate 2012, dashes (blue filling) the sustainability-focused scenario (SF2050), and dots (red filling) the economy-focused scenario (EF2050). Please note that in the top panels each density plot per scenario describes the spread over 3482 lakes for an initial clear and turbid state (i.e., 6964 data points), the middle and bottom panels differ in the number of lakes per density curve (for details see Table A.1 in Supplementary material A).

outflow than in the inflow (see the spread of values around the dashed 1:1 line in Fig. 5.3). This pattern differs between equilibrium ecosystem states, with the regression line of macrophyte-dominated lakes deviating more from the 1:1 line (i.e., larger slope) than for phytoplankton-dominated lakes (Fig. 5.4). Thus, whether and how strongly the in- and outflow TN:TP ratios of lakes differ (i.e., deviating from the 1:1 line) depends on both the TN:TP loading of the inflow and the ecosystem state.

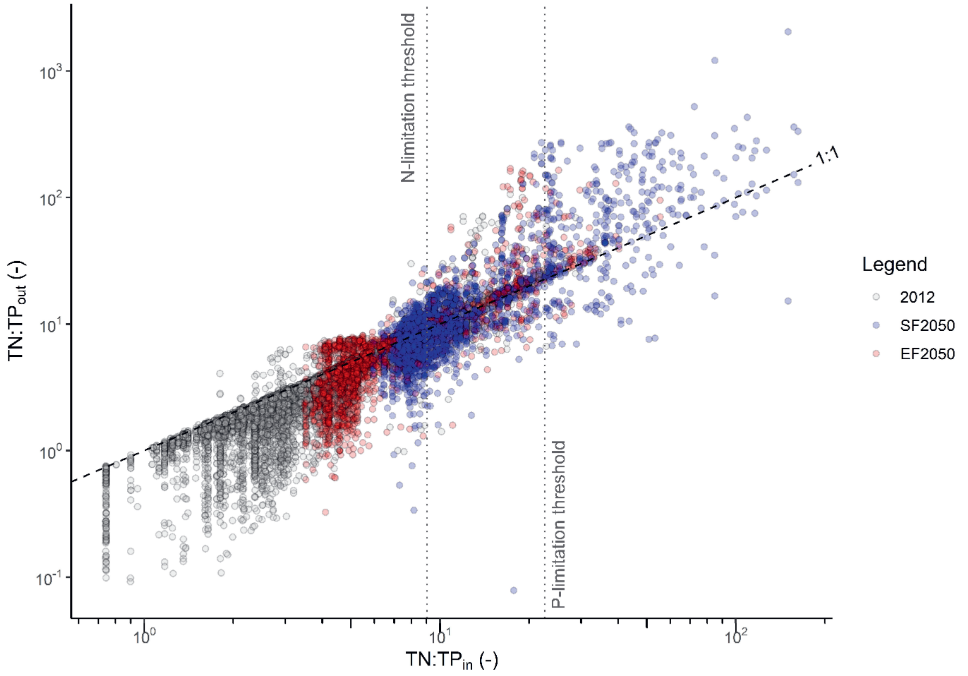

Figure 5.3. TN:TP ratios of the outflow and inflow for 2012 (gray), the sustainability-focused scenario (SF2050, blue) and the economy-focused scenario (EF2050, red). The dark gray dashed line is the 1:1 line indicating where the TN:TP ratio of the outflow equals that of the inflow. The vertical dotted lines represent the N- and P-limitation threshold for phytoplankton as defined by (Guildford and Hecky 2000), converted to mass TN:TP ratios.

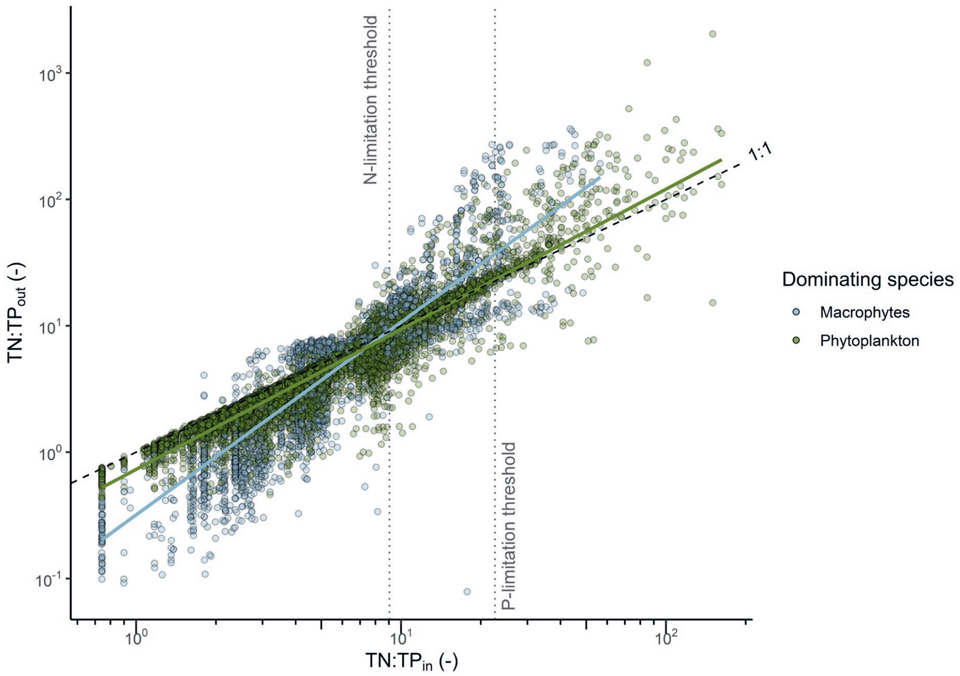

Figure 5.4. TN:TP ratios of the outflow and inflow per equilibrium ecosystem state (macrophyte-dominated in blue and phytoplankton-dominated in green) for 2012 and the 2050 scenarios combined. The light blue and dark green lines are the linear regression lines in log-log space (i.e., power functions in non-log space) for macrophyte- and phytoplankton-dominated lakes, respectively. The dark gray dashed line is the 1:1 line indicating where the TN:TP ratio of the outflow equals that of the inflow. The vertical dotted lines represent the N- and P-limitation threshold for phytoplankton as defined by (Guildford and Hecky 2000), converted to mass TN:TP ratios.

5.4 Discussion

5.4.1 In-lake water quality and nutrient retention

Our scenario analysis showed that more lakes are expected to be macrophyte-dominated and have higher nutrient retention fractions in 2050 than in 2012, with the strongest changes for the sustainability-focused scenario. This increase in the number of macrophyte-dominated lakes conforms to the decreased nutrient loadings but may seem unexpected based on the temperature increases from the 2050 scenarios. In both scenarios, especially TP loadings decrease by among others improved connection to, and treatment of, sewage (see section 5.2.2). In the sustainability-focused scenario this is a result of deliberate actions to reduce nutrient pollution, whereas in the economy-focused scenario this is merely a result of technological developments. The lower TP loadings and a corresponding increase in TN:TP ratios in the 2050 scenarios compared to 2012 may decrease the risk of dominance by toxic phytoplankton species (Chen et al. 2013). Nevertheless, the effect of TN:TP ratios on phytoplankton nuisance is debatable (see section 5.1 and 5.4.2) and the rising water temperatures in our scenarios potentially increase the risk of phytoplankton instead of macrophyte dominance (Mooij et al. 2007; Paerl and Huisman 2008). Though, the latter also depends on the top-down control by the food web (Fragoso Jr et al. 2011).

In our 2050 scenarios, the increase in temperature is small relative to the decrease in TP loading (Fig. D.1 in Supplementary material D). We see a shift to more macrophyte-dominated lakes in 2050, especially for the sustainability-focused scenario with the lowest nutrient loadings. This suggests that the effect of nutrient load reduction prevails. Similarly, across 55 European lakes studies, eutrophication was the overriding stressor and in cases of paired nutrient-thermal stress, nutrient effects were more pronounced in (cross-)basin studies (cf., our study) than in mesocosm experiments (Birk et al. 2020). Other model simulations have also shown the negligible effect of temperature increase (i.e., less than 1 °C in our study) for the establishment of macrophytes, and chlorophyll-*a* levels at low nutrient loadings (Rolighed et al. 2016), potentially due to nutrient limitation (Fragoso Jr et al. 2011). On the other hand, warming may even improve water quality in subtropical lakes with year-round macrophyte presence (Fragoso Jr et al. 2011). Nevertheless, in the far future (e.g., 2100) when climate change is expected to play a larger role, the positive effect of nutrient reduction could be diminished, especially under the RCP8.5 scenario (van Vuuren et al. 2011; Golub et al. 2022).

Nutrient retention fractions mostly shifted to higher values between 2012 and the 2050 scenarios. We found a bimodal pattern in nutrient retention fractions that is explained by the ecosystem state, especially for the sustainability-focused scenario. The effect of macrophyte versus phytoplankton dominance on the nutrient retention fraction may have been even stronger when distinguishing an intermediate state of co-existence, in addition to strongly macrophyte- and algae dominated states sensu Bachmann et al. (2002). The bimodal pattern is in line with the theory that macrophyte-dominated lakes have a higher nutrient retention capacity than phytoplankton-dominated lakes (Hilt et al. 2017; van Wijk et al. 2021). The increase in the number of macrophyte-dominated lakes by decreased nutrient loading is thus accompanied by higher nutrient retention fractions. Also, temperature could affect nutrient retention, since higher epilimnion temperatures may directly lead to higher biochemical process rates and thus potentially more nutrient retention. However, direct temperature effects might be counteracted by an ecosystem state shift to phytoplankton dominance or by temporary stratification which may increase P release from the sediment (Woolway et al. 2021). The net effect of temperature thus depends on the sensitivity of lake system processes and state shifts to changes in temperature and nutrient loading, as well as on stratification regimes. Especially in the sustainability-focused scenario, the effect of change in ecosystem state on nutrient retention by strong nutrient load reductions prevails.

We chose to focus on nutrient retention fractions (i.e., nutrient retention efficiency) because they correct for the influence of nutrient loading on the absolute amount of nutrients retained. Still, the absolute amount of nutrients retained might be important in the context of nutrient conservation sensu van Wijk et al. (2021a). The lower the nutrient loading, the more lakes will have low absolute nutrient retention values (Supplementary material E) and the less nutrients are available for harvest and reuse. Nevertheless, macrophytes may be easier to harvest and reuse (e.g., Quilliam et al. (2015) and Bartodziej et al. (2017)) than phytoplankton. Thus, although the chance of macrophyte dominance is higher in lakes with low nutrient loading, they may still contribute to higher nutrient conservation potential. Our results show that even with relatively high nutrient loading (i.e., 2012 in Fig. 5.2), nutrient retention fractions are generally higher in macrophyte- than in phytoplankton-dominated lakes. This shows the importance of ecosystem state-dependent nutrient retention fractions versus absolute amounts. Furthermore, the nutrient retention fraction can directly be used to translate nutrient inflows into nutrient outflows. For example, higher nutrient retention fractions in macrophyte- compared to phytoplankton-dominated lakes result in relatively lower throughflow of nutrients to downstream systems. As such, low nutrient retention in phytoplankton-dominated lakes could result in downstream eutrophication issues.

5.4.2 TN:TP ratios of lake outflows

Lakes may alter TN:TP ratios between the in- and outflow depending on lake characteristics such as water depth and hydraulic residence time. For example, deeper waterbodies may retain relatively more P through settling whereas in shallower systems more sediment-water contact leads to higher denitrification rates (Maranger et al. 2018). Therefore, TN:TP ratios may positively correlate with water depth. Moreover, reservoirs have shorter residence times and lower TN:TP ratios than natural lakes (Maranger et al. 2018). Nevertheless, in our study differences among outflow TN:TP ratios of lakes were not related to lake depth or hydraulic residence time (Supplementary material F). We found that the effect of lakes on TN:TP ratios depends on the inflow TN:TP ratio and lake ecosystem state (Fig. 5.3 and 5.4).

A one-to-one relationship between in- and outflow TN:TP ratio would be expected when nutrients are proportionally retained. However, lakes are often nutrient sinks and nutrient-limited. Hence, relatively larger parts of the major limiting nutrient are used in biotic processes and can contribute to nutrient retention. The major limiting nutrient is thus expected to be relatively well retained, whereas the surplus of the other nutrients will remain in the water column and can flow out to downstream systems. As such, nutrients are retained in different proportions and, consequently, the nutrient ratio of the outflow of a lake may differ from the inflow. This nutrient limitation effect may also explain why in our study lakes with a low inflow TN:TP ratio (i.e., more likely N-limited) tend to have a lower TN:TP ratio at the outflow (i.e., relatively more P in the water column) than at the inflow, whereas lakes with higher TN:TP ratios (i.e., more likely P-limited) more often tend to have higher TN:TP ratios at the outflow (i.e., relatively more N in the water column) than in the inflow. Indeed, Elser et al. (2009) found that lakes with high TN:TP ratios were consistently P-limited. In general, the out- and inflow TN:TP ratios correlate positively, explaining the higher outflow TN:TP ratios in the 2050 scenarios compared to 2012 through lower inflow TN:TP ratios in 2012 (Fig. 5.3).

Furthermore, the regression line of macrophyte-dominated lakes deviates more from the 1:1 line than for phytoplankton-dominated lakes (Fig. 5.4). The different correlations between in- and outflow TN:TP ratios may be explained by the distinct nutrient uptake mechanisms of the dominating group of primary producers. Phytoplankton directly consumes nutrients from the water column. Though, next to some direct uptake by their leaves, rooting macrophytes may take up nutrients from the sediment (Granéli and Solander 1988). We assume that the sediment nutrient content depends on the nutrient loading into the water column at equilibrium, but the nutrient availability to macrophytes is modified by sediment characteristics and in-sediment nutrient retention. This decoupling of macrophyte nutrient uptake from the water column (Bachmann et al. 2002) may explain why in- and outflow TN:TP ratios correlate less in macrophyte- than phytoplankton-dominated lakes. Moreover, the interpretation of the TN:TP ratio relationships is complicated by the fact that, contrary to macrophytes, in our study the phytoplankton nutrient content is part of the total nutrient concentrations of the water column and water outflow. This might also explain the closer correlation between in- and outflow TN:TP ratios in phytoplankton- than in macrophyte-dominated systems.

Contrary to other studies, we found that whether lakes increase or decrease outflow TN:TP ratios depends on whether a lake is N- or P-limited. For example, studies of hundreds of US lakes found mostly higher out- than inflow TN:TP ratios, explained by relatively higher in-lake retention of P by burial compared to N loss by denitrification (Grantz et al. 2014; Maranger et al. 2018; Wu et al. 2022). According to our results, this would be expected to be lakes with relatively high inflow TN:TP ratios. Nevertheless, these US lake studies include relatively low input TN:TP ratios (e.g., on average 7.5 on a mass basis in Wu et al. (2022)). Thus, other studies do not report the TN:TP decreasing effect of more N-limited systems (i.e., low inflow TN:TP ratios) that we found. This might be explained by the relatively low TN:TP ratios captured in our 2012 simulations for China compared to historic (before 2007) data of temperate to tropical lakes with median in-lake TN:TP mass ratios of 10-32 (Abell et al. 2012). The relatively low TN:TP ratios in our study might be caused by the generally decreased inflow TN:TP ratios as calculated based on the in-river retention equation from (Behrendt and Opitz 2000) (Supplementary material B).

Our results suggest that when nutrient loading and inflow TN:TP ratios are sufficiently reduced to enable macrophyte dominance, macrophytes will augment the decrease in TN:TP ratios in the water outlet. However, when TN:TP ratios are too high, macrophyte dominance may aggravate TN:TP ratios. Furthermore, care should be taken in conclusions on the effect of TN:TP ratios on water quality because this, among others, depends on which nutrient is limiting in the receiving system. For example, higher outflow TN:TP ratios may improve the water quality of downstream P-limited lakes, but threaten N-limited coastal ecosystems (Wu et al. 2022). Moreover, which (toxic) phytoplankton species dominates depends on TN:TP ratios (Dolman et al. 2012), the nutrient forms (Glibert 2017), and the actual nutrient loading (Smith 1982; Guildford and Hecky 2000). Furthermore, which nutrient is limiting in the receiving waterbody may differ per season (Xu et al. 2015). Therefore, we call for more research on the combined effect of nutrient loadings and alterations in their TN:TP ratios on water quality, and careful consideration of how nutrient- and lake management will influence TN:TP ratios.

5.4.3 Social and scientific outlook

Our scenario study considers the effect of changes in nutrient loading and epilimnion temperatures through SSP and RCP scenarios. However, climate change may also alter precipitation which is positively related to nutrient loading by runoff (Özen et al. 2010; Jeppesen et al. 2011; Meerhoff et al. 2022). For example, in the far future, large increases in riverine N loading are projected by precipitation increases in highly-fertilized eastern China (Sinha et al. 2017). Moreover, changes in precipitation will affect water residence times and therewith nutrient retention. We did not include such changes in hydrology and associated nutrient loading and nutrient retention in our scenario study because of uncertainty in how precipitation regimes will change. In China, expected changes in precipitation may differ per region and season (Gao et al. 2012). For example, in the Yangtze River basin, it has been shown that this depends on interplays of local, regional, and global drives of change (Li et al. 2021a) but insignificant changes in annual mean precipitation are expected in the 2050s compared to 1961-1990 (Huang et al. 2011). When the effect of climate change on precipitation becomes more certain, future scenario studies can support water managers' understanding of the interplay between hydrology, nutrient loading, and nutrient retention.

In our study, we lumped the results into net retention of TN and TP, and their ratios. Through this, we made a first step to explore what water quality, nutrient retention, and downstream nutrient ratios may look like in 2050 for a large number of Chinese lakes. In the future, more detailed studies may help to better understand how TN:TP ratios will change based on specific nutrient retention processes such as denitrification and P retention by settling and consecutive burial. Also, exploration of the speciation of nutrients (e.g., particulate versus dissolved forms) in pollution sources and their role in nutrient retention processes is important to get a more thorough insight into how systems function and how water quality may develop in the future. The process-based PCLake+ model may be used for this because it includes the effect of different nutrient forms and retention processes. Moreover, the model is applied to various world regions (Janse et al. 2008; Janssen et al. 2019a; Coppens et al. 2020) and may, therefore, be used to test our findings for lakes around the world.

We analyzed the effect of lakes on nutrient transport to downstream systems as the change in nutrient loading between the lakes' in- and outflow. However, studies of how connected waterbodies influence each other's water quality through nutrient loading and nutrient retention are needed in more complex network settings to prevent inconvenient surprises. For example, flushing may decrease the likelihood of alternative stable states in chains of lakes but still, abrupt changes between states may be possible in time and space (Hilt et al. 2011). Also, water quality may be surprisingly uniform among waterbodies in a homogenous network despite a downstream increase in water and nutrient flows (van Gerven et al. 2017). Moreover, other means of connectivity could be considered, such as transport by organisms (Teurlincx et al. 2019). For example, in heterogeneous landscapes with many lakes, the degree of mobility of anglers can lead to three types of spatial patterns in fish populations, including sequential collapses (cf., the collapse of a line of dominoes) (Carpenter and Brock 2004). Carpenter and Brock (2004) conclude that a one-size-fits-all policy makes lake districts more vulnerable to change and this may be overcome by more lake-specific management approaches. We believe that studies of spatially connected systems may increase system understanding and help to find optimal water quality management strategies in hydrological networks.

5.5 Conclusion

We performed a scenario analysis of the effect of anthropogenic alterations of water temperature and (the ratio of) nutrient inputs on water quality and nutrient retention in 3482 Chinese lakes, and downstream nutrient loading. The effect of nutrient load reductions prevailed, showing that improved lake water quality (i.e., more macrophyte-dominated lakes), increased nutrient retention fractions and lower downstream nutrient loading go hand in hand. This is in line with the spatial feedback theory used in the Smart Nutrient Retention Network concept (van Wijk et al. 2021). However, TN:TP ratios may be altered more in macrophyte- than phytoplankton-dominated lakes, and the impact of this on downstream waterbodies depends on the inflow TN:TP ratios, the nutrient loadings, and the limiting nutrient in the receiving system. In our 2050 scenarios, increases in the inflow TN:TP ratio result in higher outflow TN:TP ratios in many of the studied lakes compared to 2012. The impact of these higher outflow TN:TP ratios on downstream systems will be waterbody-specific, therefore, we call for careful analysis of connected systems and goal setting to guide water quality management.

Despite the uncertainties around the downstream impacts of alterations in TN:TP ratios, our simulations show that a number of Chinese lakes are projected to have better ecological water quality in 2050 than in 2012. Still, most of the simulated lakes were phytoplankton-dominated. In the economy-focused scenario, water quality, nutrient retention, and nutrient loading (ratios) to downstream systems change only slightly compared to 2012. The sustainability-focused scenario shows a more promising future with 45% of the lakes being macrophyte-dominated with higher nutrient retention fractions and thus less nutrient loading to downstream ecosystems. The main reason for the expected water quality improvement lies in nutrient load reductions and the reinforcing feedback between nutrient loading, water quality and nutrient retention. Therefore, we conclude that earnest efforts are needed to drastically reduce nutrient loadings to reach this more sustainable future scenario for Chinese lakes, whilst minimizing epilimnetic temperature rise. Moreover, our study illustrates that water quality management around the globe could benefit even more from nutrient pollution reduction than one would expect at first sight.

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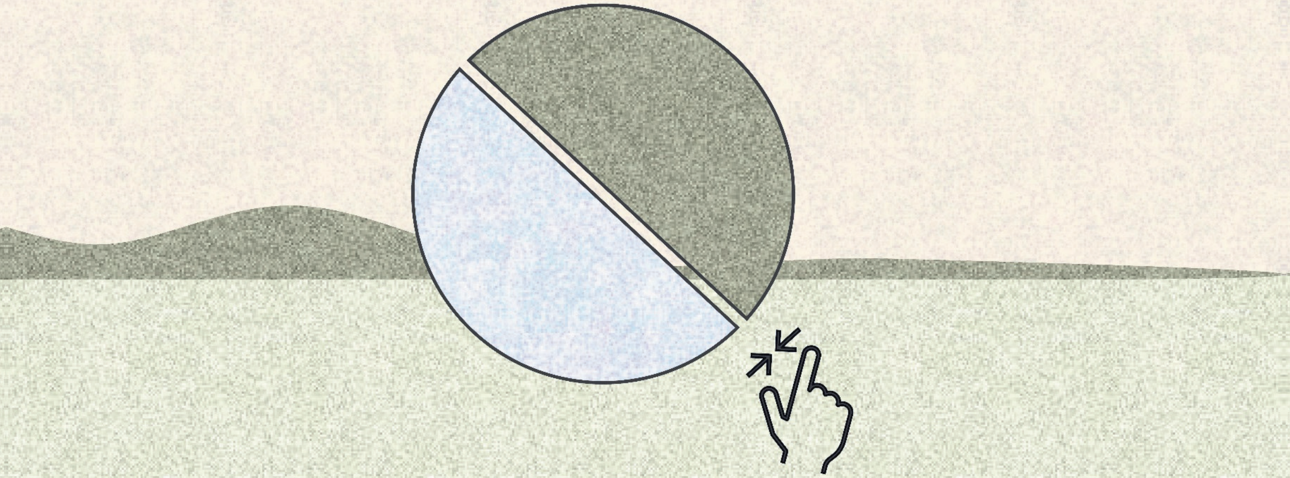
Chapter 6

A serious game approach for lake modeling and management: the EscapeBLOOM



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Abstract

Environmental models are valuable tools, yet, communication about model results between modelers and non-modelers is complicated by different levels of understanding. Game design may help to bridge this gap through learning by playing. Here we present the "EscapeBLOOM", a digital "Escape Room" in which teams aim to save a lake from a harmful algal bloom while learning about lake models. The game consists of multiple puzzles reflecting the process and choices made by professional modelers in a specific lake management case. We show that the EscapeBLOOM was positively received in multiple countries and cultures, and significantly contributed to perceived learning on lake modeling and nutrient management by non-modelers. Finally, we discuss the challenges and opportunities of our serious game to introduce models and related concepts. We envision that our serious game approach can inspire others to create their own "Escape-game" to aid the communication of environmental modeling cases.

6.1 Introduction

Mathematical models are valuable tools to study environmental systems in various ways including hypothesis formulation, improved understanding, prediction, and finding solutions (Janssen et al. 2015). Already in the second half of the 20th century, Vollenweider and colleagues built stochastic models to formulate hypotheses on the relationship between TP and chlorophyll-*a* (Vollenweider 1975; Rast and Lee 1978; Rast et al. 1983). Later, various aquatic ecosystem models were developed that led to a better understanding of, for example, connectivity between lakes, alternative stable states (Scheffer et al. 1993), and, aquatic food webs (Christensen and Pauly 1992). Moreover, various models are used for the prediction of global change in freshwater systems (Vanderkelen et al. 2020; Grant et al. 2021) or for finding solutions to environmental degradation (Janssen et al. 2019b).

All these purposes have led to a diverse modeling landscape with various model approaches, theories, and applications. As such, today's models fulfill a role that is synergistic to lab and field studies providing inspiration, filling in data gaps, and allowing for virtual experiments that are impossible in the real world (Janssen et al. 2019b). Although this model diversity should be celebrated for the provisioning of rich scientific insights (Janssen et al. 2015), communicating model results with non-modeling communities is complicated by different perspectives and disciplinary knowledge among people. The scientific community is therefore in need of a tool that bridges the gap between modelers and non-modelers, for example, by introducing environmental models and related concepts.

Challenges regarding communication and understanding of the complexity of problems are also recognized in participatory modeling processes and, in this context, game design (including gamification and serious games) is suggested as a promising approach to support social learning, engagement and motivation in an enjoyable environment (Bakhanova et al. 2020). Moreover, digital game-based learning, and serious games can supplement formal teaching through their potential to increase student's motivation and engagement to enhance learning outcomes (Madani et al. 2017). Especially when games have a friendly competition element (i.e., ludus games), they can stimulate motivation and contribute to more effective application of the learned material (Madani et al. 2017). A serious game distinguishes itself from other games by having a specific aim (e.g., an explicit educational purpose) in addition to mere entertainment (cf., Susi (2007); de Suarez et al. (2012); Aubert et al. (2018)). They support learning through trial and error by providing a safe learning environment (Aubert et al. 2018) and have been developed for numerous purposes in environmental management and real-word water issues (e.g., (Madani et al. 2017; Aubert et al. 2018).

Here, we propose a serious game approach in the form of a digital "Escape Room". An Escape Room typically is a physical room in which players are locked in order to solve a series of puzzles to escape from the room within a certain amount of time. In our digital serious game called the "EscapeBLOOM", players are taken along a storyline reflecting the process and choices made by professional modelers in a specific lake management case. By solving multiple challenges, players can find the single solution which represents the historic management of that lake. We created the game in Microsoft Excel in such a way that new challenges, additional background information, and clues appear when players provide correct (intermediate) answers. The game introduces three lake models (the lake branch of the 1-D hydrodynamic model GOTM (Burchard 1999; Golub et al. 2022), the simple lake eutrophication model GPLake (Chang et al. 2019) and the complex lake ecosystem model PCLake (Janse 1997)) and water quality management concepts in an interactive way, whilst having a time limitation to find the final solution. By allowing the players to experience modeling steps, we aim to increase the non-modelers' understanding of concepts and results that arise from a modeling exercise. Although we applied the serious game approach to a specific case, we envision that our methods can be employed beyond this case.

First, we present the storyline and challenges included in our EscapeBLOOM game. Next, we show how we used this serious game to effectively communicate modeling concepts and results of an environmental management case to non-modelers, and give some recommendations for game moderation. Finally, we discuss the challenges and opportunities of using a serious game approach to introduce models and related concepts by highlighting the key features of the EscapeBLOOM, discussing what sets our game apart and providing a future outlook. We envision that our serious game approach can inspire other modelers to create their own "Escape-game" to aid the communication of environmental modeling cases.

6.2 Methods of the EscapeBLOOM

The EscapeBLOOM takes players along on a story where they will help the fictitious "Prof. Clearwater" to find a solution to save a lake that experiences a harmful algal bloom, by solving multiple puzzles. The game story is introduced by Prof. Clearwater in the form of this text:

"Dear team, I'm sure that you know why I summoned you: I received a pressing phone call that there is a lake with a harmful algal BLOOM. I have to find a solution within one hour! Because otherwise the fish for today's dinner will die and I will be fired! Luckily I know 100 combinations of solutions to get lakes clean again! But which one to choose? I need your help to find the right solution. But time is limited… You will have to find the solution within one hour!"

When players continue to read the instructions from Prof. Clearwater, they will be guided through multiple challenges that they can find in the different sheets of the Microsoft Excel document of the game. The challenges reflect the process and choices made by a modeler for the management of a real lake (see Box 6.1), these include: getting to know the lake, collecting data, running and interpreting models, and deciding on individual measures. Once

Box 6.1: The example case of the EscapeBLOOM

This example of a historic case is captured in the EscapeBLOOM game. We anonymized the case to not give away the answers of the game.

The solution of the EscapeBLOOM presents the historic management of a real, man-made lake. Important ecosystem services of the lake are tourism, water regulation, and commercial shipping. Rich and diverse aquatic vegetation emerged soon after the creation of the lake, providing food for many water birds visiting the lake in late summer and autumn. The lush biodiversity was short-lived and, in the late 1960s, algal blooms developed as a result of eutrophication from multiple pollution sources. Bream became the dominant fish species while the flourishing bird population collapsed.

To turn the tide, in the 1970s nutrient pollution sources were reduced to such an extent that the algal blooms were diminished, though macrophytes did not recover yet. To reinforce the nutrient load reduction, two other measures were taken in the following decades. In the 1990s, the macrophytes in the lake reappeared, and algal blooms were reduced.

Which measures were being taken to reach this result? In the game, players will find the answer.

players complete one challenge, the next challenge will open up and they will be able to get another step closer to the final solution. When all challenges are completed within one hour, this will be celebrated in the "The grand finale" sheet.

Here, we first present the challenges as included in our player version of the EscapeBLOOM (available through https://doi.org/10.5281/zenodo.8116796 upon publication) without giving away the answers. Thereafter, we introduce multiple applications of the game, including an assessment of perceived learning by 30 students. Please note that the game's storyline can be adjusted to the wishes of the game moderators, like using a specific case study or different challenges. See Supplementary material A and B for details on how the game was technically created and designed, which can provide guidelines for potential new game development.

6.2.1 The challenges in the EscapeBLOOM

6.2.1.1 Challenge 1: Which lake?

The first challenge is to find out which lake has to be saved. For this, players have to 1) find a relevant scientific paper and 2) find the coordinates of the respective lake. The players are provided with text with clues towards the paper, a picture with hints about the lake, and table with lake coordinates. By combining information from all clues (empirical data, and information in openly available literature) it is possible to discover which lake the game is about.

6.2.1.2 Challenge 2: Diving into the lake

In the second challenge, players need to increase their understanding of the lake in terms of 1) lake stratification and 2) the maximum amount of chlorophyll-*a* as a measure of algae. The text of the challenge includes a table introducing two online available simple-to-use models (i.e., GOTM and GPLake). By applying the models with input data from literature (from challenge 1), this challenge can be solved.

6.2.1.3 Challenge 3: Where do the nutrients come from?

The aim of challenge 3 is to find the best management options to sufficiently reduce nutrient pollution. The challenge is split up into multiple tasks: 1) Identify the critical nutrient loading; 2) calculate current nutrient loading; 3) calculate nutrient load reduction per measure and find the most effective two measures; 4) evaluate whether these measures will sufficiently reduce the nutrient loading. Players are given a graph with output of the PCLake model on critical nutrient loading, a "Background report" with many numerical details on the nutrient pollution sources of the lake, and a storyline-text including suggested nutrient load reduction measures. The text of the storyline also provides more background information related to the results of challenge 2. By interpreting the graph and other information, a nutrient balance calculation can be performed to answer each sub-question.

6.2.1.4 Challenge 4: Additional measures

In the last challenge, Prof. Clearwater explains that more measures are needed to really restore the lake. The aim is to find two other measures in addition to nutrient load reduction. For this, players are provided with more storyline-text and a new sheet with a graphical “Decision Tree”. Questions in the Decision Tree help to decide on which measures would be worth considering. Players can make a management decision by combining all information provided throughout the game.

6.2.1.5 The grand finale

The game ends on the “The grand finale” sheet. Here, the storyline ends with a congratulatory message. Also, it provides instructions for the players to indicate that they solved the EscapeBLOOM. Based on this, game moderators are given the opportunity to declare a winner. After playing the game, the players have been introduced to three different lake models, and a whole suite of modeling related terms, methods and results.

6.2.2 Game application and perceived learning

The EscapeBLOOM was tested in a trial run and applied on multiple occasions with different audiences and purposes (Table 6.1). The game was generally played in teams of about 4 people, both in online meetings as well as in real life on one or multiple laptops. In each case, we asked the participants for qualitative feedback after playing the game. During an MSc course on water quality and quantity modeling, we also assessed the perceived learning of 30 students. During this course, in total 41 students played the EscapeBLOOM in teams of 2-4 people. They assessed their knowledge of 32 concepts and skills by filling out a questionnaire

(Supplementary material C). Per concept, each student was asked to give a rating of their perceived knowledge on a scale from 1 (not familiar) to 10 (expert). The questionnaire was filled out directly before and after playing the game to analyze whether playing the game influenced the perceived learning of these items. To correct for potential influences of conducting the questionnaire twice, control concepts were included in the questionnaire that are related to, but not included in the game. For these concepts, no perceived learning would be expected. In the end, 30 participants gave consent for the use of the outcomes in this study and fully completed the two questionnaires. We analyzed these results using a paired Two-sample Fisher-Pitman permutation test (R package coin; (Hothorn et al. 2013; Team 2021) for each concept.

6.3 Results

6.3.1 General reception of the EscapeBLOOM

The game received positive responses in terms of being well-designed and architected, clear, fun, and (moderately) challenging. Players expressed their appreciation for the interactive way of learning that the game offers (e.g., bringing fun and knowledge in water quality modeling and management). More specifically, they valued the gradual build-up of the game to introduce players to lake modeling (including model application), which also showed the importance of small details like recalculating and double-checking information. Additionally, they appreciated that the game is about a real case and concrete measures to address water quality issues (Box 6.1). The time limitation and competitive element that we as moderators included in the game received mixed responses. Where some participants appreciated the deadline, others felt their learning process was hampered by their ambition to be the first to finish the game. Multiple participants indicated interest in a publication of the game to be able to re-play it with colleagues, students or water authorities, or to adjust the game for application for other lakes or water management cases. This desire also proved itself in the application of the game in a Department Christmas Party

Table 6.1. EscapeBLOOM trail runs and applications.

Date	Purpose	Audience	Occasion	Location	Country
14 July 2022	Introduction to topic	11 Early career nutrient pollution scientists	Pilot run for conference workshop	Wageningen	The Netherlands
7 August 2022	Introduction to topic, networking	10 Limnologists with varying modeling experience	SIL22 Topical Workshop	Online, hosted from UFZ Magdeburg	Germany
1 December 2022	Fun and challenging activity with aquatic ecological content	20 Aquatic ecologists (i.e., stream ecologists, modelers, remote sensers, cyanobacterial experts)	Department Christmas Party	IGB Berlin	Germany
7 December 2022*	Learning by playing	41 Master students	MSc course “Modelling Future Water Stress”	Wageningen University & Research	The Netherlands
31 March 2023	Learning by playing	15 Master students	MSc course “Water & Environment Module 3 Integrated Catchment Modeling”	University of Chinese Academy of Sciences, Sino-Danish Center	China
25 June 2023	Introduction to topic, networking	21 Limnologists with varying modeling experience	GLEON 2023 Workshop	Ryn	Poland

*30 Students participated in the quantitative assessment of their perceived learning.

at IGB Berlin (Table 6.1). Moreover, players saw potential for the game to be applied as an educational tool on decision making and models for different audience levels if it would be simplified. We tested the EscapeBLOOM as an educational tool on modeling concepts, for which the results are presented below.

6.3.2 Perceived learning

The paired Two-sample Fisher-Pitman permutation test showed that there was a significant difference in the distribution of perceived knowledge by the MSc course students (*n* = 30) before and after playing the game for 12 of the 24 relevant concepts (Fig. 6.1). The EscapeBLOOM is focused on lake modeling and nutrient management in the context of alternative stable states. This is reflected in the concepts for which perceived knowledge increased, such as "Critical nutrient loading", "Ecological engineering", "Lake models", and "Nutrient load reduction" (Fig. 6.1). Furthermore, for example, the perceived knowledge of "Nutrient balance calculation" increased, which is a specific skill introduced in multiple steps in the game and a major input to models (Fig. 6.1). "Lake stratification" also stands out, which was a relatively new concept for the students that they explored in the game themselves and/or for which they asked support from the moderators. The six control concepts gave insignificant results, as would be expected for concepts that are irrelevant to the game (Fig. D.1 in Supplementary material D). Other concepts with insignificant differences were only briefly touched upon in the game, such as "Hydrological regulation", "Impact of fishery on water quality", and "Point/non-point sources of nutrients" (Fig. D.2 in Supplementary material D). The general skills of "Analytical thinking" and "Literature search" are applied in the game, but may not have been novel enough for the students to perceive learning (Fig. D.2 in Supplementary material D). Indeed, most students that played the game are MSc students who already have experience in these general skills from previous courses.

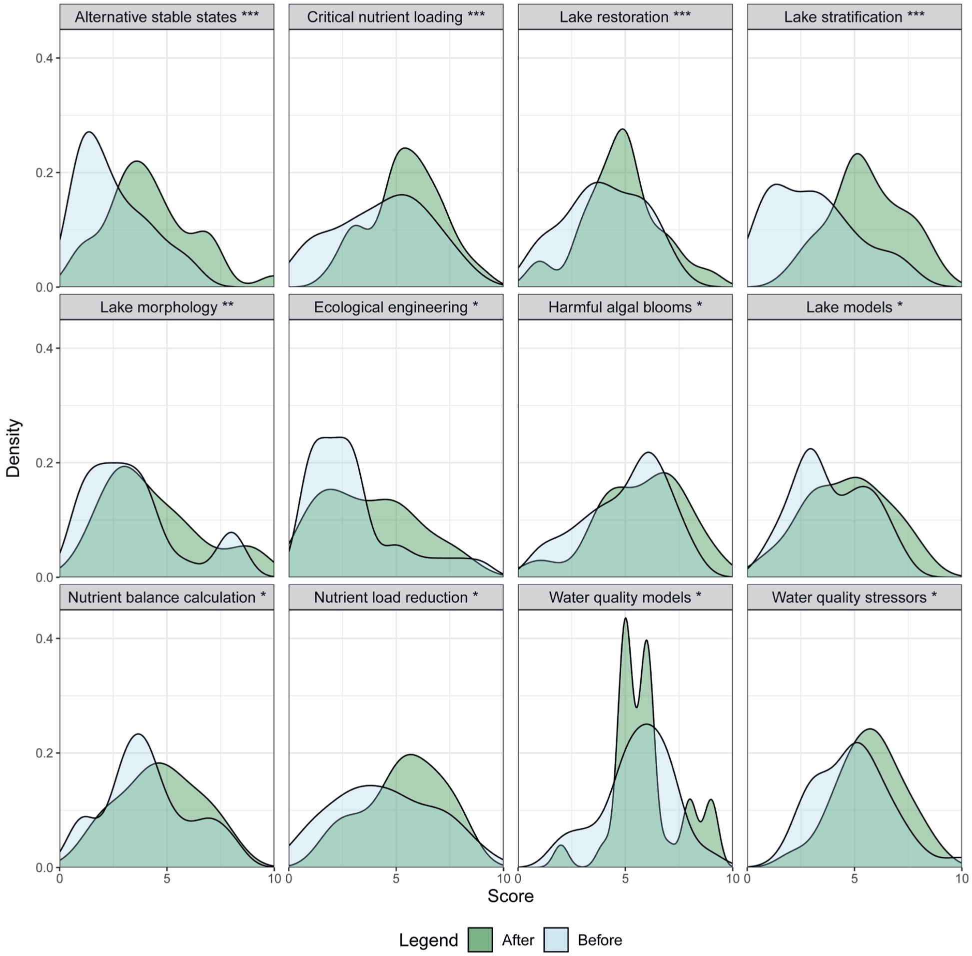

Figure 6.1. Kernel distribution of perceived learning scores (*n* = 30) with significant differences between scores before (light blue) and after (dark green) playing the game. The scores (x-axis) range between 0 (not familiar with the concept) to 10 (expert on the concept) and the y-axis gives the cumulative probability density (fraction of participants) based on the kernel density estimation method of Sheather and Jones (1991). The results of the students' scores were analyzed using a paired Two-sample Fisher-Pitman permutation test. Symbols indicate significance with ***: P<0.001, **: P<0.01, *: P<0.05).

6.3.3 Recommendations for game moderation

Based on our experience with application of the game on several occasions (Table 6.1), we have developed recommendations to organize and moderate the game. In our game applications, we always started and ended plenary, with an introduction before and discussion after playing the game to ensure a smooth start of the game and to enhance learning. During the gameplay, we were present as moderators for technical (e.g., see Supplementary material E) and some content-related questions without giving away answers to the game. We recommend tailoring the plenary sections to the background knowledge of the audience and the purpose of the game application. A pre-game verbal instruction on how to save the game on one's device and an introduction into how the game will be played is recommended to enhance clarity, solve technical issues, and help teams to start playing the game at the same time. Though, with the instructions in the game, it should be self-explanatory for players who would like to play the game on their own without a moderator. An additional introduction into water quality management and modeling is useful to get players on the same starting ground (e.g., course for MSc students in environmental sciences) but is redundant for people working in this field (e.g., limnologists). We recommend keeping such content-related introductions brief to allow players to explore the related concepts, and develop skills, through learning by playing.

During the gameplay, players may ask content-related questions which offer an opportunity for the moderator to explain concepts on a level that matches the player's background knowledge. Such interactions enhance the learning process. Hints are provided in the game at certain times to help players to proceed (see Supplementary material A and B for how these are automated by the use of a timer). If players keep struggling for a long time after these hints are provided, the moderator may give some tactical clues to ensure some progress. The latter is recommended to maintain the balance between challenging the players, and warranting a fun environment whilst going through the steps in the game, which all contribute to the learning process of the players.

After playing the game, we recommend a plenary recap and discussion of the solutions as a debriefing moment which is an important element of effective game-based learning (Madani et al. 2017). This includes a discussion of concepts and steps that were not yet clear to the players, helping players to reflect on all steps of the game, also if players failed to solve the game in time. It deepens knowledge and ascertains players to understand why they found the correct solution. Additionally, in this post-game plenary, it is recommended to demonstrate the relevance of the game by discussing the real case it represents. Although we excluded the discussion part in the quantitative assessment of perceived learning, both the discussion of the answers with the reasoning behind them and the explanation of the real case and solutions that the game is based on, were also highlighted by players as a one of the strong points of the game application. Additionally, for players that were more focused on quickly solving the game rather than the learning process, the post-game plenary provides a moment to learn and focus on the content. Furthermore, a discussion moment creates space to receive feedback to keep improving the game and to award a small prize to the team that solved the game first.

6.4 Discussion

6.4.1 Key features of the EscapeBLOOM

The EscapeBLOOM game is expected to be a useful educational tool for scientific research and practice in water quality management in lakes. During one round of the game spanning a time of 1-2 hours, the players apply and interpret three state-of-the-art mathematical models for water ecosystems across hydrodynamics and ecological processes (GOTM, PCLake, GPLake). As a result, the game would be highly valuable for those participants who do not have experience in environmental modeling, to rapidly acquire an idea of and experience with how the models work and how their results are interpreted. Moreover, such experience would be even more valuable for players who plan to use models for research and management. The game provides a shortcut for them to start learning about modeling in a unique way and pave the way for them towards a modeler.

Moreover, this game exhibits potential to connect modelers and non-modelers. Linking the communities of modelers (e.g., AEMON) and non-modelers (e.g., stakeholders, managers, policymakers) is essential to bring model outcomes to practice because many decision makers who are responsible for lake restoration have limited modeling research background but eagerly need the modeling outcomes to guide the management strategies. Despite the recent advances in modeling, communicating model results and their uncertainties with non-modeling communities remains challenging (Liu et al. 2008; Bannister et al. 2021). To this end, we deem that the EscapeBLOOM could bridge the gap between modelers and non-modelers. The EscapeBLOOM delivers the scientific background of modeling to non-modelers, and communicates the needs of non-modelers to modelers in occasions when non-modelers participate and inquiry about the modeling results, via a relaxing communication that is unique from other ways of interactions such as conferences. As a result, the EscapeBLOOM may increase the potential for successful communication and mutual understanding from both modelers and non-modelers.

In addition, the EscapeBLOOM game shows several strengths for education in water quality management. First, the game combines both technical details (i.e., referring to scientific publications and models) and non-scientific aspects (i.e., game, competition, entertainment), thereby aiming to be educative on scientific concepts and modeling whilst players are enjoying themselves at the same time. Second, by the “Escape Room” feature of the game, the players are actively engaged into the development of the storyline, thereby processing the information and knowledge in a more effective way. Such active learning has a clear advantage over the other ways of education (e.g., unidirectional report or presentation), where the participants usually acquire knowledge in a passive way and often experience lower efficiency in learning (Freeman et al. 2014). Finally, this game asks the participants to play in groups, so that the players from the same group work interactively to resolve the puzzles together. Such team-work has clear advantages, such as that the intellectual inputs from more than one person may increase the efficiency in work, and the participants could learn from each other and identify the strengths from other participants. The gaming process may increase the efficiency of learning while enhancing the entertainment experience. Indeed, the game has been tested in different countries and cultures, and it was well received (Table 6.1) so that it contributed to the perceived learning in water quality management (Fig. 6.1).

6.4.2 What sets the EscapeBLOOM apart

The EscapeBLOOM game has multiple strengths that set it apart from other serious games in the field of water quality management and its potential application. First, the EscapeBLOOM is a serious game that allows for preference elicitation. Such a type of game is particularly lacking for environmental management according to a systematic review among 43 existing serious games (Aubert et al. 2018). A typical serious game that enables eliciting the management preferences would have the following features: 1) allows the participation of both experts and citizens; 2) provides sufficient background information in a neutral way; 3) includes real world data; 4) allows the players to provide options for management and also the manager to make a decision on preference; and 5) has an IT interface to facilitate easy access and engagement. The EscapeBLOOM involves all the features above to promote the preference elicitation, thereby filling in the gap for serious games in environmental management, especially for water pollution. For example, in challenge 4 (Section 6.2.1.4), players can select different combinations of management strategies. Nevertheless, the EscapeBLOOM has been designed to evaluate the effectiveness of various potential management actions in advance (e.g., different management strategies in challenge 4). As a result, there is an optimized and right answer for each challenge in this game. In the future, the game could be redesigned to incorporate an algorithm without a right or a wrong answer concerning preferences (Aubert et al. 2018), whilst relaxing the Escape Room format.

Second, the EscapeBLOOM is among the few serious games that allows for both problem structuring and alternative exploration. Problem structuring includes procedures of cognitive mapping and stakeholder analysis, which helps to learn about the objectives to be considered and serve as an effective tool to frame the decision and identify who makes the decision (Marttunen et al. 2017; Aubert et al. 2018). In addition, alternative exploration allows the players to try out alternative management options in a safe trial environment before implementing in a real world (Tanes and Cemalcilar 2010), which could help to resolve a “wicked problem” that is difficult or impossible to solve because of the interconnected nature. The EscapeBLOOM starts from the point of view of a stakeholder and provides a storyline to help the players define the problem and objectives. Then, with a focus on modeling, this game allows the players to predict the outcomes of alternative management strategies. Therefore, the EscapeBLOOM further fulfills another expectation for serious games in environment management (Aubert et al. 2018).

Third, the EscapeBLOOM is the first game that focuses on lake restoration and management with a specific emphasis on in-lake processes. This is different from most existing serious game products that are designed from catchment management perspectives (Madani et al. 2017; Aubert et al. 2018). In fact, lakes are unique from one to another, thereby management strategies differ per lake (Abell et al. 2020). For example, many deep lakes with stable stratification would be prone to P precipitation (Kong et al. 2023), while shallower lakes could be more effectively (and more practical) restored by biomanipulation (e.g., fish removal) (Søndergaard et al. 2008). This poses a challenge in selecting management approaches for lake restoration. Here, the EscapeBLOOM provides an example for setting up the management strategy for a certain lake with 4 steps (challenges), which own the potential to be generalized and applied to many other lakes.

6.4.3 Future outlook

Based on the numerous feedback we have received after each game application (Table 6.1), there are multiple ways to further improve the EscapeBLOOM or to expand its application domain. Participants indicated options to adjust and apply the game to other cases, to include multiple management trajectories, and to simplify it for more general educational and entertainment purposes. We foresee that an easier and shorter version with less calculation-based challenges, more visuals, and more interactive clues on whether you are on the right track may be more suitable in an entertaining context (such as the Department Christmas Party at IGB Berlin). A version with hardly any drop-down answer options and mostly open questions (e.g., including answer ranges as explained in Supplementary material B) may be most suitable in educational settings to prevent guessing for solutions. Moreover, the game design can be tailored to specific learning outcomes since concepts or skills that received specific attention in the EscapeBLOOM were also the ones on which perceived knowledge increased (Fig. 6.1). Since the game is designed in Microsoft Excel, it is relatively easy to implement such adjustments, also when having little experience with coding. Nevertheless, Microsoft Excel does not run on every computer, therefore it could be worth to invest in a software independent version (e.g., using Java).

In our EscapeBLOOM, players were taken along steps that reflect the process and choices made by professional modelers in a specific lake management case including data collection, running models, interpreting model output, performing nutrient balance calculations and assessing management options. This design aimed to allow the players to experience different modeling steps to increase the non-modelers' understanding of concepts and results that arise from a modeling exercise. The storyline and outcomes of the challenges can easily be adjusted to apply the EscapeBLOOM approach to other lake management cases. With more effort, the challenges in the game can also be modified for other environmental management cases or different learning outcomes. Alternative learning outcomes may be to focus more on specific modeling steps, for example, on the input of models (e.g., data collection, processing and evaluation), model runs (e.g., adding other models or focus on one model more specifically), the model outcomes (e.g., interpreting and validating results) or management options (e.g., exploring the effect of measures by the application of models, discussing trade-offs between measures). A practical challenge is that one needs to invest time to create the game but we hope that we provided the tools to facilitate this approach (Supplementary material A, B, and a dummy version available through https://doi.org/10.5281/zenodo.8116796 upon publication). Even without adjusting the game as it is, different learning objectives may be achieved by giving specific attention to certain additive steps in the plenary discussion after playing the game (e.g., discussing the management options from a natural science and political perspective). The game itself can be used to make models, their input and output, and their processes more accessible.

6.5 Conclusion

We developed the EscapeBLOOM as a serious game to communicate environmental management and modeling concepts and results to non-modelers. The game was positively received during multiple applications in different countries and cultures, and was shown to contribute to perceived learning on lake modeling and nutrient management by non-modelers. We believe that the Escape Room feature of our game and its focus on lake models and water quality management make our game unique, yet its format is generally applicable. The EscapeBLOOM can be adjusted to target different audience groups and learning outcomes to expand its application range. We envision that our serious game approach can inspire others to create their own "Escape-game" to aid the communication of environmental modeling cases.

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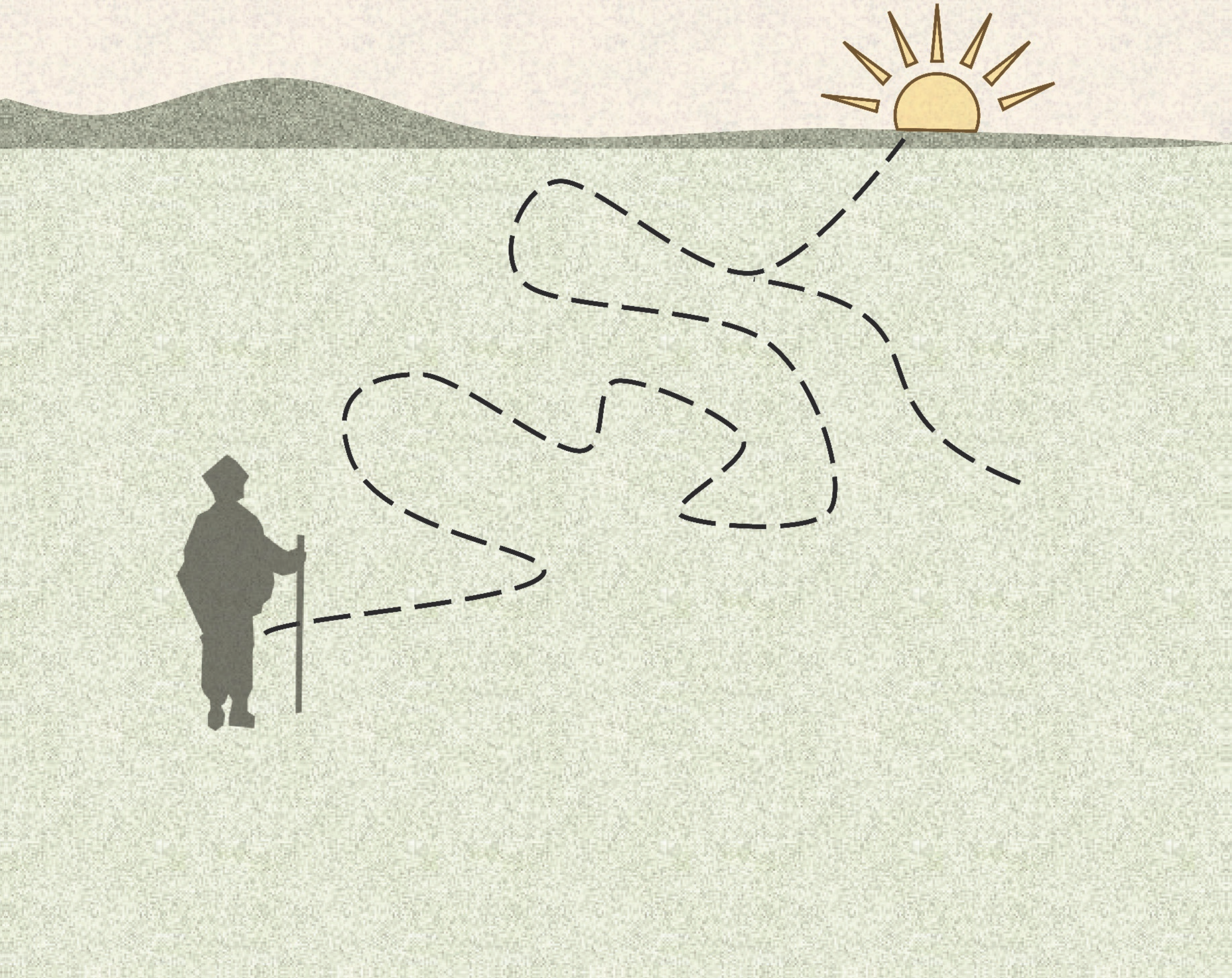
Chapter 7

General discussion



7 General discussion

Through this thesis I aimed to increase our understanding of nutrient retention in connected surface waters, to contribute to more sustainable management of water and nutrients. This Chapter, first, summarizes the main findings per research objective (Section 7.1 and Fig. 7.1). From Section 7.2 onwards, the implications of these findings are discussed in a broader context. For each research chapter, I indicate strengths and weaknesses (overview in Table 7.1) as well as lessons for the future. Here, I focus on how my thesis contributed to the advancements of *perspectives* (Section 7.2 and 7.4), *theories* (Section 7.2.1, 7.3.1 and 7.4.1) and *tools* (Section 7.3 and 7.5), to support water quality management. Lastly, I provide an outlook for SNRNs (Section 7.7).

7.1 Main findings

In short, first, I developed and presented the Smart Nutrient Retention Networks (SNRNs) concept as a novel *perspective* to focus water quality management on nutrient retention in networks of surface waters to support nutrient conservation (Chapter 1 and 2, objective 1). The effect of ecosystem state on nutrient retention as part of the newly developed spatial feedback *theory* is an important new focus, but I conclude that relatively simple and versatile dynamic models are lacking to model this in hydrological networks. Therefore, I developed two model *tools* to fill this gap: GPLake-M and GPLake-R (Chapter 3 and 4, objective 2). Moreover, I performed a scenario analysis of thousands of Chinese lakes to inform management *perspectives* by increasing understanding of how nutrient retention may influence nutrient ratios and their transport to downstream systems (Chapter 5, objective 3). The development of GPLake-M and the scenario analysis of Chinese lakes contributed to *theoretical* insights in lake ecosystem state and feedbacks of nutrient retention. Lastly, I developed the EscapeBLOOM as a communication *tool* to increase the non-modelers' understanding of concepts and results that arise from a modeling exercise (Chapter 6, objective 4).

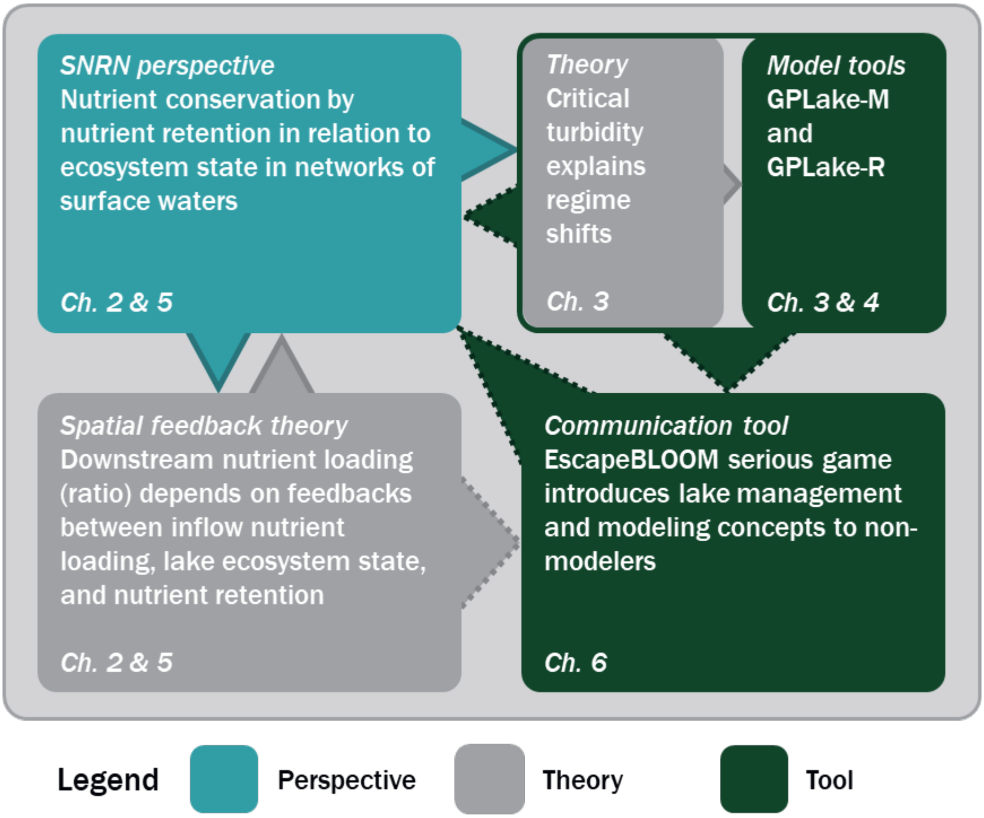


Figure 7.1. Overview of the interconnectedness of the main perspective, theories, and tools (colored boxes) resulting from the research chapters (Ch.) of this thesis. Closed triangles represent connections strongly present in this thesis, dashed triangles indicate connections that can be further developed in the future.

7.1.1 Develop the SNRN concept based on existing knowledge of nutrient retention in surface waters (objective 1)

In Chapter 2, I presented existing literature to develop and introduce the SNRN concept. SNRNs are aimed at nutrient conservation by focusing water quality management on nutrient retention in networks of surface waters (Fig. 7.1). Interventions to alter hydrology or to stimulate the presence of macrophytes can be used to shape local nutrient retention with potential network-wide cascading effects of improved water quality. I argued that successful nutrient conservation – even at a local level – through SNRN management strategies requires clearly formulated goals and catchment-wide system understanding. To support such system understanding and the development of SNRN management strategies, I identified a lack of nutrient retention models that include the self-reinforcing feedback loop of ecological water quality, nutrient retention, and nutrient loading in networks of inland waters in relation to management options. More broadly, I concluded that SNRNs can be one component of a sustainable future as they are designed around biogeochemical nutrient cycling processes and contribute directly to at least 3 UN Sustainable Development Goals (SDGs): zero hunger (SDG 2), clean water and sanitation (SDG 6), and responsible consumption and production (SDG 12) (United Nations 2015).

7.1.2 Support the development of SNRNs through relatively simple and versatile dynamic models that are rooted in resource competition theory (objective 2)

In Chapter 3 and 4 I presented two novel models that I developed as building blocks to simulate nutrient retention in relation to ecosystem state in networks of lakes: GPLake-M and GPLake-R (Fig. 7.1). In Chapter 3, I presented the new graphical and mathematical GPLake-M model as a novel approach to describe regime shifts in shallow lakes that is rooted in resource competition *theory* and the critical turbidity concept. This work supports the fundamental understanding of regime shifts in shallow lakes (Fig. 7.1) and provides a starting point for further mechanistic and management-focused explorations and model development. Especially the critical turbidity concept and the relation between light-limited submerged macrophytes and nutrient-limited phytoplankton might provide a new focus for empirical aquatic ecological research and water quality monitoring programs. Next, in Chapter 4, I build on the GPLake-M model to develop the new GPLake-R model. To my knowledge, this is the first versatile process-based and mass-balanced model of nutrient retention in relation to ecosystem state under alternative stable states in shallow lakes. GPLake-R captures the hysteretic pattern from the more complex PCLake model, with macrophyte-dominated lakes having higher P retention than phytoplankton-dominated lakes. I believe that the relatively simple and versatile GPLake-R model is a major step in the development of a model *tool* to support development of Smart Nutrient Retention Networks because it includes the feedback between ecosystem state, nutrient retention, and nutrient loading.

7.1.3 Increase understanding of how nutrient retention may influence nutrient ratios and their transport to downstream systems (objective 3)

In Chapter 5, I analyzed lake ecosystem state, in-lake nutrient retention, and nutrient transport (ratios) to downstream systems by 2050 under a low climate change and sustainability-focused, and a high climate change and economy-focused scenario for 3482 Chinese lakes using the relatively complex lake ecosystem model PCLake+. This is an example of how modeling *tools* can be used to increase *theoretical* insight (i.e., system understanding), eventually aiming to support the development water quality management *perspectives*. Here, a number of Chinese lakes was projected to have better ecological water quality in 2050 than in 2012. More specifically, the effect of nutrient load reductions prevailed in the scenario analysis, showing that improved lake water quality (i.e., more macrophyte-dominated lakes), higher in-lake nutrient retention fractions, and lower nutrient transport to downstream waterbodies go hand in hand (Fig. 7.1). Furthermore, TN:TP ratios may be altered more in macrophyte- than phytoplankton-dominated lakes, and the impact of this on downstream waterbodies depends on the inflow TN:TP ratios, the nutrient loadings, and the limiting nutrient in the receiving system (Fig. 7.1). Altogether, Chapter 5 concludes that earnest efforts are needed to drastically reduce nutrient loadings to reach the more sustainable future scenario for Chinese lakes, whilst minimizing temperature rise. On the positive side, this study illustrates that water quality management could benefit even more from nutrient pollution reduction than one would expect at first sight.

7.1.4 Develop a tool to interactively increase the non-modelers' understanding of concepts and results that arise from a lake modeling exercise (objective 4)

When we have *theoretical* insights, novel *perspectives*, or *tools*, science communication is essential to put it into practice. As an — hopefully inspirational — example, in Chapter 6, I presented the EscapeBLOOM. This is a newly developed serious game to interactively communicate lake management and modeling concepts and results to non-modelers (Fig. 7.1). The game was positively received during multiple applications in different countries and cultures, and significantly contributed to perceived learning on lake modeling and nutrient management by students in environmental sciences. Based on the feedback on the EscapeBLOOM, I envision that this serious game can be applied, modified, or serve as inspiration for others to create their own "Escape-game" as *tool* to aid the communication of water quality management — or other environmental — modeling cases.

7.2 The Smart Nutrient Retention Network perspective

7.2.1 Nutrient retention theories and perspectives

The SNRN *perspective* to use nutrient retention in water quality management and to reuse retained nutrients (Chapter 1) is in itself not new, but the focus that I put on ecosystem states in networks of surface waters is. Examples from nutrient retention and reuse range from traditional approaches to recycle water and nutrients in rice fields (Yin et al. 1993), up to constructed wetlands as green treatment technology (Wu et al. 2015). Whereas nutrient conservation is more common in (sub)tropical regions, the water systems in the northern temperate zone tend to be strongly influenced by humans. Here, for example, legacies of inefficient nutrient use across watersheds hamper effective nutrient load reduction (Jarvie et al. 2013; Sharpley et al. 2013). Over the last decades, Nature Based Solutions have been gaining ground to modulate natural process to, amongst others, contribute to water purification (Jarosiewicz et al. 2022). SNRN management strategies would fit in such nature-based solutions approach, especially in highly modified and controlled water systems such as lowland western Europe.

With the development of the SNRN concept, also a new spatial feedback *theory* emerged that includes the role of ecosystem state in nutrient retention in networks of surface waterbodies (Table 7.1). The network *perspective* of SNRNs is also present in other concepts and *theories* on hydrologically connected systems, but these are not as explicitly focused on the effect ecosystem state on nutrient retention (Table 7.1). For example, the Nutrient Spiraling concept applies to stream-lake-stream systems (Newbold et al. 1981; Baker et al. 2016), the Serial Discontinuity Concept for running waters such as rivers and streams (Stanford and Ward 1983), and the Nitrogen Cascade phenomenon between the atmosphere, terrestrial ecosystems and aquatic ecosystems (Galloway et al. 2003). I think SNRNs are most closely linked to the freshwater pipe concept which focusses on biogeochemical processing in freshwaters along the terrestrial-ocean continuum (Cole et al. 2007; Maranger et al. 2018).

Originally the freshwater pipe concept was presented as a carbon (C) cycling model (Cole et al. 2007)). Recently, Maranger et al. (2018) developed a framework to explore C:N:P stoichiometry along the freshwater pipe. Here an “active pipe” refers to aquatic systems that influence C:N:P ratios between the terrestrial inputs and eventual export into the ocean (Maranger et al. 2018). Since lakes — and their ecosystem state — influence N:P ratios (Chapter 5), they can be considered an important element of an active pipe. Also SNRNs may form an active pipe, however this may not always be desirable. Nutrient load reduction in freshwater systems is generally beneficial to reduce eutrophication, but the change in nutrient ratios may be undesirable because it may alter food web dynamics and which (phytoplankton) species proliferate (Elser et al. 2009; also see Chapter 5 and Section 7.4).

The focus on ecosystem states in the SNRN *perspective* was inspired by *theory* on alternative stable states in shallow lakes (Scheffer et al. 1993) (Scheffer et al. 1993). Nevertheless, the general applicability of such abrupt regime shifts between alternative stable states is under debate, since also more gradual or non-hysteretic shifts between ecosystem states in shallow lakes are possible (Jeppesen et al. 2007; Sayer et al. 2010). I consider lakes with hysteretic relations between nutrient loading and ecosystem states as the most ideal case to influence ecological nutrient retention in networks of connected shallow lakes. Especially under such circumstances, local management actions may have more effect than one would expect at first sight (e.g., Chapter 5). In waterbodies with less abrupt nutrient load-response curves (also see Chapter 4), the dominance of macrophytes instead of phytoplankton is still relevant for nutrient retention and may support downstream water quality and the potential for nutrient conservation.

7.2.2 Lessons from nutrient retention models

In Chapter 2, I discussed existing freshwater models that account for nutrient retention (overview table in Supplementary material C of Chapter 2). Here the analysis was focused on models at a catchment or global scale, and models for individual waterbodies. I concluded that nutrient retention models are missing that include management options and the self-reinforcing feedback loop of ecological water quality, nutrient retention, and nutrient loading in networks of inland waters. Still, nutrient transport in connected waterbodies (mostly chains of lakes) has been modeled in process-based ways before.

Two examples show that internal nutrient loading may complicate modeling of nutrient retention and transport. First, already in the 1980’s, (Ahlgren 1980) performed computer simulations of a chain of four shallow eutrophic, N-limited lakes in Sweden where sewage input was diverted. For P, the model worked best without nutrient retention, probably because excessive internal P loading driven by wind mixing counterbalanced sedimentation

(Ahlgren 1980). Second, Epstein et al. (2013) applied the Lake2K model to a hypothetical chain of four oligotrophic sub-alpine lakes that form net nutrient sources in summer. This ecosystem model for stratifying lakes among others includes nutrient mass balances and phytoplankton biomass (Epstein et al. 2013). A simple constant estimate of nutrient loading was applied to represent internal loading by benthic primary producers (i.e., benthic algal N-fixation and submerged macrophyte senescence in summer) (Epstein et al. 2013). The model exercise showed that the upstream lakes had most effect on nutrient conversion and buffering, and that mass export increases in downstream direction. When developing SNRNs, this possibility of (oligotrophic) lakes being nutrient sources should be kept in mind. Although exceptions exist, still, most lakes are expected to be net sinks of N and P (Wu et al. 2022).

Despite serving different purposes, these examples can give insights on how to model connected systems. For the water balance, the easiest approach is to assume that evaporation and precipitation at the lake surfaces are balanced, leading to an outflow that equals the inflows (Ahlgren 1980). The study by Epstein et al. (2013) exemplifies that the effect of the spatial configuration of lakes can be easily interpreted by assuming all lakes have the same watershed (and thus water balance). Moreover, they argue that in small, lake-populated watersheds the effect of connecting streams channels may be negligible (Epstein et al. 2013). Also, therefore, when starting to model lake networks to develop SNRNs, it would be easiest to start off with example cases in which these three hydrological assumptions are justified. Based on the latter requirement, simple cases of lake networks to explore in the context of SNRNs could, for example, be the connected lakes in Attenborough Nature Reserve in the United Kingdom (Cross et al. 2014), the Frisian Lakes in the Netherlands (Kramer et al. 2023), the Masurian Lake District in Poland, and many other lake-rich areas in Europe.

7.3 Theories and tools for SNRN development

7.3.1 Mechanistic understanding and modeling of regime shifts

The GPLake-M and GPLake-R models (Chapter 3 and 4) build on Tilman's (1982) seminal resource competition *theory*, and Huisman and Weissing's (1994; 1995) *theoretical* models of phytoplankton under nutrient- and light limitation. However, when using empirically relevant parameter settings for competitive strength for nutrients and light, and the relative nutrient to light limitation switch points for submerged macrophytes and phytoplankton, these *theoretical* models suggest co-existence at intermediate nutrient loadings rather than alternative stable states described by Scheffer (1990) and Scheffer et al. (1993) (Supplementary material A of Chapter 3). Still, Scheffer's (1990) critical turbidity concept helps to describe regime shifts in shallow temperate lakes in GPLake-M. At the same time, each model equilibria set of GPLake-M can be understood by the *theoretical* models of Tilman (1982) and Huisman and Weissing (1994; 1995), and layered extensions thereof by van Gerven et al. (2015) (Table 7.1). However, the abrupt regime shifts in GPLake-M are unlikely to be found in empirical data (Jeppesen et al. 2007; Sayer et al. 2010; Davidson et al. 2023). In GPLake-R this modeling approach is advanced to dynamically capture either gradual or abrupt responses of lake ecosystem state to nutrient loading with potential coexistence of macrophytes and phytoplankton around critical nutrient loadings (Table 7.1). By its dynamic nature, the GPLake-R model is both suitable to model long-term equilibrium ecosystem states, as well as temporal processes (e.g., hydrological interventions and timing of regime shifts). Moreover, by explicitly incorporating the relation between ecosystem state and nutrient retention, GPLake-R provides a basis to model the spatial feedback underlaying the SNRN *perspective* (Chapter 2; Table 7.1).

Next to abrupt regime shifts, GPLake-M applies Liebig's law of the minimum so that either nutrients or light are limiting. This approach is in line with the original GPLake model (Chang et al. 2019), and the more recent GPLake-S model to give a worst case estimate of phytoplankton levels under P and N loading (Chang et al. 2022). Still, co-limitation of nutrients and light may occur (cf., Huisman and Weissing (1995)) and could theoretically lead to either stable species coexistence or alternative stable states (Brauer et al. 2012). With GPLake-R it is now possible to simulate co-limitation of nutrients and light in macrophytes and phytoplankton, and coexistence of macrophytes and phytoplankton around critical nutrient loadings. Nevertheless, co-limitation of nutrients and light is most pronounced in N-limited systems (Healey 1985) and may therefore not be as relevant to the P focused GPLake-type of models.

Finally, both GPLake-type models presented in this thesis use areal units. This may be less intuitive for those with an empirical water quality background, where concentration units are more common (Table 7.1). However, in the PCLake+ model all state variables are expressed in masses per m^2 to maintain the mass balance in the exchange between compartments with different water volumes (Janssen et al. 2019a). Additionally, in GPLake-M, state variables are expressed per m^2 to enhance the comparison between macrophytes and phytoplankton (Chapter 3; Table 7.1). Moreover, the graphical GPLake-M model is in line with typical PCLake(+) output, presenting ecosystem state in relation to areal nutrient loading (e.g., Janse et al. (2010) and Janssen et al. (2019b)). Additionally, Chapra (1975) argued that areal P retention processes should better correlate to areal than volumetric water loads. This may translate to nutrient retention rates being more strongly related to areal nutrient loading rather than nutrient concentrations. In this line, in the GPLake-R model the nutrient retention rate is coupled to the incoming areal nutrient loading through the load-response curves (Chapter 4). In the end, model and measurement results with areal and volumetric units can easily be converted into one another using lake depth. Still, awareness and expression of the use of different units among communities is important to avoid communication issues. This also holds for other unit confusions that may arise due to (de)coupling of nutrient and water inflows (Supplementary material F of Chapter 3) and the concentration unit of Vollenweider's normalized nutrient loading (Supplementary material G of Chapter 3).

7.3.2 Future outlook for SNRN modeling tools

In this thesis, I showed that GPLake-M and GPLake-R capture the main patterns from the more complex PCLake model, however these two models are not yet applied to real world cases which limits assessment of their performance in practice (Table 7.1). Olson and Jones (2022) developed another numerical and conceptual model that — at first sight — produces a similar chlorophyll (i.e., for phytoplankton) to TP load-response curve as the GPLake-type models. They calibrated their model with chlorophyll and TP concentration data from the U.S. National Lakes Assessment, whilst lacking hydrologic and elemental load data (Olson and Jones 2022). In the original GPLake model, such data lacks were overcome by using normalized P loading (Vollenweider 1975; Jones and Lee 1986) for field, lab and model data (Chang et al. 2019). GPLake-M and GPLake-R could still benefit from empirical testing for macrophyte versus phytoplankton dominance, and nutrient retention, respectively. For future application and testing of these mass-balanced models, nutrient loadings can be calculated from hydrological loading data together with inflowing nutrient concentrations. Moreover, GPLake-M and GPLake-R are in principle suitable to study different spatial patterns of nutrient and water inflows, which have been shown to be important for the success of lake restoration measures (Janssen et al. 2019b) and may be especially relevant in networks of lakes.

The GPLake-type models developed in this thesis (Chapter 3 and 4) are currently parameterized to for summer averages (Table 7.1), following the example from Supplementary material A of Chapter 1. Summer averages are relevant for eutrophication management because they present maximum levels of phytoplankton (and macrophytes) that can cause nuisance, whereas annual averages may be more relevant in the context of long-term nutrient retention management in hydrological networks.

Summer average nutrient retention can potentially be higher due to temporary nutrient storage in (dead) primary producer biomass, which may partly be released again in other seasons (Landers 1982). In the scenario analysis for Chinese lakes (Chapter 5) this was considered by analyzing annual averaged model output. Therefore, the resulting insights in nutrient retention and downstream nutrient loading may inform long-term management of nutrient retention and transport. Especially for GPLake-R (Chapter 4) to be applied in an SNRN modeling *tool*, a next step would be to also parameterize the model for annual averages. The model is then expected to capture the nutrient retention pattern as presented for a chain of lakes in Supplementary material B of Chapter 1.

To fill the gap in modeling *tools* on the level of lake ecosystem networks, recently, PCLakeS+ was developed as a complex lake meta-ecosystem version of the PCLake+ model (Kramer et al. 2023). With PCLakeS+ complex lake networks can be modeled, showing the importance of the spatial configuration of lakes and the influence of the food web on nutrient retention and transport (Kramer et al. 2023). Whereas GPLake-type models (Chapter 3 and 4) are intended to be relatively simple and to give a first diagnosis of lake water quality (e.g., Chang et al. (2019)) (Table 7.1), the PCLakeS+ approach is more detailed and complex, both in terms of model input and output. These differences result in a trade-off between input data requirements, model run times, and skills required to run the model (lower in GPLake approach) versus the level of detail at which conclusions can be drawn (higher in PCLakeS+ approach). In line with Janssen et al. (2015), I see the parallel development of these diverse approaches as a strength because each approach may serve its own nice. Therefore, I also introduced models of diverse levels of complexity in the EscapeBLOOM serious game (Chapter 6). Time will tell whether one, the other or both approaches are more suitable to support the development of SNRNs.

7.4 Scenario analysis using a lake modeling tool

7.4.1 Theoretical insights for SNRNs

The scenario analysis with the PCLake+ model confirmed the spatial feedback *theory* introduced in Chapter 2 and provided a *theoretical* direction on how downstream TN:TP ratios are influenced by nutrient retention in lakes (Chapter 5; Table 7.1). First, I found that the bimodal pattern of in-lake nutrient retention fractions among the simulated lakes correspond with the lake ecosystem states, with macrophyte-dominated lakes having a higher nutrient retention fraction. Also, the scenarios resulted in higher numbers of macrophyte-dominated lakes when nutrient loading decreased. Together with the reasoning that nutrient flows to downstream systems decrease when nutrient retention increases, this supports the spatial feedback *theory* (Chapter 2) that when nutrient loading decreases, ecosystem state improves, which after a regime shift enhances nutrient retention and decreases nutrient loading to downstream systems, where the process may repeat itself. Nevertheless, this scenario analysis is based on a single lake model (PCLake+) and an earlier version of the model (PCLake) has shown such relationships before (Supplementary material A of Chapter 2; Table 7.1). Therefore, additional studies with different models or empirical data are welcome to confirm our findings. Still, this study (Chapter 5) for the first time demonstrated that this relationship also holds under plausible future scenarios for a wide variety of lakes.

Second, I showed that TN:TP ratios of lake outflows only partly correlate with inflow TN:TP ratios, and also depend on nutrient retention through nutrient limitation and lake ecosystem state. Maranger et al. (2018) suggested that nutrient retention may alter TN:TP ratios because N and P retention processes differ. Additionally, Wu et al. (2022) found most of the 5622 lakes in their global study to more strongly retain P than N, thus increasing TN:TP ratios. I showed a mixed picture, with low TN:TP inflow lakes decreasing outflow TN:TP ratios and high TN:TP inflow lakes increasing outflow TN:TP. Moreover, this pattern is amplified in macrophyte-dominated lakes. As a *theoretical* explanation I suggest that the major limiting nutrient is relatively well retained, resulting in increased TN:TP ratios in P-limited lakes (i.e., more likely at high inflow TN:TP (Guildford and Hecky 2000; Elser et al. 2009)) and vice versa for N-limited lakes. I did not find scientific evidence for disproportional N and P retention in macrophyte- or phytoplankton-dominated lakes, but the stronger correlation between in- and outflow TN:TP ratios in phytoplankton-dominated lakes may be explained by their stronger coupling to nutrients in the water column.

7.4.2 Lessons for scenario analyses

In Chapter 5, I performed a scenario analysis to explore different plausible futures for water quality in Chinese lakes. This type of scenario analysis is also called an "explorative scenario" (IPBES 2016) and typically is used to explore multiple alternative futures (e.g., Wang et al. (2020)). I focused on two alternative scenarios for 2050, to keep run times in check to study >3000 lakes. In our study, a number of Chinese lakes are projected to have better ecological water quality in 2050 than in 2012 (Chapter 5). This trend is in line with the reduction in risk of harmful algal brooms in freshwater ecosystems according to the high ambition scenario for 2070 from the PBL Netherlands Environmental Assessment Agency (Ligtvoet et al. 2023). Alternatively, "target-seeking scenarios" can be used to develop multiple pathways (e.g., alternative management options in Table 7.1) to reach an agreed-upon future target (IPBES 2016), as applied in the back-casting approach of Li et al. (2019). They found that in >9 out of 54 nutrient use efficiency scenarios, coastal eutrophication targets for nutrient export by three rivers in China would be met (Li et al. 2019). Target-seeking scenario analyses may be more suitable to inform management decisions for specific case studies, whereas our exploratory approach was aimed at providing insight in potential water quality futures (e.g., under different climate change scenarios; Table 7.1).

In our study, the effect of nutrient load reduction prevailed over that of climate change. Moe et al. (2019) also concluded that nutrient concentrations were a more important driver that climate change in their worst-case scenario (cf., economy-focused scenario in Chapter 5) for a Norwegian lake. Similar to our study, they neither accounted for the indirect effects of climate change on nutrient loading and water flows (Table 7.1), and they suggest that their Bayesian network modeling approach could be an underestimation of the future lake status (Moe et al. 2019). Because of the large spatial coverage of our study, the uncertainty in the local climatic changes on precipitation patterns (Gao et al. 2012; Li et al. 2021a) hampers us to draw such conclusions. Here, additional explorative scenarios could advance insight in the relative importance of potential changes in precipitation patterns and whether this should be considered when developing management strategies.

7.5 Serious games as science communication tool

7.5.1 Serious game availability and development

In Chapter 6, I presented the newly developed digital EscapeBLOOM serious game that among others introduces freely available lake models. There are ample serious games about water-related issues with formats and aims varying from board games to IT interfaces and awareness raising to training (e.g., see the review by Aubert et al. (2018)). Although many serious games are available for free (Stanitsas et al. 2019), in scientific publications the availability of the serious games often remains unexplained (Madani et al. 2017). I intend to make the EscapeBLOOM game freely available, together with a dummy version displaying the techniques to create a similar digital escape room, upon publication of Chapter 6 in a scientific journal. Additionally, details on how the game was technically created and designed can already be found in Supplementary material A and B of Chapter 6. By sharing the techniques to create the serious game, I hope to open opportunities for others to modify and apply the serious game for their own purposes.

During the development and application of the EscapeBLOOM, I experienced that it may be challenging to specify the target audience and game format suitable for the aim of the game and its success. In case of the EscapeBLOOM, the audience turned out larger than expected. After initially being designed for limnologists with limited modeling background, multiple people showed interest in application of the game in (university) education. In both professional scientific and educational settings, the game was well received (Table 6.1). The digital escape room format worked well to introduce lake models and concepts (Table 7.1). However, when aiming for in-depth discussions and development of management strategies, other game formats (e.g., including role-play (Dahdouh-Guebas et al. 2022)) may be more suitable (Table 7.1). Lastly, I included a quantitative analysis of perceived learning in one application of the game but got the impression that this scientific endeavor may influence the enjoyment and learning process. In such studies it is essential to include controls (e.g., control concepts, Chapter 6) to correct for such effects on the learning, but it may be impossible to avoid any effect on the process.

7.5.2 Lessons for serious games for SNRNs

In the context of water quality management, our EscapeBLOOM game stands apart by being focused on lake restoration, in-lake processes, and lake modeling. Others have also expressed the desire to develop games related to lakes and models, for example, with a focus on social-economic decision making dynamics (Carpenter and Brock 2004). In the EscapeBLOOM (Chapter 6), the aim was to introduce water quality management concepts and lake modeling *tools*. The game significantly contributed to perceived learning on concepts that lay at the core of this thesis and the SNRN concept, being alternative stable states and critical nutrient loading (i.e., the nutrient loading at which regime shifts occur) (Table 7.1).

Nevertheless, catchment scale games might be more relevant to communicate the network *perspective* of SNRNs (Table 7.1). For example, the Flipping Lakes game is well suited to explain pollution transport and retention, and the role of lake-ecosystem state for pollution management in catchments (Armstrong et al. 2021). The board game format of Flipping Lakes strongly differs from the digital escape room feature of the EscapeBLOOM, both having their merits and weaknesses. Where board games may be more strongly associated with games for entertainment and give more room for open discussions on the content, the digital escape room format guides players to one final solution. Together with the time limitation in the EscapeBLOOM, this may limit open discussion about potential solutions during the game, but it allows for more steering on learning outcomes. Also, the digital format of the EscapeBLOOM appeared beneficial in times when physical meetings are limited, since it can be played in hybrid or fully online settings (e.g., the workshop at SIL22 in Table 6.1). Therefore, in the future, I would like to develop an SNRN focused game using insights and techniques from the EscapeBLOOM, to help to bring the SNRN concept from *theory* to practice.

Table 7.1. Overview of main strengths and weaknesses of the perspectives, theories and tools of the research chapters as discussed in Chapter 7.

Research chapter	Strengths	Weaknesses
2. SNRNs	SNRNs are based on a novel spatial feedback theory on nutrient loading, ecosystem state and nutrient retention.	SNRNs do not directly apply existing concepts and theories of hydrologically connected systems.
	The SNRN perspective highlights the dual nature of nutrients as pollutant and resource.	The SNRN perspective is only focused on nutrients.
3-4. GPLake-M and GPLake-R	GPLake-M describes regime shifts through critical turbidity	The presented models are only suitable for first diagnosis.

	whilst being based on resource competition theory. GPLake-R dynamically includes the spatial feedback theory on nutrient loading, ecosystem state and nutrient retention. The presented models capture patterns from the PCLake model. Areal units enhance comparison between primary producers.	The presented models are not yet applied to real world cases. The presented models are parameterized for summer averages. Areal units may be counterintuitive for empiricist.
5. Scenario analysis	The scenario analysis confirms the spatial feedback theory on nutrient loading, ecosystem state and nutrient retention. A theoretical explanation was found for TN:TP ratios related to in-lake nutrient retention. The scenario analysis of socio-economic development and climate change gives insight in potential water quality futures.	Theoretical insights are based on only one lake ecosystem model. Alternative management options were not explored. Indirect effects of climate change on nutrient loadings and water flows were not assessed.
6. EscapeBLOOM	The EscapeBLOOM was well received in introducing lake models and water quality management concepts. The EscapeBLOOM significantly contributed to perceived learning on critical nutrient loading and alternative stable states.	The EscapeBLOOM is limited in raising in-depth discussions and development of management options. The EscapeBLOOM is not directly applicable to the network perspective of SNRNs.

7.6 Future outlook for SNRNs in water quality management

I hope this thesis will serve as an inspiration for (collaborations with) water quality mangers, to start designing management strategies based on lessons from the SNRN *perspective*. I believe modeling studies of lake networks together with lake managers will stimulate the uptake of the SNRN approach, and serious games may also play a role in such endeavors. The relatively complex PCLakeS+ modeling approach is already available to simulate networks of lakes, including feedbacks between ecosystem state, nutrient retention, and nutrient loading. After implementation on a networks scale, also the relatively simple GPLake-R model can be used to support explorations of SNRN management strategies. At the same time, water quality managers may already start to include the core principles of the SNRN *perspective* in their management strategies by considering that:

- Connected waterbodies may influence each other's water quality,
- nutrients are both a pollutant and a resource,
- nutrient retention followed by nutrient removal and reuse will contribute to nutrient conservation,
- nutrient retention can be enhanced by hydrological and macrophyte-focused management, and
- regime shifts from phytoplankton to macrophyte dominance will enhance in-lake nutrient retention and may contribute to downstream water quality improvement.

In a broader context, SNRN management strategies should also consider potential tradeoffs of interventions, such as risks of undesired changes in ecosystem state and nutrient retention potential by harvesting practices (Chapter 2). Also, I call for awareness on risks of nutrient retention in terms of altering TN:TP ratios (e.g., Chapter 5), retention of other pollutants that may complicate reuse of nutrient retaining substances (Hoellein and Rochman 2021; Haynes and Zhou 2022; Table 7.1), and potential long-term internal P-loading when retained nutrients are insufficiently removed

(Søndergaard et al. 2001). Finally, there may also be potential for synergies to tackle major sustainability challenges beyond eutrophication and nutrient availability. For example, reduction of eutrophication and stimulation of macrophyte dominance in networks of waterbodies could reduce greenhouse gas emissions (Li et al. 2021b; Aben et al. 2022), and restoration and construction of nutrient retaining wetlands may provide habitat to support biodiversity (Mitsch et al. 2014).

Foremost, the SNRN *perspective* acknowledges the importance interconnectivity of waterbodies and therefore suggests to smartly position and time management strategies within the hydrological network. This may call for combinations of measures — as suggested for individual waterbodies (Lürling and Mucci 2020) — to have a larger effect than would be expected at first sight. To make informed management decisions, the individual waterbodies and the system as a whole should be understood (Van Liere and Gulati 1992). A systems analysis including determination of water- and nutrient balances, biological compositions of the waterbodies, and socio-economic costs and benefits may help to acquire and strengthen such understanding (Lürling et al. 2016). Although this thesis has a strong ecological focus, ideally, in the future SNRNs management strategies will be further developed from a social-ecological systems *perspective* that fully acknowledges the intertwined and dynamic nature of human and natural systems (Biggs et al. 2021). I hope this PhD thesis will increase understanding of nutrient retention in connected surface waters to contribute to more sustainable management of water and nutrients, and therewith to the UN Sustainable Development Goals (SDGs) of zero hunger (SDG 2), clean water and sanitation (SDG 6), and responsible consumption and production (SDG 12).

7.7 Final thoughts

This thesis arose from numerous concerns about the future of our planet because of environmental pollution, overexploitation, climate change, and biodiversity loss. Historical examples of collapsing societies because of —

amongst others — unsustainable human exploitation of the environment (Costanza et al. 2007), together with fictitious but realistic literature warning for the future collapse of Western civilization due to insufficient translation of such knowledge into power (Oreskes and Conway 2013), and the unsustainable use of valuable nutrients (Hugo 1862) strengthen and express such concerns. Moreover, during my PhD project, the COVID-19 pandemic and the Russian invasion of Ukraine have shown the fragility of our seemingly safe living environments in a highly connected world, for example, threatening food security and aggravating inequality around the globe (Bin-Nashwan et al. 2022; Hammad et al. 2023; Mottaleb and Govindan 2023). Additionally, global challenges such as climate change, and food and water security interact, potentially aggravating each other (Moss et al. 2011; Wicaksono et al. 2017).

Oreskes and Conway (2013) indicate a lack of truly holistic approaches that integrate natural and social components to address climate change. I argue that such a holistic system *perspective* is especially important to find synergies when addressing complex, intertwined challenges, but at the same time, the details matter and may provide a starting point to give courage to act. Most broadly, through my PhD work I tried to contribute to sustainable development regarding climate change, food security and stainable use of resources. These challenges are connected through water and nutrients, on which I focused in this PhD thesis. Through the SNRN concept that I developed, I highlight the dual nature of nutrients being a pollutant and resource that can influence — and are influenced by — ecological water quality (Table 7.1). In this thesis, the vision for SNRNs provided a holistic-type of *perspective* by looking at networks at surface waters (Chapter 2). Additionally, I dove into the ecological details of individual lakes, with nutrient retention forming a bridge toward the network *perspective* (Chapter 3-5).

The scenario analysis of thousands of Chinese lakes gives some hope that in the future ecological water quality may improve, but this requires drastic changes from current practices (Chapter 5). In addition to efforts needed to reduce nutrient loading and temperature rise to reach the sustainability-oriented scenario, the SNRN concept provides a direction to improve the management of nutrients within surface waters (Chapter 2). The other chapters in this thesis present relatively simple models as *tools* to help to explore ecological water quality and nutrient retention in lakes (Chapter 3 and 4) and to introduce such modeling *tools* to potential users (Chapter 6). Therewith, this thesis makes small steps to help to inform water quality management, but there is still a long way to go to reach a sustainable future.

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Supplementary materials

The supplementary materials are organized per research chapter (2-6). Additional documents — such as the GPLake-M model tool — are, or will be made, available online with the published articles.

Table of contents

Supplementary materials of Chapter 2

Supplementary material A

Most studies in the review by Hilt et al. (2017) show higher nutrient retention in macrophyte-dominated over phytoplankton-dominated shallow lakes. Indeed, an exploration with lake ecosystem model PCLake (Janse 2005; Supplementary material C) revealed that these alternative stable states are reflected in the lake-wide N and P retention (Fig. A.1).

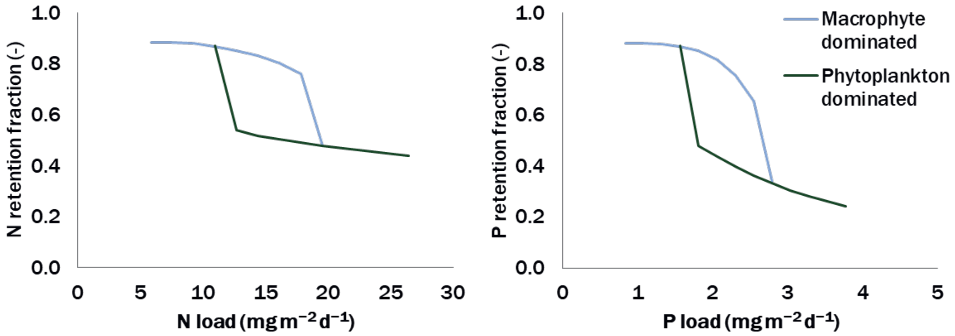

Figure A.1. Summer averaged N and P retention fractions for a macrophyte- (light blue line) and phytoplankton- (dark green line) dominated lake under different nutrient loadings (with 7 g g^{-1} N to P loading ratio).

To make these graphs, first, a bifurcation analysis (Janse 2005; Jansen et al. 2019) was performed to determine the summer average nutrient concentrations at the outflow, depending on the initial ecosystem state and the nutrient loading. Standard PCLake settings were applied (Janse 2005), with a depth of 2 m and a 7 g g^{-1} N to P ratio in the nutrient loading, and the model was run for 40 years to reach equilibrium. Next, the nutrient retention fractions (-) were calculated as:

$$N\ retention\ fraction = \frac{mPLoad \times cNPLoadMeas - wNOutflTot \times sDepthW}{mPLoad \times cNPLoadMeas} \quad \text{Eq. (A.1a)}$$

and

$$P\ retention\ fraction = \frac{mPLoad - wPOutflTot \times sDepthW}{mPLoad} \quad \text{Eq. (A.1b)}$$

with mPLoad being the P loading (g m^{-2} d^{-1}), cNPLoadMeas the N to P ratio of the nutrient loading (g g^{-1}), wNOutflTot and wPOutflTot the total amount of N and P flowing out with the water discharge (g m^{-3} d^{-1}), and sDepthW the water depth (m).

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Supplementary material B

Methods

We used model output from Janssen et al. (2019) to calculate nutrient retention in a chain of lakes in a fashion similar to Hilt et al. (2011). Janssen et al. (2019) modeled longitudinal lake profiles with 10 homogenous segments to study the effect of spatial nutrient loading and hydrology on lake restoration success. Each segment was modeled using the lake ecosystem model PCLake. Here we interpret each lake segment as a completely mixed individual lake in a chain of 10 lakes and calculated nutrient retention (Fig. B.1). The underlying nutrient retention processes are natural internal retention per lake (e.g., sedimentation and burial) and natural losses per lake (i.e., denitrification). Retention is calculated as the difference between total nutrient loading into the lake and nutrients flowing out of the lake along with the water discharge.

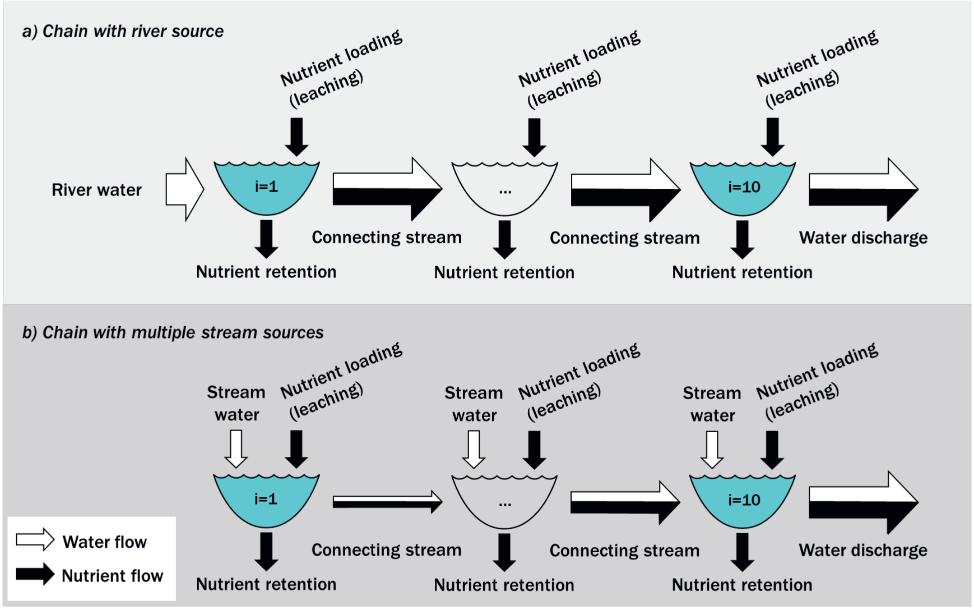

Figure B.1. Schematic of the modeled chains of lakes with a) a river water source, and b) multiple stream sources of water. Please note that the size of the white arrows gives an indication of the size of the water flow.

We selected model output with low external nutrient loading (e.g., leaching) into each lake (9.16 N and 1.31 P in mg m^{-2} d^{-1}), with initially clear states. These results represent chains of 10 shallow lakes (2 m depth) which are macrophyte dominated (55.6-62.9 dry weight in g m^{-2} d^{-1}). We assume that no nutrient retention occurs in the streams connecting the lakes. Thereby, the chain length or number of lakes per chain gives an indication of the effect of lake density in, for example, a catchment of a river retaining relatively few nutrients.

Two different spatial patterns of water supply were compared to assess the effect of hydrological connectivity. The first is a single source into the most upstream lake (20 mm d^{-1}), for example, a clear river (Fig. B.1a). The second are multiple water sources, each into one lake (2 mm d^{-1} per lake), for example, a clear stream into each lake (Fig. B.1b). Furthermore, in both cases the water entering the first lake flows out into the next lake through a connecting stream, and this is repeated in a downstream direction till the water is discharged from the 10th lake in the chain. Along with this outflow of water, nutrients are transported downstream. Thereby, each lake in the chain receives water from the discharge of upstream lakes and, in the case of situation b (Fig. B.1b) also from side-streams or groundwater. Likewise, each lake in the chain receives nutrients from the discharge of upstream lakes and from leaching from surrounding land or groundwater seepage.

The concentration of nutrients (g m^{-3}) in the outflow of lake i was calculated as:

$$N\ concentration_i = sNH4W + sNO3W + sNDetW + sNDiatW + sNGrenW + sNBlueW + sNZoo \qquad \text{Eq. (B.1a)}$$

and

$$P\ concentration_i = sPO4W + sPAIMW + sPDetW + sPDiatW + sPGrenW + sPBlueW + sPZoo \qquad \text{Eq. (B.1b)}$$

with all terms on the right being N and P concentrations in the lake water (g m^{-3}) for: NH_4 (sNH4W), NO_3 (sNO3W), detritus (sNDetW and sPDetW), diatoms (sNDiatW and sPDiatW), green algae (sNGrenW and sPGrenW), blue-green algae (sNBlueW and sPBlueW), zooplankton (sNZoo and sPZoo), PO_4 (sPO4W), and P absorbed onto inorganic matter (sPAIMW).

These nutrient concentrations were converted to nutrient loading out of lake i, which equals the nutrient loading discharging into the next lake (i+1) (g m^{-2} d^{-1}) by:

$$N\ loading\ (discharging)_{i+1} = N\ concentration_i \times \frac{uQin_{i+1}}{1000} \qquad \text{Eq. (B.2a)}$$

and

$$P\ loading\ (discharging)_{i+1} = P\ concentration_i \times \frac{uQin_{i+1}}{1000} \qquad \text{Eq. (B.2b)}$$

with $uQin_{i+1}$ being the amount of water flowing into the next lake, which equals the discharge out of lake i (mm d^{-1}).

Supplementary materials

In addition to this nutrient loading discharging from one lake into the next, every lake receives an external nutrient loading (g m^{-2} d^{-1}) representing nutrient inflow by leaching from the lakeshores, which results in a total nutrient loading per lake (i) (g m^{-2} d^{-1}) of:

$$Total\ nutrient\ loading_i = Nutrient\ loading\ (discharging)_i + Nutrient\ loading\ (leaching)_i \qquad \text{Eq. (B.3)}$$

where nutrients can be N or P, and lake i=1 receives nutrient loading by leaching only.

Next, N and P retention per lake (i) (g m^{-2} d^{-1}) was calculated according to:

$$Nutrient\ retention_i = Total\ nutrient\ loading_i - Total\ nutrient\ loading_{i+1} \qquad \text{Eq. (B.4)}$$

and the nutrient retention fraction (-) over a chain of j lakes:

$$Nutrient\ retention\ fraction_j = \frac{\sum_{i=1}^{j} Nutrient\ retention}{\sum_{i=1}^{j} Total\ nutrient\ loading} \qquad \text{Eq. (B.5)}$$

Results and discussion

The results show that in a chain of macrophyte dominated shallow lakes, the amount of nutrients retained per lake increases and tends to reach a plateau with increasing chain length if the chain is river-fed (light blue bars in Fig. B.2). With multiple stream sources of water, the amount of nutrients retained per lake is independent of the position within the chain (dark blue bars in Fig. B.2). The retention fraction over the chain shows similar patterns (grey lines in Fig. B.2).

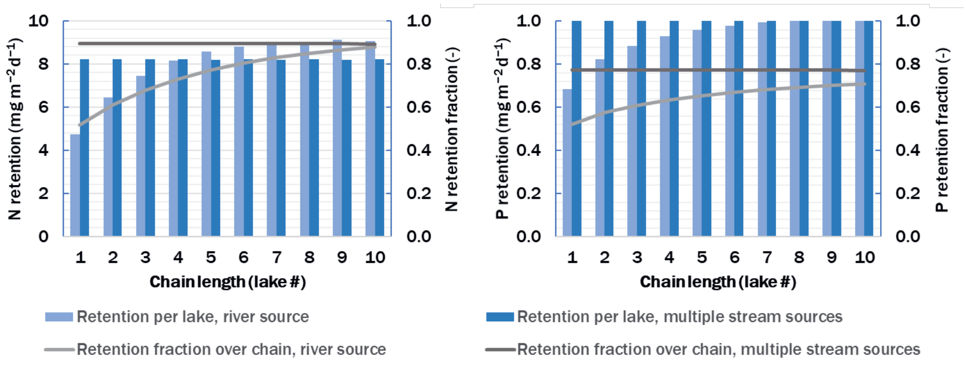

Figure B.2. N (left graph) and P (right graph) retention per lake # (mg m^{-2} d^{-1}) (blue bars with left y-axis) and retention fraction for a lake chain with a length of # lakes (-) (grey lines with right y-axis). Lake chains with a river water source and multiple stream sources of water (see Fig. B.1) are presented by light and dark colors, respectively.

These results demonstrate that, depending on the hydrological connections to water sources, the overall nutrient retention in a chain of lakes may depend on the number of lakes in that chain. With a river source of water, an increase in lake density from 1 to 7 lakes per chain enlarges the N and P retention fractions over the entire chain. Increasing lake densities above 7 lakes per chain here hardly affected the overall nutrient retention fraction, because the addition of each lake is accompanied by additional nutrient loading and thereby dampens the nutrient retention fraction.

With multiple stream sources of water, the constant nutrient retention per lake and nutrient retention fraction over the chain of lakes may be explained by the relative water and nutrient supply. The addition of the same amount of clean water to every new lake in the chain, plus the amount of water delivered by lakes upstream in the chain, increases the amount of water flowing through the chain. This implies a decrease in hydraulic residence time with increasing chain length and could explain a decrease in relative nutrient retention fraction per lake in the downstream direction (reflected by the slower increase in nutrient retention fraction over the chain with chain length). Apparently, the decrease in nutrient retention fraction per lake in combination with the increasing total nutrient loading downstream here balance out, resulting in a similar amount of nutrients retained in each lake.

Independent of the hydrological connectivity, the total amount of nutrients retained increases with chain length. Thus, a larger upstream lake density contributes to some extent to the reduction of eutrophication problems downstream. Furthermore, potentially more nutrients can be harvested and reused for nutrient conservation with increasing lake densities. Here one should note that N retention is probably largely caused by denitrification which results in gaseous losses in the form of N_2 and possibly the greenhouse gas N_2O. The amount of nutrients that can potentially be reused on land is likely to be much smaller than the nutrient retention values presented here.

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Supplementary material C

Table C.1. Overview of selected freshwater models that account for nutrient retention, at various spatial scales. For each model is given: waterbody types included, primary producer groups (i.e., macrophytes, phytoplankton, non (-)) and nutrient species included, model output related to water quality, modelling approach, which nutrient retention processes and management options at the waterbody level are included, and major references describing these models. *TN = Total nitrogen, (D)ON = (dissolved) organic nitrogen, (D)IN = dissolved inorganic nitrogen, PN = particulate nitrogen, NO_3 = nitrate, NH_4 = ammonium, TP = total phosphorus, OP = organic phosphorus, (D)IP = (dissolved) inorganic phosphorus, (T)DP = (total) dissolved phosphorus, PP = particulate phosphorus, PIN = phosphorus adsorbed to inorganic matter, PO_4 = phosphate.

Table C1. Continued.

Spatial scale	Model name	Waterbody						Primary producer	Nutrient species*	Model output related to water quality	Modelling approach	Nutrient retention processes in inland waters	Management options	Literature
		Reservoirs	Lakes	Rivers	Streams	Ditches	Wetlands							
Individual waterbody	AquaVenus				X	X		Submerged macrophytes	PN, NO_3, NH_4, DIP, PP	Macrophyte biomass and nutrient concentrations that can be transformed to N and P retention rates	Process-based	Sediment release/absorption, sedimentation, resuspension, decomposition, mineralization, nitrification, macrophyte uptake (net growth), epiphytic biofilm denitrification, sediment denitrification	-	(de Klein 2008)
	Delft3D-WAQ	X	X	X				Phytoplankton, submerged and emergent macrophytes	TN, ON, DIN, PN, NO_3, NH_4, TP, OP, IP, PO_4, PP	Nutrient concentrations	Process-based	Storage, transformation, removal	Macrophyte harvesting	(Van Gerven et al. 2009; Deltares 2020)
	Dillon and Rigler model		X					-	TP	P concentration and retention	Empirical	Sedimentation	-	(Dillon and Rigler 1974)
	Internal load model		X					-	TP	P concentration and retention	Empirical	Sedimentation and internal loading (negative retention)	-	(Nürnberg 1984)
	NUSWALITE				X			Phytoplankton, rooting, emergent and floating macrophytes	ON, IN, OP, IP	Nutrient concentrations	Process-based	Denitrification, sedimentation (burial), and adsorption to sediment	Biomass removal by mowing and dredging	(Siderius et al. 2009)

Table C1. Continued.

	Papyrus Simulator						X	Macrophytes (*Cyperus papyrus*)	TN, NO_3, NH_4	N retention and removal	Process-based	Nitrification, plant mortality, detritus mineralization, settling and denitrification	Macrophyte harvesting	(Van Dam et al. 2007)
	PCDitch				X	X		Phytoplankton, rooting, emergent and floating macrophytes	TN, NO_3, NH_4, TP, PIN, PO_4	Critical nutrient loading	Process-based	Adsorption to sediment, sedimentation (no resuspension), burial, mineralisation (incl. denitrification) and uptake by vegetation	Mowing and dredging	(Janse and Van Puijenbroek 1997; Janse 2005)
	PCLake / PCLake+		X					Phytoplankton, rooting, emergent and floating macrophytes	TN, NO_3, NH_4, TP, PIN, PO_4	Critical nutrient loading	Process-based	Adsorption to sediment, sedimentation (no resuspension), burial, mineralisation (incl. denitrification), uptake by biota and indirect relations such as the impact of fish and macrophytes on resuspension	Grazing by birds, biomanipulation, fishery, mowing, dredging, reducing fetch, sediment traps and including a wetland zone with marsh vegetation	(Janse 2005; Janssen et al. 2019)
	SALMO	X	X					Phytoplankton	TN, NO_3, NH_4, TP, PP, PO_4	Nutrient, phytoplankton and zooplankton concentrations	Process-based	Denitrification, PO_4 co-precipitation by calcite, sedimentation and release from sediment, phytoplankton settling and nutrient cycling by zooplankton and fish	-	(Benndorf and Recknagel 1982; Recknagel et al. 2008; Chen et al. 2014)
	Wetland in front of Lake Erie						X	Phytoplankton, macrophytes (*Nelumbo lutea*)	TP	P retention	Process-based	Direct P sedimentation and resuspension, and specific plankton and macrophyte sedimentation	-	(Mitsch and Reeder 1991)
	WETSAND						X	Macrophytes (not specified, dense versus	TN, ON, NO_3, NH_4, TP	Nutrient distributions	Process-based	Vegetation uptake, biomass decay and nutrient returns	-	(Kazezyılmaz-Alhan et al. 2007)

Table C1. Continued.

								sparse vegetation)						
Catchment	Flow-path attenuation model		X					-	TP	P concentration	Hybrid empirical and process-based	Retention fraction depending on hydraulic residence time and first-order rate coefficient for P loss	-	(Zhang et al. 2012)
	General analytical model		X	X			X	-	TN, TP	Pollutant retention	Empirical	Retention fraction depending on transport length and retention parameter specific for lakes, wetlands and other physical features and biogeochemical processes	-	(Quin et al. 2015)
	HYPE		X	X				-	TN, ON, IN, TP, DP, PP	Nutrient concentrations	Process-based	Sedimentation, resuspension, primary production by phytoplankton, mineralization and denitrification	-	(Lindström et al. 2010)
	INCA				X			-	NO_3, NH_4	Nutrient concentrations	Process-based	Nitrification and denitrification depending on NO_3 and NH_4 concentration	-	(Wade et al. 2002)
	INCA-P				X			Macrophytes (not specified), epiphytic algae	TDP, PP	P mobilisation, transport and retention	Process-based	Sedimentation, resuspension, sorption, uptake by macrophytes and epiphytes	-	(Jackson-Blake et al. 2016)
	MARINA	X		X				-	DON, DIN, PN, DOP, DIP, PP	Nutrient transport to sea	Hybrid empirical and process-based	Removal fraction for water consumption, and DIN and DIP retention specified for rivers and dammed reservoirs, representing denitrification,	-	(Strokal et al. 2016)

Table C1. Continued.

												sedimentation and accumulation		
	PolFlow		X	X				-	TN, TP	Nutrient transport to sea	Hybrid empirical and process-based	Retention fraction depending on discharge, slope, occurrence of lakes and calibrated loss term representing denitrification, sedimentation, etc.	-	(de Wit 2001)
	SPARROW	X	X		X			-	TN, TP	Nutrient loading	Hybrid empirical and process-based	Decay function for lakes and reservoirs depending on settling velocity and overflow rate (outflow/area), first-order decay function for streams depending on stream reach length with decay functions depending on discharge rate. Corrected with downstream monitoring data	-	(Elliott et al. 2005)
	VEMALA		X	X	X			Phytoplankton	TN, TP	Nutrient loading, retention and removal, and transport to sea	Empirical	Calibrated sedimentation and release rates. Retention depending on lake volume, water residence time and lake nutrient concentrations	-	(Huttunen et al. 2016)
Global	GlobalNEWS	X		X				-	DON, DIN, PN, DOP, DIP, PP	Nutrient transport to sea	Hybrid empirical and process-based	Retention fractions for water consumption, retention in river corridor, and in reservoirs based on empirical parameterizations and for DIN and DIP based on change in water	-	(Seitzinger et al. 2002; Mayorga et al. 2010)

Table C1. Continued.

												residence time over undammed conditions and mean reservoir depth in case of DIN. Dissolved organic forms are not retained		
	IMAGE-GNM	X	X	X			X	-	TN, TP	Nutrient loading, retention and removal, and transport to sea	Hybrid empirical and process-based	Retention fraction depending on hydraulic residence time and nutrient uptake velocity, with the latter depending temperature and N concentration, representing denitrification, sedimentation and sorption by the sediment	-	(Beusen et al. 2015)
	NiRReLA		X	X			X	-	TN, NO_3	N retention and removal	Empirical	Retention fractions depending on hydraulic load and lake and reservoir specific settling velocities, with the latter representing denitrification and burial	-	(Harrison et al. 2009)
	WaterGAP3 / WorldQual							-	TP	P loading and concentrations	Empirical	Retention fractions depending on hydraulic load	-	(Fink et al. 2018)

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Supplementary materials of Chapter 3

Supplementary material A: Resource competition theory of alternative stable states

When species compete for the same resources, their competitive strength and requirement (i.e., limitation) of these resources will determine which species wins the competition, or whether coexistence or alternative stable states are possible (Tilman, 1982). Huisman and Weissing (1994; 1995) developed a mechanistic model explaining such competition effects for phytoplankton communities in a mixed water column. Here we provide four theoretical scenarios to explain why the mixed model of Huisman and Weissing is inherently unsuitable to model empirically observed alternative stable states of macrophytes and phytoplankton.

Empirical patterns

Empirical observations show that macrophytes dominate in freshwater ecosystems at low nutrient loading and phytoplankton at high nutrient loading, and that they can show alternative stable states at intermediate nutrient levels (Jeppesen et al. 1990; Scheffer, 1990). Thus, macrophytes are the stronger competitor for nutrients, whereas phytoplankton is the stronger competitor for light. In terms of the above-mentioned resource competition theory by Tilman (1982) and Huisman and Weissing (1994, 1995), this implies that macrophytes have a lower R^* than phytoplankton while phytoplankton has a lower I^*_{out} than macrophytes. Furthermore, the empirically validated PCLake model (Janse, 2010) shows that the GPLake-M Slope of macrophytes is larger than that of phytoplankton and that their Plateaus are similar (Supplementary material E). This implies that macrophytes are light-limited at lower nutrient loadings (i.e., Plateau over Slope) than phytoplankton.

Four scenarios with the Huisman and Weissing model

Below we consider four possible scenarios of the Huisman and Weissing model in terms of competitive strength and nutrient to light limitation switch points of macrophytes and phytoplankton, thereby ignoring the trivial scenarios that either macrophytes or phytoplankton are the superior competitor for both nutrients and light and therefore always wins the competition irrespective of the environmental conditions. For each scenario, we ask ourselves whether it 1) complies with the empirical knowledge on the relative competitive strength and nutrient to light limitation switch points of macrophytes and phytoplankton, 2) results in empirically expected pattern of macrophyte dominance at low nutrient loading and phytoplankton dominance at high nutrient loading, and 3) results in coexistence of macrophytes and phytoplankton at intermediate nutrient loading or in alternative stable states (Table A.1).

Table A.1. Four scenarios of the Huisman and Weissing model in terms of competitive strength and nutrient to light limitation switch points of macrophytes (macr) and phytoplankton (phyt), and whether these parameter settings and model output comply with empirical knowledge.

Scenario	Parameter settings		Compliance with empirical knowledge		
	Relative competitive strength	Relative nutrient to light limitation switch points	Parameter setting	Dominance at extremes	Competition outcome at intermediate nutrient loadings
1	$R^*_{macr} < R^*_{phyt}$ $I^*_{out,macr} > I^*_{out,phyt}$	$\frac{Plateau_{macr}}{Slope_{macr}} < \frac{Plateau_{phyt}}{Slope_{phyt}}$	Yes	Yes	Coexistence
2	$R^*_{macr} > R^*_{phyt}$ $I^*_{out,macr} < I^*_{out,phyt}$	$\frac{Plateau_{macr}}{Slope_{macr}} < \frac{Plateau_{phyt}}{Slope_{phyt}}$	No	No	Alternative stable states
3	$R^*_{macr} > R^*_{phyt}$ $I^*_{out,macr} < I^*_{out,phyt}$	$\frac{Plateau_{macr}}{Slope_{macr}} > \frac{Plateau_{phyt}}{Slope_{phyt}}$	No	No	Coexistence
4	$R^*_{macr} < R^*_{phyt}$ $I^*_{out,macr} > I^*_{out,phyt}$	$\frac{Plateau_{macr}}{Slope_{macr}} > \frac{Plateau_{phyt}}{Slope_{phyt}}$	No	Yes	Alternative stable states

Scenario 1: Coexistence with empirically relevant parameters

For the empirically observed relative competitive strengths and nutrient to light limitation switch points, the model of Huisman and Weissing results in potential coexistence of macrophytes and phytoplankton at equilibrium. At low nutrient loadings macrophytes win the competition and at high nutrient loading the phytoplankton wins, but at a range of intermediate nutrient loadings coexistence occurs. At these intermediate nutrient loadings macrophytes are light-limited and phytoplankton is nutrient-limited, so they are limited by the resource they are the weaker competitor for. Therefore, they are not able to outcompete each other and can coexist. Thus, this theoretical scenario does not result in the alternative stable states of Scheffer (1990).

Scenario 2: Alternative stable states for switched competitive strength

When switching the competitive strength of macrophytes and phytoplankton, alternative stable states can occur. Now phytoplankton is the better competitor for nutrients and wins the competition at low nutrient loadings. On the other hand, macrophytes are now the stronger competitor for light and win the competition at high nutrient loadings. Because the nutrient to light limitation switch points remain unaltered, at intermediate nutrient loadings, phytoplankton is still nutrient-limited and macrophytes are light-limited. Thus, the species are limited by the resource they are the stronger competitor for. Therefore, they can outcompete each other at these intermediate nutrient loadings, depending on whether they were initially dominant or not. In other words, here one species cannot invade once the other species is present. This is the zone of alternative stable states. Concludingly, this theoretical scenario can produce alternative stable states, however the pattern of when which species dominates and the competitive strength of the species is not in line with empirical knowledge.

Scenario 3: Coexistence for switched parameters

When also the relative nutrient to light limitation switch points is reversed, the model again produces coexistence. Phytoplankton (i.e., stronger nutrient-competitor) dominates at low nutrient loadings and macrophytes (i.e., stronger light-competitor) dominate at high nutrient loadings. Because of the reversed nutrient to light limitation switch points, now phytoplankton is light-limited and macrophytes are nutrient-limited at intermediate nutrient loadings. Thus, the species cannot outcompete each other because they are limited by the resource they are the weaker competitor for and, hence, coexist. This theoretical scenario with only empirically unjustified species characteristics neither results in the empirical pattern of when which species dominates, nor alternative stable states.

Scenario 4: Alternative stable states for reversed nutrient to light limitation switch points

When reversing the nutrient to light limitation switch points but using the empirically expected competitive strength of macrophytes and phytoplankton, alternative stable states can occur. Now macrophytes (i.e., stronger nutrient-competitor) dominate at low nutrient loadings and phytoplankton (i.e., stronger light-competitor) dominates at high nutrient loadings. Moreover, phytoplankton is light-limited and macrophytes are nutrient-limited at intermediate nutrient loadings because of the reversed nutrient to light limitation switch points. Thus, the species are limited by the resource they are the stronger competitor for and can outcompete each other, depending on whether they were initially dominant or not. Hence, alternative stable states occur. This theoretical scenario can produce an empirically relevant pattern of alternative stable states, though only for empirically unjustified relative nutrient to light limitation switch points.

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Supplementary material B: Differential equations and equilibrium solutions of mixed and layered models of macrophyte-phytoplankton competition

Huisman and Weissing (1994; 1995) developed a mechanistic model for competition among phytoplankton species for nutrients and light in a mixed water column. Van Gerven et al. (2015) expanded this model to capture competition for nutrients and light in layered communities of floating and submerged plants. Both models are based on the same basic set of differential equations and only differ essentially in the way the competitors shade each other. Here we define and study these generalized differential equations, and provide the specifics on shading for each setting of the model. Next, we show the qualitative outcomes of competition through invasion experiments, and provide the quantitative outcomes of the different layering of the model by bifurcation analysis. Here we express macrophyte and phytoplankton in areal nutrient content to clarify the link with GPLake-M, still the model would also be applicable for competition between other primary producers. Model symbols with their units and description are provided in Table B.1.

Table B.1. Symbols, units and description of the generalized differential equations for nutrient-light competition, applied to macrophytes and phytoplankton. The parameter setting given in this table are chosen such that they match the parameters of GPLake-M ($\mathrm{Slope_{phyt}} = 47.3$ d, $\mathrm{Slope_{macr}} = 237$ d and $\mathrm{Plateau_{phyt}} = \mathrm{Plateau_{macr}} = 259$ mg P m^{-2}).

Symbol	Unit	Description	Category	Value
$Pphyt$	mg P m^{-2}	Areal phytoplankton P content	Output variable	Variable
$Pmacr$	mg P m^{-2}	Areal phytoplankton P content	Output variable	Variable
$Pwater$	mg P m^{-3}	P concentration in the water	Output variable	Variable
$Pload$	mg P m^{-2} d^{-1}	Areal P loading	Input variable	0.0-6.6
D_{in}	d^{-1}	Dilution rate	Physical parameter	0.01
I_{in}	J s^{-1} m^{-2}	Intensity of the incoming light	Physical parameter	200
K_{bg}	m^{-1}	Background extinction	Physical parameter	0.0
z	m	Depth	Physical parameter	2.0
$p_{max,phyt}$	d^{-1}	Max. per capita growth rate of phytoplankton	Biological parameter	0.1057
$p_{max,macr}$	d^{-1}	Max. per capita growth rate of macrophytes	Biological parameter	0.0211
l_{phyt}	d^{-1}	Per capita loss rate of phytoplankton	Biological parameter	0.0211
l_{macr}	d^{-1}	Per capita loss rate of macrophytes	Biological parameter	0.00422

$\boldsymbol{H_{nut,phyt}}$	m^2 mg P	Half-saturation constant of nutrient limitation of phytoplankton	Biological parameter	2.59
$\boldsymbol{H_{nut,macr}}$	m^2 mg P	Half-saturation constant of nutrient limitation of macrophytes	Biological parameter	2.33
$\boldsymbol{H_{light,phyt}}$	J m^{-2} s^{-1}	Half-saturation constant of light limitation of phytoplankton	Biological parameter	57.4
$\boldsymbol{H_{light,macr}}$	J m^{-2} s^{-1}	Half-saturation constant of light limitation of macrophytes	Biological parameter	118.3
$\boldsymbol{k_{phyt}}$	m^2 mg P^{-1}	Per capita extinction coefficient of phytoplankton	Biological parameter	0.0290
$\boldsymbol{k_{macr}}$	m^2 mg P^{-1}	Per capita extinction coefficient of macrophytes	Biological parameter	0.0191
$\boldsymbol{E_{phyt}}$	-	Total extinction coefficient over the relevant part of the water column for phytoplankton	Biological parameter	Variable
$\boldsymbol{E_{macr}}$	-	Total extinction coefficient over the relevant part of the water column for macrophytes	Biological parameter	Variable

Generalized differential equations for nutrient-light competition

The generalized differential equation for areal phytoplankton nutrient content (Pphyt, mg P m^{-2}) is:

$$\frac{dPphyt}{dt} = p_{max,phyt} \times min\left(\frac{Pwater}{H_{nut,phyt}+Pwater}, \frac{1}{E_{phyt}} \times LN\left(\frac{H_{light,phyt}+I_{in,phyt}}{H_{light,phyt}+I_{in,phyt} \times e^{-E_{phyt}}}\right)\right) \times Pphyt$$
$$-l_{phyt} \times Pphyt \qquad \text{Eq. (B.1a)}$$

The generalized differential equation for areal macrophyte nutrient content (Pmacr, mg P m^{-2}) is:

$$\frac{dPmacr}{dt} = p_{max,macr} \times min\left(\frac{Pwater}{H_{nut,macr}+Pwater}, \frac{1}{E_{macr}} \times LN\left(\frac{H_{light,macr}+I_{in,macr}}{H_{light,macr}+I_{in,macr} \times e^{-E_{macr}}}\right)\right) \times Pmacr$$
$$-l_{macr} \times Pmacr \qquad \text{Eq. (B.1b)}$$

The dynamics of the concentration of free nutrients (Pwater mg P m^{-3}) with a unit conversion to mg P m^{-2} d^{-1} by multiplication with depth z (m) are described by:

$$\frac{dPwater}{dt} = Pload - z \times D_{in} \times Pwater$$
$$-p_{max,phyt} \times min\left(\frac{Pwater}{H_{nut,phyt}+Pwater}, \frac{1}{E_{phyt}} \times LN\left(\frac{H_{light,phyt}+I_{in,phyt}}{H_{light,phyt}+I_{in,phyt} \times e^{-E_{phyt}}}\right)\right) \times Pphyt$$

$$-p_{max,macr} \times min\left(\frac{Pwater}{H_{nut,macr}+Pwater}, \frac{1}{E_{macr}} \times LN\left(\frac{H_{light,macr}+I_{in,macr}}{H_{light,macr}+I_{in,macr}\times e^{-E_{macr}}}\right)\right) \times Pmacr$$

Eq. (B.1c)

And the mass balance equation for the whole lake system, that should hold at any moment in time, is:

$$Pload = z \times D_{in} \times Pwater + l_{phyt} \times Pphyt + l_{macr} \times Pmacr \qquad \text{Eq. (B.2)}$$

Considerations about the function describing the effect of light limitation

Given the complexity of the function $\left(\frac{1}{E} \times LN\left(\frac{H_{light}+I_{in}}{H_{light}+I_{in}e^{-E}}\right)\right)$ describing the average effect of light limitation on the per capita growth rate over the water column – as opposed to the simplicity of the Monod function $\left(\frac{Pwater}{H_{nut}+Pwater}\right)$ describing the effect of nutrient limitation – it may not directly be clear how the light limitation function responds to changes in $\mathrm{H_{light}}$, $\mathrm{I_{in}}$ and E. Therefore, we here give the limits of the light limitation function for each of its parameters either going to zero or infinity.

In case the half saturation constant $\mathrm{H_{light}}$ goes to infinity, no growth is possible irrespective of the other parameters:

$$\lim_{H_{light}\to\infty}\left(\frac{1}{E} \times LN\left(\frac{H_{light}+I_{in}}{H_{light}+I_{in}e^{-E}}\right)\right) = 0 \qquad \text{Eq. (B.3a)}$$

and when $\mathrm{H_{light}}$ goes to zero, light is not limiting growth irrespective of the other parameters:

$$\lim_{H_{light}\to 0}\left(\frac{1}{E} \times LN\left(\frac{H_{light}+I_{in}}{H_{light}+I_{in}e^{-E}}\right)\right) = 1 \qquad \text{Eq. (B.3b)}$$

In case the amount of incoming light $\mathrm{I_{in}}$ goes to zero, no growth is possible irrespective of the other parameters:

$$\lim_{I_{in}\to 0}\left(\frac{1}{E} \times LN\left(\frac{H_{light}+I_{in}}{H_{light}+I_{in}e^{-E}}\right)\right) = 0 \qquad \text{Eq. (B.3c)}$$

and when light $\mathrm{I_{in}}$ goes to infinity, $\mathrm{H_{light}}$ light is not limiting growth irrespective of the other parameters:

$$\lim_{I_{in}\to\infty}\left(\frac{1}{E} \times LN\left(\frac{H_{light}+I_{in}}{H_{light}+I_{in}e^{-E}}\right)\right) = 1 \qquad \text{Eq. (B.3d)}$$

In case the extinction E goes to infinity, no growth is possible irrespective of the other parameters:

$$\lim_{E\to\infty}\left(\frac{1}{E} \times LN\left(\frac{H_{light}+I_{in}}{H_{light}+I_{in}e^{-E}}\right)\right) = 0 \qquad \text{Eq. (B.3e)}$$

In case the extinction E goes to zero, application of the rule of L'Hôpital allows us to simplify the complex light limitation term to the simpler Monod term which resembles the way nutrient limitation is implemented in the Huisman and Weissing (1994; 1995) model and the layered extension thereof by van Gerven et al. (2015):

$$\lim_{E\to 0}\left(\frac{1}{E}\times LN\left(\frac{H_{light}+I_{in}}{H_{light}+I_{in}e^{-E}}\right)\right)=\left(\frac{I_{in}}{H_{light}+I_{in}}\right) \quad \text{Eq. (B.3f)}$$

The derivation for the function $\left(\frac{1}{E}\times LN\left(\frac{H_{light}+I_{in}}{H_{light}+I_{in}e^{-E}}\right)\right)$ describing the average effect of light limitation on the per capita growth rate over the water column can be found in Supplementary material H.

Cases of the Huisman and Weissing (1994; 1995) and the van Gerven et al. (2015) model
Having defined and studied these generalized differential equations, we can now derive specific cases that represent the Huisman and Weissing (1994; 1995) model for vertically mixed communities and the van Gerven et al. (2015) model for layered communities. To do so, we need to define I_{in} and E.

The terms for the vertically mixed communities according to Huisman and Weissing (1994; 1995) are:

$$I_{in,phyt}=I_{in,macr}=I_{in} \quad \text{Eq. (B.4a)}$$

$$E_{phyt}=E_{macr}=k_{phyt}\times Pphyt+k_{macr}\times Pmacr+K_{bg}\times z \quad \text{Eq. (B.4b)}$$

and for layered communities with floating macrophytes above submerged macrophytes *sensu* van Gerven (2015):

$$I_{in,macr,float}=I_{in} \quad \text{Eq. (B.5a)}$$

$$E_{macr,float}=k_{macr,float}\times Pmacr,float \quad \text{Eq. (B.5b)}$$

$$I_{in,mact,subm}=I_{in,macr,float}\times e^{-E_{macr},float} \quad \text{Eq. (B.5c)}$$

$$E_{mact,subm}=k_{mact,subm}\times Pmacr,subm+K_{bg}\times z \quad \text{Eq. (B.5d)}$$

The terms for layered communities with phytoplankton above submerged macrophytes are:

$$I_{in,phyt}=I_{in} \quad \text{Eq. (B.6a)}$$

$$E_{phyt}=k_{phyt}\times Pphyt+K_{bg}\times z \quad \text{Eq. (B.6b)}$$

$$I_{in,macr,subm}=I_{in,phyt}\times e^{-E_{phyt}} \quad \text{Eq. (B.6c)}$$

$$E_{macr,subm}=k_{macr,subm}\times Pmacr,subm \quad \text{Eq. (B.6d)}$$

and for layered communities with floating macrophytes above phytoplankton:

$$I_{in,macr,float}=I_{in} \quad \text{Eq. (B.7a)}$$

$$E_{macr,float}=k_{macr,float}\times Pmacr,float \quad \text{Eq. (B.7b)}$$

$$I_{in,phyt} = I_{in,macr,float} \times e^{-E_{macr,float}} \tag{Eq. (B.7c)}$$

$$E_{phyt} = k_{phyt} \times Pphyt + K_{bg} \times z \tag{Eq. (B.7d)}$$

Monoculture equilibria and invasion experiments

In case of a monoculture of either phytoplankton or macrophytes (identified as i in the formula's below), the model has the following equilibria when species i is nutrient-limited:

$$Pwater^* = R_i^* = \frac{l_i \times H_{nut,i}}{p_{max,i} - l_i} \tag{Eq. (B.8a)}$$

$$Pi^* = \frac{Pload - z \times D_{in} \times Pwater^*}{l_i} \tag{Eq. (B.8b)}$$

Here Pwater^* is the minimum nutrient concentration needed by primary producer i, hence R_i^* in the model of Tilman (1982).

Furthermore, when species i is light-limited and $\mathrm{K}_\mathrm{bg} = 0$, the equilibria of a monoculture are:

$$Pwater^* = \frac{Pload - l_i \times Pi^*}{z \times D_{in}} \tag{Eq. (B.9a)}$$

$$Pi^* = \frac{p_{max,i}}{k_i \times l_i} \times LN\left(\frac{H_{light,i} + I_{in,i}}{H_{light,i} + I_{in,i} \times e^{-k_i \times Pi^*}}\right) \tag{Eq. (B.9b)}$$

Please note that Pi occurs both in the left hand and the right-hand term of the latter equation and we lack an explicit expression to calculate Pi^* under light limitation.

For a given set of parameters (Table B.1), the outcome of the competition between phytoplankton and macrophytes in the Huisman and Weissing (1994; 1995) model and the layered versions thereof can be evaluated by performing mutual invasion experiments of both groups of species (phytoplankton and macrophytes) in the monoculture equilibrium of the other group of species. In case both groups can invade in the other's monoculture equilibrium, they will coexist. When neither group can invade in the others monoculture equilibrium, we get alternative stable states where the outcome of competition is determined by the initial conditions. Finally, when one group can invade in the other's monoculture equilibrium but not vice versa, the group that is able to invade will dominate.

The invasion experiment showed that at intermediate loadings where macrophytes would be light-limited and phytoplankton would be nutrient-limited if they occur, the outcome of competition depends both on the layering of the system and the amount of nutrient loading. When macrophytes occur above phytoplankton, macrophytes can invade phytoplankton and phytoplankton cannot invade macrophytes, leading to macrophyte dominance. When the system is mixed, both groups can invade the macrophyte monoculture equilibrium for all loading levels, but macrophytes can only invade phytoplankton at lower loadings. This results in coexistence at lower loadings but phytoplankton dominance at higher loadings. The same result is obtained for the situation where phytoplankton occurs above macrophytes but in this situation the switch from coexistence to phytoplankton dominance takes places at a lower level of nutrient loading compared with the mixed system. These outcomes are also visible in the bifurcation plots below (Fig. B.1).

Bifurcation plots for nutrient loading

Having shown the outcome of competition in qualitative terms in the invasion experiments, we can now study the quantitative outcomes of the different layering of the model by bifurcation analysis. The bifurcation plots (Fig. B.1) show that sets I, III and IV are irrespective of the layering, and set II strongly depends on how the system is being layered. Sets I, III and IV shown here correspond with their counterparts in GPLake-M whereas both models diverge in the outcomes for phase II (a and b).

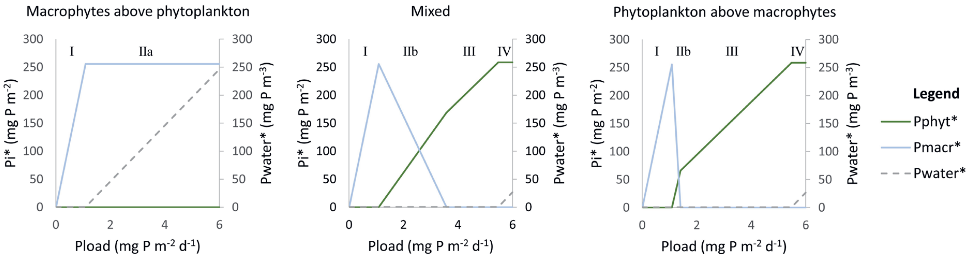

Figure B.1. Equilibrium results of the generalized differential equations for the case of a macrophyte layer above phytoplankton (left panel), vertically mixed communities (middle panel), and a phytoplankton layer above macrophytes (right panel). Roman numbers indicate qualitatively different sets of equilibria of the model: I) monoculture of nutrient-limited macrophytes, IIa) monoculture of light-limited macrophytes, IIb) coexistence of light-limited macrophytes and nutrient-limited phytoplankton, III) monoculture of nutrient-limited phytoplankton, and IV) monoculture of light-limited phytoplankton. For parameter settings see Table B.1.

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Supplementary material C: Relationship between light-limited macrophytes and phytoplankton

The relation between light-limited macrophytes and phytoplankton was explored by bifurcation analysis with PCLake. PCLake was run for a range of hydrological loadings (Qin; 5.5, 13.3, 16, 40 mm d^{-1}) to explore the effect of hydraulic residence time (τ; 50-364 d; Table 3.1, set 2-5). Moreover, PCLake was run for various depths (z; 1, 1.5, 2.5, 3,5, 4 and 5 m) whilst maintaining a τ of 100 days (set 6-11 in Table 3.1). The P content of both vegetation and phytoplankton (aPVeg and PPhyt in g P m^{-2}) was plotted against P loading (0.00001-0.02 g P m^{-2} d^{-1}). To enable this, PPhyt was added to the derivatives in PCLake by the function:

$$PPhyt = oPPhytW \times sDepthW \qquad \text{Eq. (C.1)}$$

First, we explored whether macrophytes and phytoplankton are nutrient- or light-limited in the hysteretic range and whether the theory that macrophytes are light-limited sooner than phytoplankton is captured by PCLake (see section 3.1.2). For this we visually analyzed the bifurcation plots: when the state depends on the nutrient concentration, nutrient limitation is assumed, and if the state is independent of nutrient concentration, light is assumed to be limiting. Second, the relationship between areal P content of macrophytes and phytoplankton during light limitation (i.e., Plateau) was explored. We visually estimated the Plateau value of macrophytes as the middle of macrophyte peak (i.e., decreasing segment just above the drop to zero-biomass), and of phytoplankton as the leveling off of the areal P content.

Limitation phases in PCLake output

Around the hysteretic range, the macrophytes have reached a maximum (i.e., are light-limited) whilst the amount of phytoplankton is dependent on the nutrient loading (i.e., are nutrient-limited) (Fig. C.1 and C.2). Even beyond the hysteretic range (i.e., once phytoplankton outcompeted macrophytes) the amount of phytoplankton keeps increasing with P loading for a while until it reaches a maximum. Hence, macrophytes are light-limited and phytoplankton nutrient-limited during hysteresis in the PCLake output.

Furthermore, the transition from nutrient to light limitation of macrophytes corresponds with the onset of phytoplankton occurrence (Fig. C.1 and C.2). This can be explained as once macrophytes are light-limited, they will not take up all nutrients and some free nutrients will be available for phytoplankton. These free nutrients enable phytoplankton growth in the presence of macrophytes up to the point where phytoplankton outcompete macrophytes by crossing the critical turbidity (Supplementary material D).

Additionally, PCLake output shows a decrease in the amount of phytoplankton with P loading in the light-limited phase. This can be explained by the increasing fraction of detritus that is included in the incoming P loading, hence light limitation increases with nutrient loading in PCLake.

Areal P content in PCLake output

The areal P content of macrophytes and phytoplankton was found to be similar in their respective light-limited phases (Fig. C.1 and C.2). Therefore, the macrophyte Plateau in GPLake-M is assumed to equal the phytoplankton Plateau (g P m^{-2}):

$$Plateau_{macr} = Plateau_{phyt} \qquad \text{Eq. (C.2)}$$

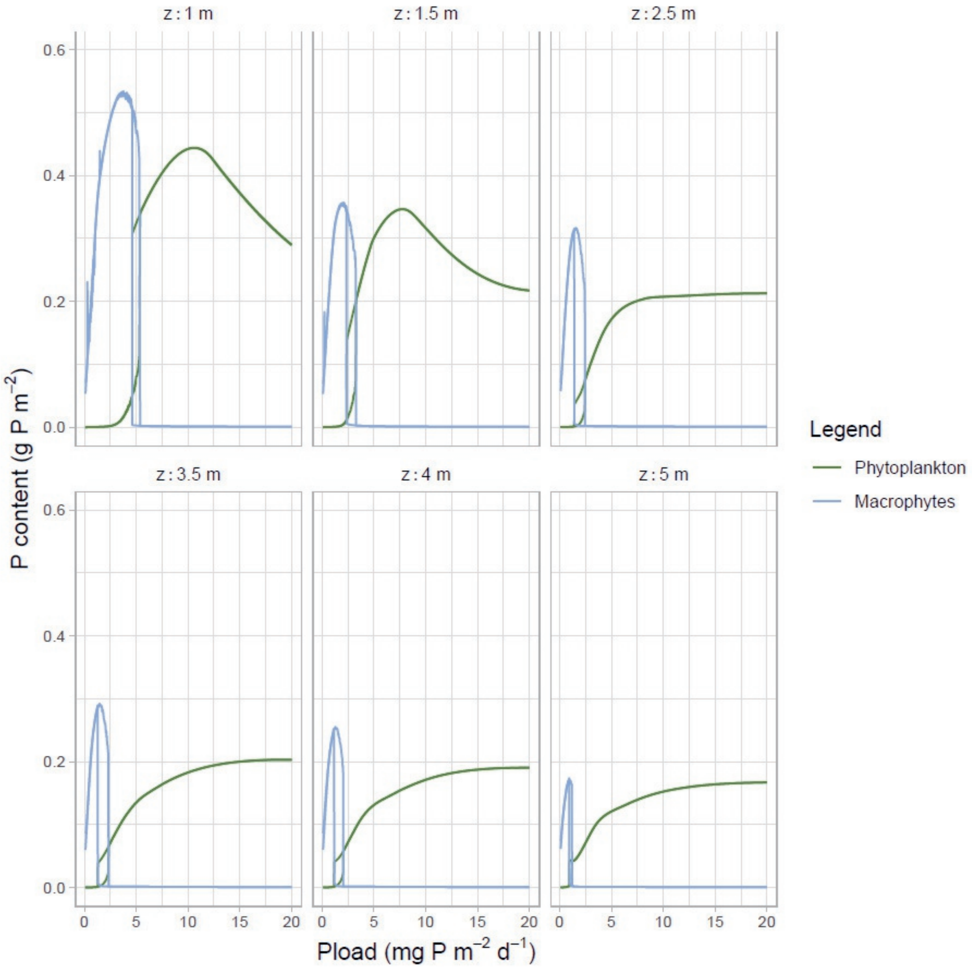

Figure C.1. PCLake bifurcation plots for phytoplankton (dark green) and macrophyte (light blue) P content (g P m^{-2}) for a range of lake depths (z: 0.5-5 m) and a constant hydraulic residence time (*τ*: 100 d).

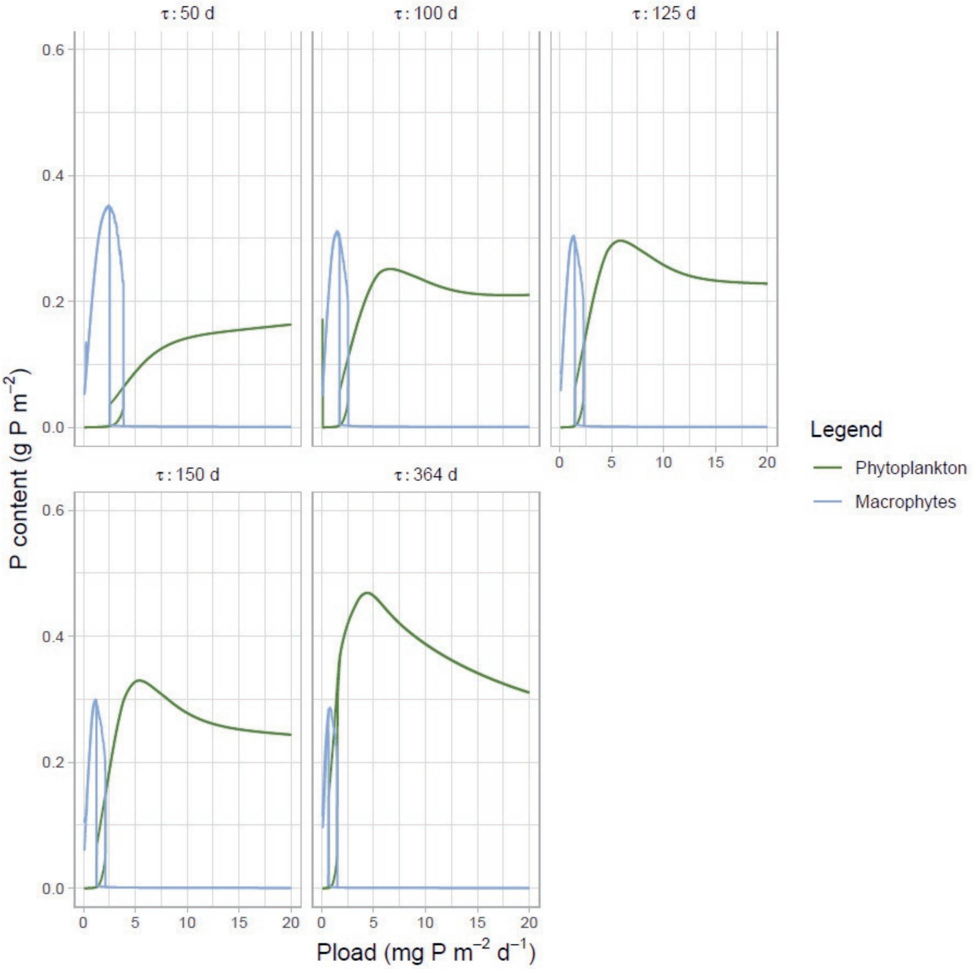

Figure C.2 PCLake bifurcation plots for phytoplankton (dark green) and macrophyte (light blue) P content (g P m^{-2}) for a range of hydraulic residence times (*τ*: 50-364 days; i.e., Qin: 5.5-40 mm d^{-1}) and a constant lake depth (z: 2 m).

Supplementary material D: Critical turbidity

To parameterize GPLake-M, the critical extinction coefficient was determined as the total light extinction coefficient at which regime shifts occur, based on bifurcation analyses of a standard lake in PCLake (set 1 in Table 3.1) and lakes of +/- 0.5 m depth. Next, the critical extinction coefficient was converted into a critical P content as a measure of critical turbidity.

Critical turbidity and light extinction

Critical turbidity can be understood from the total light extinction coefficient in Lambert Beer's law, as formulated by Huisman and Weissing (1994):

$$I_{out} = I_{in} \times e^{-k \times w \times z} \qquad \text{Eq. (D.1)}$$

with I_{out} being the light intensity at the bottom of the water column (J m^{-2} s^{-1}), I_{in} the light supply intensity at the top of water column (J m^{-2} s^{-1}), k the light extinction coefficient (m^2 g^{-1}), w the biomass density (g m^{-3}) and z the total depth of the water column (m). The term k×w×z (-) represents the total light extinction coefficient (i.e., total light attenuation coefficient) which we added as aExtTot (-) in PCLake by:

$$aExtTot = aExtCoef \times sDepthW \qquad \text{Eq. (D.2)}$$

Here aExtCoef is the total community-specific extinction coefficient (equals k×w or extinction coefficient, m^{-1}) and sDepthW is the depth of the water column (m). By this we assume that phytoplankton is the major source of light extinction (see section 3.1.3).

For GPLake-M, the critical extinction coefficient (Ext_{crit}, -) was determined as the total light extinction coefficient at which regime shifts between macrophyte and phytoplankton dominance occur. For this, bifurcation analyses were performed in PCLake by plotting aExtTot on the y-axis and mPLoad on the x-axis. First, mPLoad (P loading) was set in the range of 0.001-0.005 g P m^{-2} d^{-1}. Next, the mPload range was fine-tuned until it captured the regime shifts in both directions to get a first impression of the critical nutrient loadings. These analyses were performed for a standard lake of 2m depth with a Qin of 20 mm d^{-1}, as well as for deviating depths (+/- 0.5 m, set 7 and 8 in Table 3.1) and Qin (40 mm d^{-1}, set 2 in Table 3.1). In all runs, the critical extinction coefficient visually fell in the range of 6-7. The widest range of aExtTot was covered by the runs of 1.5 and 2.5 m depth (and a standard Qin of 20 mm d^{-1}). Therefore, the PCLake runs with deviating depths (1.5, 2.0 and 2.5 m depth, Qin of 20 mm d^{-1}) were selected to mathematically derive the critical extinction coefficient. For this, these runs were repeated at a higher resolution by using a narrower mPLoad range (within +/- 0.0002 g P m^{-2} d^{-1}) around their critical nutrient loadings.

First, aExtTot was averaged over 6 reported points around the highest slope between neighboring reported points. The slope between points was calculated as:

$$Slope\ between\ points = \frac{aExtTot\ at\ high\ Pload\ point - aExtTot\ at\ low\ Pload\ point}{high\ Pload\ point - low\ Pload\ point} \quad \text{Eq. (D.3)}$$

Averaging all resulting critical extinction coefficients (at 1.5, 2.0 and 2.5 m depth for both directions of the regime shift) gave an average critical extinction coefficient (Ext_{crit}, -) of 6.4. This critical extinction coefficient value also visually fits the results from PCLake runs for a wider range of depths (1-5 m) and Qin (5.5-40 mm d^{-1}) (Fig. D.1 and D.2).

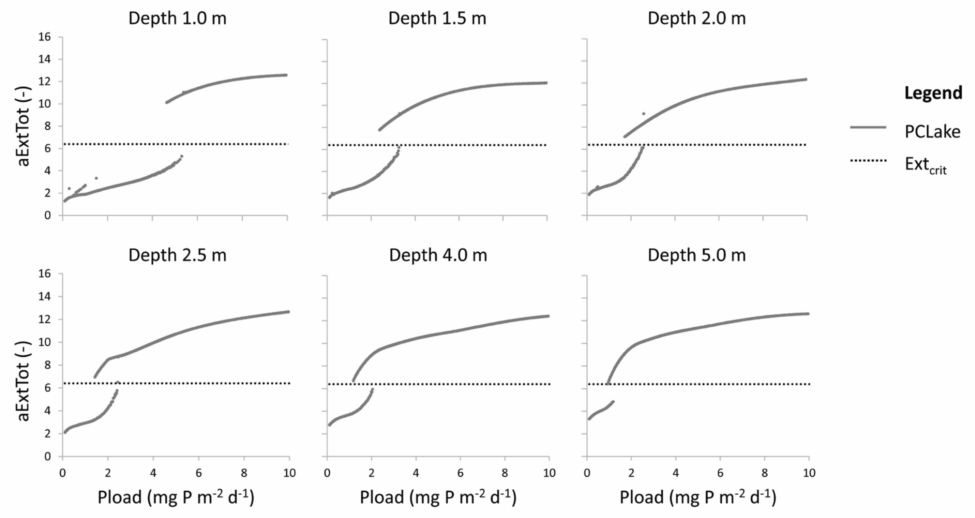

Figure D.1. PCLake bifurcation plots of total extinction coefficient (aExtTot, -) and the average critical extinction coefficient (Ext_{crit}, -) against P loading (mg P m^{-2} d^{-1}) for multiple lake depths (m).

Conversion to critical P content

Next, the critical extinction coefficient was converted into a critical P content (Pcrit, g P m^{-2}) as a measure of critical turbidity by:

$$Pcrit = \frac{Ext_{crit}}{ExtSpSest} \times cSest \quad \text{Eq. (D.4)}$$

Where ExtSpSest is the average seston species-specific extinction coefficient of 0.25 m^2 g DW^{-1} (similar to k in Lambert Beer's Law), derived from PCLake based on cExtSpDiat, cExtSpGren, cExtSpBlue and cExtSpDet. The latter species-specific extinction coefficients refer to the components of seston: diatoms, green and blue-green algae and detritus, respectively. And cSest is the seston P to dry weight ratio of 0.00286 g P g DW^{-1}, determined from PCLake output as oPSestW over oDSestW for a standard lake (2m depth, Qin 20 mm d^{-1}) at a mPLoad of 0.0026 g P m^{-2} d^{-1}. This stoichiometric ratio is used to convert the biomass unit to P. This resulted in a Pcrit of 0.073 g P m^{-2} at which regime shifts between macrophytes and phytoplankton are expected.

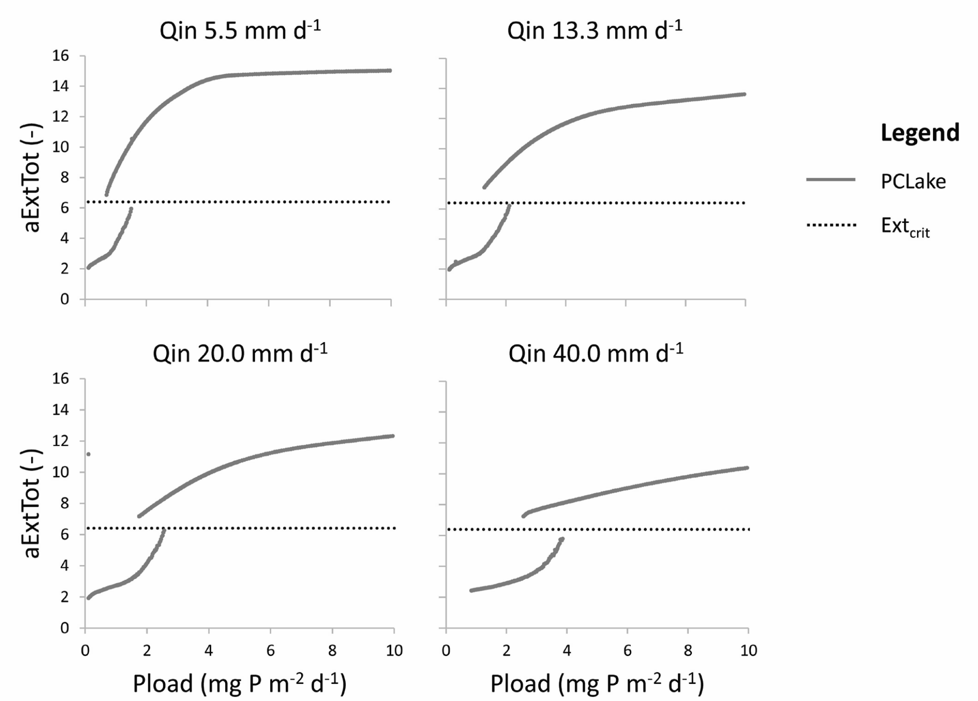

Figure D.2. PCLake bifurcation plots of total extinction coefficient (aExtTot, -) and the average critical extinction coefficient ($\mathbf{Ext_{crit}}$, -) against P loading (mg P $\mathbf{m^{-2}}$ $\mathbf{d^{-1}}$) for multiple hydrological loadings (Qin, mm $\mathbf{d^{-1}}$).

Supplementary material E: Plateau and Slope

Plateau and Slope values for GPLake-M were parameterized by analysis of nutrient-response curves, based on bifurcation analysis of a standard lake in PCLake (set 1 in Table 3.1). Slopes and Plateaus were determined for both an initial clear and turbid state. Because the values hardly differed among the initial states, they were averaged per species.

Plateau

The Plateau was derived from a horizontal line (constant function, y = c = Plateau (g P m^{-2})) through the light-limited phytoplankton phase where the nutrient-response curve was leveling off to a constant nutrient content per nutrient loading (Fig. E.1). The Plateau was determined from phytoplankton output only, since a modeling experiment with PCLake showed that Plateaus of macrophytes and phytoplankton lie within the same range (Supplementary material C). The final Plateau of 0.259 g P m^{-2} is the average of the phytoplankton Plateaus from the initial clear and turbid state.

Slope

$\text{Slope}_{\text{phyt}}$ and $\text{Slope}_{\text{macr}}$ were parameterized by fitting a linear function (y = ax+b, with a = Slope (d)) through the nutrient-limited phase of macrophytes and phytoplankton, respectively. The Slope represents Pphyt (g P m^{-2}) or Pmacr (g P m^{-2}) over Pload (g P m^{-2} d^{-1}), hence is expressed in the unit d. Slopes were derived for both an initial clear and turbid state and averaged per species. After visual assessment of the nutrient-response curves (Fig. E.1 and E.2), the intercept was assumed to approach zero except for macrophytes with an initial turbid state. This resulted in an average $\text{Slope}_{\text{phyt}}$ of 47.3 d. Because the macrophyte parameters are completely novel in GPLake-M compared to GPLake, $\text{Slope}_{\text{macr}}$ was derived with a narrower resolution of P loading (Fig. E.2). A linear function without intercept, that goes through the macrophyte peak (highest value of aPVeg) was used to derive the $\text{Slope}_{\text{macr}}$ with an initial clear state. For the initial turbid state, a linear function with intercept was visually fitted through the sloping phase of the nutrient-response curve. This resulted in an average $\text{Slope}_{\text{macr}}$ of 237 d.

According to Chang et al. (2019), $\text{Slope}_{\text{phyt}}$ scales with hydraulic residence time τ (i.e., reciprocal of dilution rate D) and $\text{Plateau}_{\text{phyt}}$ with depth z. Therefore, we explored whether $\text{Slope}_{\text{macr}}$ varies in PCLake over a range of z (2 m +/- 0.5) and hydrological loadings (cQin; 20 and 40 mm d^{-1}, representing τ; 100 and 50 d). This revealed that the macrophyte Slope is rather invariant (Fig. E.3), therefore $\text{Slope}_{\text{macr}}$ is applied as a constant in GPLake-M.

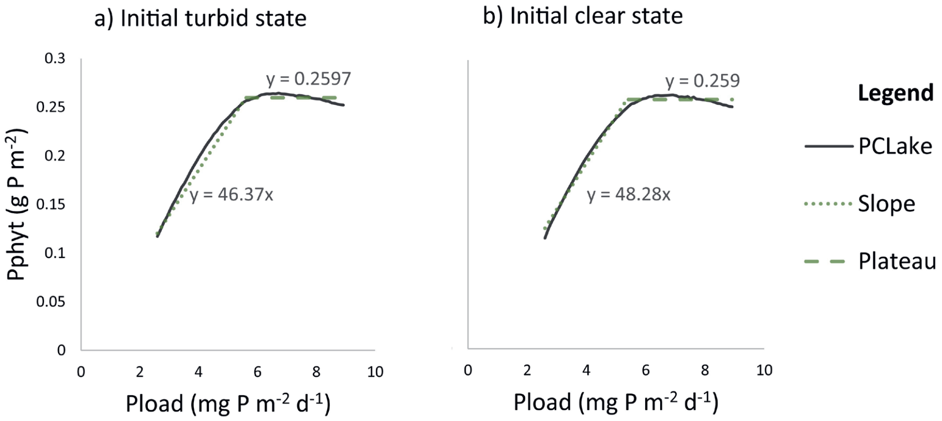

Figure E.1. Phytoplankton nutrient-response curves for a standard lake in PCLake (black line) for a) an initial turbid state and b) an initial clear state. Linear functions of the Slope (dotted green line) and Plateau (dashed green line) are displayed within the graphs.

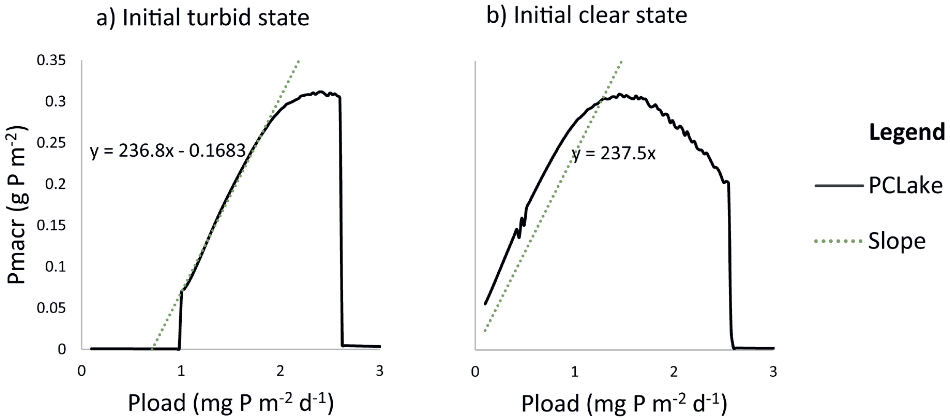

Figure E.2. Macrophyte nutrient-response curves for a standard lake in PCLake (black line) for a) an initial turbid state and b) an initial clear state. Linear functions of the Slope (dotted green line) are displayed within the graphs.

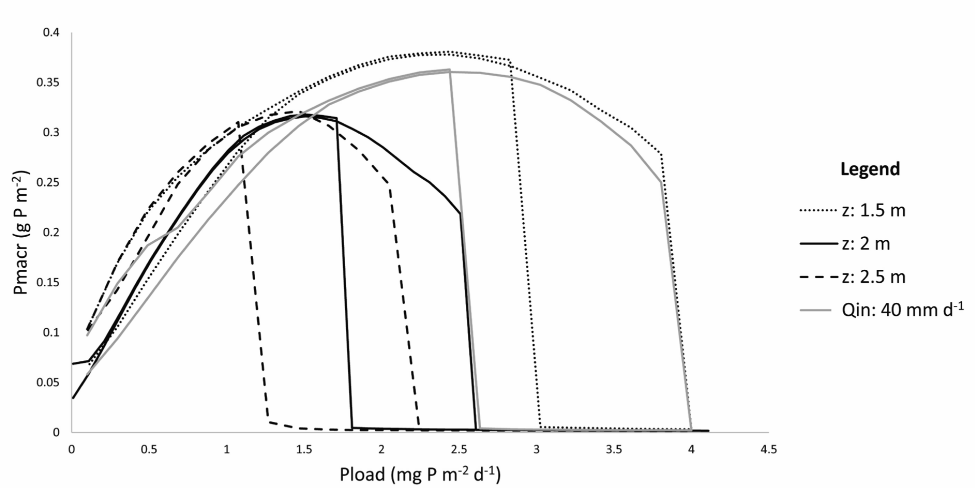

Figure E.3. Macrophyte bifurcation plots from PCLake for a standard lake (set 1 in Table 3.1) of depth z 2 m and hydrological loading Qin 20 mm d^{-1} (black), different z (dotted and dashed) and Qin (gray).

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Chang M, Teurlincx S, DeAngelis DL, Janse JH, Troost TA, van Wijk D, Mooij WM, Janssen ABG. 2019. A Generically Parameterized model of Lake eutrophication (GPLake) that links field-, lab-and model-based knowledge. Science of the Total Environment. 695:133887.

Supplementary material F: Mass balance and scaling scenarios

Various scenarios of how nutrient and water flows are coupled or decoupled are possible, as well as how nutrient retention is defined. The scenario choice influences how the model scales with hydraulic residence time and depends on the case of interest. For example, in fast flowing systems chemostat type dynamics might be relevant; with nutrients majorly entering and leaving a system along with the in- and outflow of water (i.e., coupled nutrient and water flows). In cases of concentrated point loadings, atmospheric deposition and flushing with clean water, nutrient and water inflows are decoupled. Whether nutrient and water inflows are (de)coupled influences how primary producer biomass is related to hydraulic residence time (Elliott 2021). Nutrient retention dynamics influence how strongly the outflow of nutrients is related to the outflow of water. Hydraulic residence time is one of the major factors influencing nutrient retention (Ahlgren et al. 1988; Finlay et al. 2013) but multiple relationships between the nutrient retention rate and waterflow rate are possible. Here we present a generalized mass balance equation that is open to all these different scenarios and exemplify the scaling of GPLake-M in case of Monod- and Vollenweider-type nutrient retention (see derivation in Supplementary material G).

Generalized mass balance equation

The principle of mass balance equations is that the amount of incoming mass of a substance (i.e., nutrient R) should equal the amount of outflowing mass of that substance at any moment in time. The left-hand term represents the net nutrient inflow that is available for biota and the right-hand term the total biotic nutrient loss. To generalize the mass balance equation, we first define the total nutrient loading as the sum of nutrient loading along with the water inflow z D_{in} R_{in} (g m^{-2} d^{-1}) and nutrient sources that enter the lake directly Rload (g m^{-2} d^{-1}):

$$Total\ nutrient\ loading = z \times D_{in} \times R_{in} + Rload \qquad \text{Eq. (F.1)}$$

Secondly, we consider that the loss processes of macrophytes and phytoplankton differ essentially. Rooting macrophytes are unaffected by hydrological outflow, thus are only lost by biological processes that contribute to nutrient retention within the lake (i.e., total nutrient loss rate in a macrophyte-dominated lake = $Dmacr_{ret}$ in d^{-1}). On the other hand, phytoplankton is lost by hydrological outflow and biological processes like decomposition (i.e., total nutrient loss rate in a phytoplankton-dominated lake = D_{out} + $Dphyt_{ret}$ in d^{-1}). Depending on the scenario of choice, the nutrient retention rates $Dmacr_{ret}$ and $Dphyt_{ret}$ can be constants or variables (e.g., using a Vollenweider-type function).

Altogether, this leads to the most general mass balance equation of GPLake-M:

$$z \times D_{in} \times (R_{in} - R_k^*) + Rload = Dmacr_{ret} \times Rmacr_j + (D_{out} + Dphyt_{ret}) \times Rphyt_j \qquad \text{Eq. (F.2)}$$

With depth z (m) and water inflow rate D_{in}. R_{in} and R_k^* are nutrient concentrations (g Nutrient m^{-3}) with subscript in referring to the inflowing water and subscript k to the equilibrium set (I, II, III or IV). $Rmacr_j$ and $Rphyt_j$ are the areal nutrient contents (g Nutrient m^{-2}) of macrophytes and phytoplankton, respectively. Please note that in most studies phytoplankton levels are expressed in concentration units, and macrophyte levels in units per surface area. We here chose to express both per surface area to ease comparison between the two primary producers. Subscript j indicates whether the dominant primary producer is in the zero-biomass (0), nutrient-limited (1) or light-limited phase (2). During light limitation not all nutrients are consumed and the total amount of nutrients unconsumed by phytoplankton and macrophytes, at equilibrium, is defined by R_k^*. Contrarily, in nutrient-limited systems almost all supplied nutrients are consumed, so R_k^* is assumed negligible. Note that in GPLake-M we now focused on phosphorus (P) as major limiting nutrient R.

Example mass balance and scaling scenario

Here, we first exemplify how to derive the scaling of the Slope parameters from the mass balance equations. The Slope shows how a primary producer responds to nutrient loading under nutrient limitation. In this derivation we therefore use equilibria set I and III, being the simplest cases with one primary producer in the nutrient-limited and the other in the zero-biomass phase. The resulting definitions of the Slopes can also be applied in the other equilibria sets. We focus on P in a system with only nutrient loading by inflowing water (i.e., total nutrient loading = z D_{in} P_{in} = Pload) and a simple chemostat-type mass balance where D_{in} equals D_{out}. Thereafter, we show how these equations can be used considering different scenarios for phytoplankton nutrient retention rate $Dphyt_{ret}$.

Scaling of macrophyte Slope

Set I describes nutrient-limited macrophytes and zero-biomass phytoplankton, so we assume R_I^* is zero. Given the equilibrium solution P_{phyt} equals zero (Equation 1b), this gives the mass balance equation at equilibrium:

$$z \times D_{in} \times P_{in} = Dmacr_{ret} \times Pmacr_1 \qquad \text{Eq. (F.3)}$$

Knowing that this set's equilibrium solution is $Pmacr = Slope_{macr} \times Pload = Slope_{phyt} \times z \times Din \times Pin$ (Equation 1a), this gives a $Slope_{macr}$ (d) of:

$$Slope_{macr} = \frac{1}{Dmacr_{ret}} \qquad \text{Eq. (F.4)}$$

Hence, for a constant $Dmacr_{ret}$ also the $Slope_{macr}$ is constant.

Scaling of phytoplankton Slope

Set III describes nutrient-limited phytoplankton, so we assume P_{III}^* is zero. Given the equilibrium solution P_{macr} equals zero (Equation 3a), this gives the mass balance equation at equilibrium:

$$z \times D_{in} \times P_{in} = (D_{in} + Dphyt_{ret}) \times Pphyt_1 \qquad \text{Eq. (F.5a)}$$

$$Pphyt_1 = \frac{z \times D_{in} \times P_{in}}{D_{in} + Dphyt_{ret}} \qquad \text{Eq. (F.5b)}$$

$$Pphyt_1 = \frac{1}{D_{in} + Dphyt_{ret}} \times z \times D_{in} \times P_{in} \qquad \text{Eq. (F.5c)}$$

Knowing that this set's equilibrium solution is $Pphyt = Slope_{phyt} \times Pload = Slope_{phyt} \times z \times Din \times Pin$ (Equation 3b), this gives a $Slope_{phyt}$ (d) of:

$$Slope_{phyt} = \frac{1}{D_{in} + Dphyt_{ret}} \qquad \text{Eq. (F.6)}$$

Hence, $Slope_{phyt}$ scales negatively with D_{in} and thus positively with its reciprocal τ.

Monod and Vollenweider-type nutrient retention scenarios

The nutrient retention rates $Dmacr_{ret}$ and $Dphyt_{ret}$ can be constants or variables. When using them as constants, the equations above apply directly (in the case that nutrient loading is only caused by inflowing water). This gives a constant $Slope_{macr}$, and a $Slope_{phyt}$ scaling with D_{in} and thus with hydraulic residence time τ (Fig. F.1 and F.2). Here the nutrient retention rates can be considered as half-saturation constants in a Monod-type function of the amount of primary producer. For the figures in this Supplementary material, the variable $Slope_{phyt}$ was parameterized using D_{in} is 0.01 d^{-1} and the corresponding $Slope_{phyt}$ of 47.3 d (section 3.2.1 of main text) to derive $Dphyt_{ret}$. Next this constant value of $Dphyt_{ret}$ was used to derive new $Slope_{phyt}$ values for different values of D_{in} (i.e., reciprocal of τ).

Alternatively, the nutrient retention rates can be defined as variables that, for example, depend on hydraulic residence time or temperature. As an example scenario, we here use a Vollenweider-type function for phytoplankton, as derived in Supplementary material G. In this approach, time scaling parameter s is introduced, which can be considered as the τ at which the $Dphyt_{ret}$ equals D_{in}. In the Vollenweider scenario $Dphyt_{ret}$ is defined as:

$$Dphyt_{ret} = \frac{\sqrt{s \times D_{in}}}{s} \qquad \text{Eq. (F.7)}$$

Applying this in the mass balance equations above, results in a $Slope_{phyt}$ with an alternative dependency on D_{in}. Parameterization in a similar approach as for the Monod-type function gives an s value of 81 d. Application of this s value to derive variable $Dphyt_{ret}$ and $Slope_{phyt}$ values for different values of D_{in} resulted in Fig. 3 and 5 in the main text (section 3.3). We conclude that this Vollenweider-type definition of phytoplankton nutrient retention rate gives a better fit with PCLake than the Monod-type scenario. Still, in other cases different retention scenarios might be more appropriate. The mass balance equations of GPLake-M offer flexibility to make case specific choices for such scenarios.

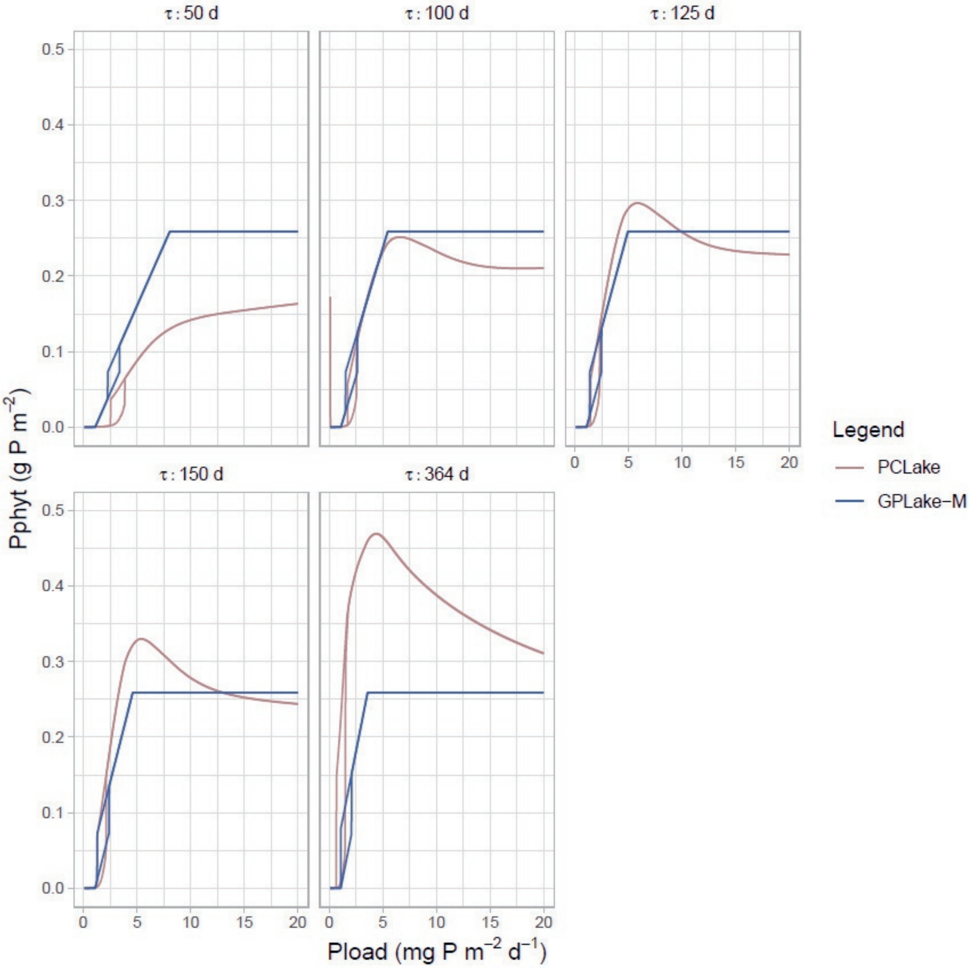

Figure F.1. Comparison of GPLake-M (blue) and PCLake (red) phytoplankton P content per residence time (*τ*: 50-364 d) for depth 2m (set 1-5, Table 3.1), assuming the Monod-type scenario in GPLake-M with constant nutrient retention rates.

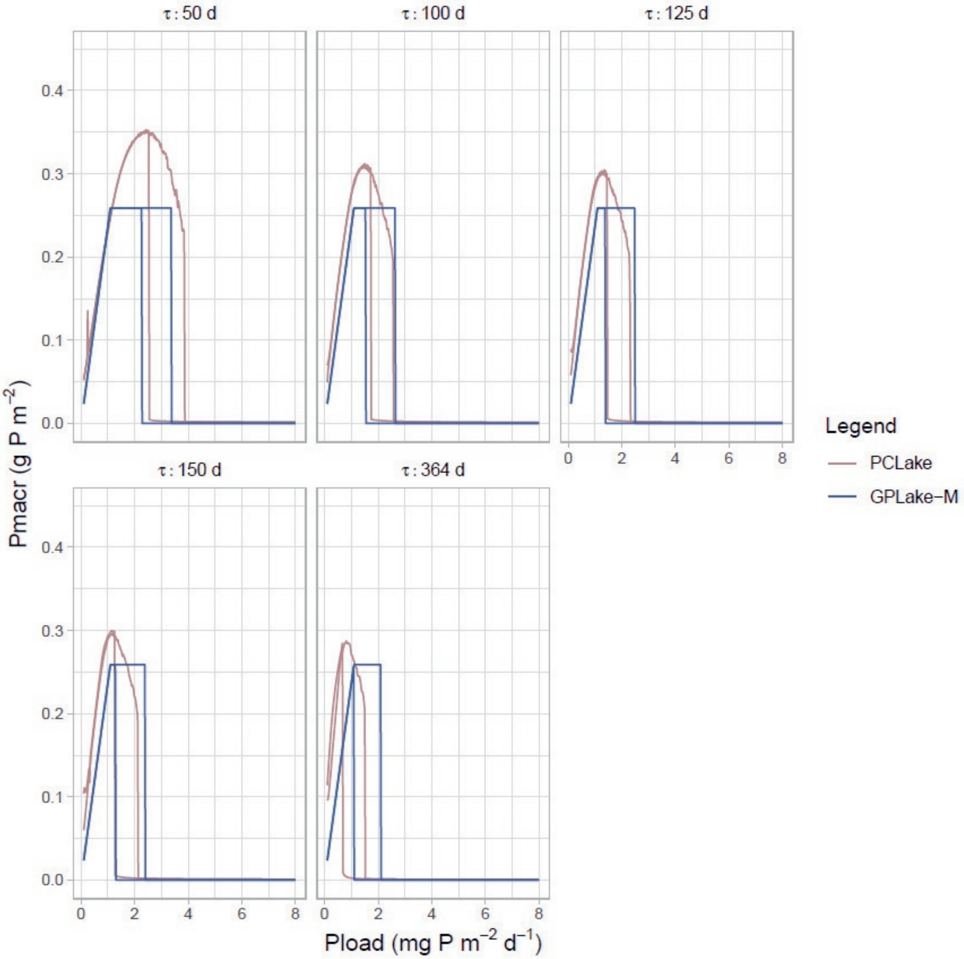

Figure F.2. Comparison of GPLake-M (blue) and PCLake (red) macrophyte P content per residence time (*τ*: 50-364 d) for depth 2m (set 1-5, Table 3.1), assuming the Monod-type scenario in GPLake-M with constant nutrient retention rates.

References

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Finlay JC, Small GE, Sterner RW. 2013. Human influences on nitrogen removal in lakes. Science. 342(6155):247-250.

Supplementary material G: Vollenweider normalization and nutrient retention

Here we dive into the Vollenweider normalization of nutrient loading that was used in GPLake (Chang et al. 2019) and derive a function that can be applied in GPLake-M in a scenario with a Vollenweider-type definition of phytoplankton nutrient retention rate. In this process, we introduce time scaling parameter s to ensure unit correctness. See Supplementary material F for an example of how to apply such scenarios using the generalized mass balance equation from GPLake-M, as used for the pattern-oriented comparison in the main text (section 3.3).

Vollenweider's normalization of nutrient loading

Vollenweider and successors showed a rather universally applicable linear relationship between P loading and the amount of phytoplankton (µg chl-*a* l^{-1}) in log-log space (Jones and Lee 1986), when P loading is normalized according to:

$$P_{cor} = \frac{\frac{L(P)}{q_s}}{1+\sqrt{\tau_\omega}} \qquad \text{Eq. (G.1a)}$$

with P_{cor} being the normalized P loading (g P m^{-3}), L(P) the annual areal P loading (g P m^{-2} y^{-1}), q_s (m yr^{-1}) the mean depth (z in m) times dilution rate (D_{in} in y^{-1}), and τ_ω the hydraulic residence time (y). Since τ_ω is the reciprocal of D_{in}, the normalized P loading is also defined as:

$$P_{cor} = \frac{\frac{L(P)}{z\times D_{in}}}{1+\sqrt{\frac{1}{D_{in}}}} \qquad \text{Eq. (G.1b)}$$

When assuming only nutrient loading by inflowing water, L(P) is the product of z, D_{in} and inflowing nutrient concentration P_{in} (g P m^{-3}) and we can rewrite Vollenweider's function in GPLake-M terms:

$$P_{cor} = \frac{\frac{z\times D_{in}\times P_{in}}{z\times D_{in}}}{1+\sqrt{\frac{1}{D_{in}}}} \qquad \text{Eq. (G.1c)}$$

Although Jones and Lee (1986) extended the application range of this relationship to higher P loading levels, the relationship holds best for phosphorus limited systems (Vollenweider and Kerekes 1982). We argue that it would not apply to light-limited systems where the amount of phytoplankton is independent of the nutrient loading, which corresponds with the flatting out of the relationship at high P loadings (Jones and Lee 1986). Moreover, it does not account for the influence of macrophytes or internal loading (Vollenweider and Kerekes 1982). Therefore, we here focus on the application of Vollenweider's normalization in GPLake(-M) to phosphorus-limited phytoplankton.

Vollenweider's normalization in GPLake

In GPLake, the phytoplankton biomass concentration during nutrient limitation (W_1 in mg chl-*a* m^{-3}) is shown to fit with multiple datasets when using Vollenweider's normalization (Chang et al. 2019) by:

$$W_1^* = Slope_{GPLake} \times P_{cor} \qquad \text{Eq. (G.2)}$$

Note that here $Slope_{GPLake}$ has a different unit and definition than the Slopes we use in GPLake-M.

When assuming only nutrient loading by inflowing water, L(P) is the product of z, D_{in} and inflowing nutrient concentration P_{in} (g P m^{-3}) (i.e., starting from Equation G.1c), we can rewrite Vollenweider's function in GPLake-M terms:

$$P_{cor} = \frac{\frac{z\times D_{in}\times P_{in}}{z\times D_{in}}}{1+\sqrt{\frac{1}{D_{in}}}} \qquad \text{Eq. (G.3a)}$$

$$P_{cor} = \frac{\frac{D_{in}\times P_{in}}{D_{in}}}{1+\sqrt{\frac{1}{D_{in}}}} \qquad \text{Eq. (G.3b)}$$

$$P_{cor} = \frac{D_{in}\times P_{in}}{D_{in}\times(1+\sqrt{\frac{1}{D_{in}}})} \qquad \text{Eq. (G.3c)}$$

$$P_{cor} = \frac{D_{in}\times P_{in}}{D_{in}+D_{in}\times\sqrt{\frac{1}{D_{in}}}} \qquad \text{Eq. (G.3d)}$$

$$P_{cor} = \frac{D_{in}\times P_{in}}{D_{in}+\frac{D_{in}}{\sqrt{D_{in}}}} \qquad \text{Eq. (G.3e)}$$

$$P_{cor} = \frac{D_{in}\times P_{in}}{D_{in}+\sqrt{D_{in}}} \qquad \text{Eq. (G.3f)}$$

$$P_{cor} = \frac{D_{in}}{D_{in}+\sqrt{D_{in}}} \times P_{in} \qquad \text{Eq. (G.3g)}$$

Applying this notation of P_{cor} in equation G.2 gives a different notation of GPLake, which shows a dependency on P_{in}:

$$W_1^* = Slope_{GPLake} \times \frac{D_{in}}{D_{in}+\sqrt{D_{in}}} \times P_{in} \qquad \text{Eq. (G.4)}$$

This shows that by the application of Vollenweider's normalization in GPLake, the effect of dilution (i.e., D_{in}) and the effect of $\sqrt{D_{in}}$ on the in lake nutrient concentration is included. In the Vollenweider scenario of GPLake-M we assume that the effect of $\sqrt{D_{in}}$ represents the nutrient retention in a phytoplankton-dominated lake. However, there seems to be a mismatch in the units of Vollenweider's normalization which we solve below, before applying this definition of nutrient retention to GPLake-M.

Unit correction of Vollenweider normalization in GPLake-M

A unit check of Vollenweider's original normalization function (Equation G.1a) reveals that $1+\sqrt{\tau_\omega}$ should be unit less. When rewritten in GPLake-M terms, $\frac{D_{in}}{D_{in}+\sqrt{D_{in}}}$ should be unit less. However, this does not seem to be the case because of the root function in both equations. We solve this by adding time scaling parameter s (with the reciprocal unit of D_{in}), being the τ_ω at which the P retention rate of a phytoplankton-dominated lake ($Dphyt_{ret}$, the same unit as D_{in}) equals the dilution rate D_{in}:

$$P_{cor} = \frac{s \times D_{in}}{s \times D_{in} + \sqrt{s \times D_{in}}} \times P_{in} \qquad \text{Eq. (G.5a)}$$

$$P_{cor} = \frac{D_{in}}{D_{in} + \frac{\sqrt{s \times D_{in}}}{s}} \times P_{in} \qquad \text{Eq. (G.5b)}$$

Note that when s is one this equals Vollenweider's function (Equation G.3g). By this unit correction, Vollenweider's normalized nutrient loading now has the same unit as P_{in} and one is free to choose the unit of D_{in} (e.g., y^{-1} or d^{-1}) as long as s has a matching reciprocal unit (i.e., y or d, respectively). In the Vollenweider scenario of GPLake-M we assume that $\frac{\sqrt{s \times D_{in}}}{s}$ is the phytoplankton nutrient retention rate $Dphyt_{ret}$, in accordance with the GPLake-M mass balance equation (Supplementary material F).

Parameterization of time scaling parameter s

The value of s can be derived bottom-up as the reciprocal of D_{in} (d^{-1}) at which half of the inflowing P is being retained. Instead, for GPLake-M we derived the value of s in a top-down approach using the constant $Slope_{phyt}$ (section 3.2.1 of main text) that was parameterized using D_{in} is 0.01 d^{-1} and the GPLake-M mass balance equation (Supplementary material F):

$$Slope_{phyt} = \frac{1}{D_{in} + \frac{\sqrt{s \times D_{in}}}{s}} \qquad \text{Eq. (G.6a)}$$

$$D_{in} + \frac{\sqrt{s \times D_{in}}}{s} = \frac{1}{Slope_{phyt}} \qquad \text{Eq. (G.6b)}$$

$$\frac{\sqrt{s \times D_{in}}}{s} = \frac{1}{Slope_{phyt}} - D_{in} \qquad \text{Eq. (G.6c)}$$

$$\frac{\sqrt{s} \times \sqrt{D_{in}}}{s} = \frac{1}{Slope_{phyt}} - D_{in} \qquad \text{Eq. (G.6d)}$$

$$\frac{\sqrt{s}}{s} = \left(\frac{1}{Slope_{phyt}} - D_{in}\right) \times \frac{1}{\sqrt{D_{in}}} \qquad \text{Eq. (G.6e)}$$

$$\frac{1}{\sqrt{s}} = \frac{1}{Slope_{phyt} \times \sqrt{D_{in}}} - \frac{D_{in}}{\sqrt{D_{in}}} \qquad \text{Eq. (G.6f)}$$

$$\frac{1}{\sqrt{s}} = \frac{1}{Slope_{phyt} \times \sqrt{D_{in}}} - \sqrt{D_{in}} \qquad \text{Eq. (G.6g)}$$

$$\sqrt{s} = \frac{1}{\left(\frac{1}{Slope_{phyt} \times \sqrt{D_{in}}} - \sqrt{D_{in}}\right)} \qquad \text{Eq. (G.6h)}$$

$$s = \frac{1}{\left(\frac{1}{Slope_{phyt} \times \sqrt{D_{in}}} - \sqrt{D_{in}}\right)^2} \qquad \text{Eq. (G.6i)}$$

References

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Supplementary material H: Phytoplankton Plateau derivation from Huisman and Weissing model

Here we provide the mathematical derivation of the GPLake(-M) phytoplankton Plateau, following the model by Huisman and Weissing (1994, 1995). The essence is that an average amount of light-limited primary producer in a water column can be calculated, despite a vertical light and biomass gradient in a water column.

Phytoplankton Plateau

The amount of phytoplankton during light limitation is expressed in mg chl-*a* m^{-3} in GPLake (W_2^* or $Plateau_{GPLake}$, and w in the model of Huisman and Weissing) (Chang et al. 2019):

$$W_2^* = \frac{p_{max}}{z \times k \times l} \times LN\left(\frac{I_{in}+H}{H}\right) \qquad \text{Eq. (H.1a)}$$

with p_{max}, being the maximum specific growth rate (d^{-1} or s^{-1} in the model of Huisman and Weissing), k the phytoplankton community light extinction coefficient (m^2 mg chl-a^{-1}), l the phytoplankton community loss rate (d^{-1} or s^{-1} in the model of Huisman and Weissing), I_{in} the light supply intensity at the top of water column (J m^{-2} s^{-1}), z the total depth of the water column (m), and H the half saturation constant of light (J m^{-2} s^{-1}).

By unit conversion to g P m^{-2} this becomes the amount of phytoplankton during light limitation in GPLake-M ($Plateau_{phyt}$):

$$Plateau_{phyt} = c \times z \times Plateau_{GPLake} = c \times \frac{p_{max}}{k \times l} \times LN\left(\frac{I_{in}+H}{H}\right) \qquad \text{Eq. (H.1b)}$$

with c being the P to chl-*a* ratio of phytoplankton (g P mg chl-a^{-1}).

Derivation of Plateau from Huisman and Weissing model

Light extinction

The GPLake(-M) Plateau values depend on the total lake depth and represent a water column averaged amount of phytoplankton, as in the model of Huisman and Weissing (1994, 1995). Still, the amount of light-limited phytoplankton depends on their position in the water column (depths s, m), because of light extinction over depth according to Lambert Beer's law:

$$I(s) = I_{in} \times e^{-k \times w \times s} \qquad \text{Eq. (H.2a)}$$

and

$$I_{out} = I_{in} \times e^{-k \times w \times z} \qquad \text{Eq. (H.2b)}$$

with I(s) being the light supply intensity at depth s (J m^{-2} s^{-1}), w the biomass density (mg chl-*a* m^{-3}) and I_{out} the light intensity at the bottom of the water column (J m^{-2} s^{-1}).

Supplementary materials

Total production rate

In general, the total production rate P (mg chl-*a* m^{-2} d^{-1}) at depth s is defined as:

$$P(s) = p(I,s) \times w\ ds \qquad \text{Eq. (H.3a)}$$

with p being the specific uptake rate (s^{-1}).

For light-limited primary producers, p is assumed to depend on light according to the Monod equation (equation 2 in Huisman and Weissing (1994)):

$$p(I,s) = p_{max} \times \frac{I(s)}{I(s)+H} \qquad \text{Eq. (H.3b)}$$

Huisman and Weissing showed that by integrating over water column depth, the average amount of light-limited phytoplankton in a water column at equilibrium can be estimated. We derive this from Equation H.3a, filling in H.3b and H.2a:

$$P = \int_0^z p_{max} \times \frac{I_{in} \times e^{-k \times w \times s}}{I_{in} \times e^{-k \times w \times s} + H} \times w\ ds \qquad \text{Eq. (H.4a)}$$

$$P = p_{max} \times w \int_0^z \frac{I_{in} \times e^{-k \times w \times s}}{I_{in} \times e^{-k \times w \times s} + H} ds \qquad \text{Eq. (H.4b)}$$

Because

$$\frac{d(I_{in} \times e^{-k \times w \times s})}{ds} = -k \times w \times I_{in} \times e^{-k \times w \times s} \qquad \text{Eq. (H.5a)}$$

Therefore

$$ds = \frac{1}{-k \times w \times I_{in} \times e^{-k \times w \times s}} d(I_{in} \times e^{-k \times w \times s}) \qquad \text{Eq. (H.5b)}$$

Assume

$$x(s) = I_{in} \times e^{-k \times w \times s} \qquad \text{Eq. (H.5c)}$$

Therefore

$$ds = \frac{1}{-k \times w \times x} dx \qquad \text{Eq. (H.5d)}$$

Substituting Equation H.5c and H.5d in H.4b gives

$$P = p_{max} \times w \int_{x(0)}^{x(z)} \frac{x}{x+H} \times \frac{1}{-k \times w \times x} dx \qquad \text{Eq. (H.6a)}$$

$$P = \frac{1}{-k \times w} \times p_{max} \times w \int_{x(0)}^{x(z)} \frac{1}{x+H} dx \qquad \text{Eq. (H.6b)}$$

$$P = \frac{p_{max}}{-k} \int_{x(0)}^{x(z)} \frac{1}{x+H} dx \qquad \text{Eq. (H.6c)}$$

Knowing

$$\int \frac{1}{x+H} dx = LN\,(x+H) \qquad \text{Eq. (H.7)}$$

Therefore, solving Equation H.6c gives

$$P = \frac{p_{max}}{-k}\left[(LN\,(x(z)+H) - (LN\,(x(0)+H)\right] \qquad \text{Eq. (H.8a)}$$

$$P = \frac{p_{max}}{k}\left[(LN\,(x(0)+H) - (LN\,(x(z)+H)\right] \qquad \text{Eq. (H.8b)}$$

$$P = \frac{p_{max}}{k} LN\left(\frac{x(0)+H}{x(z)+H}\right) \qquad \text{Eq. (H.8d)}$$

Knowing x(0) = I_{in} and substituting Equation H.2b this gives

$$P\ = \frac{p_{max}}{k} LN\left(\frac{I_{in}+H}{I_{out}+H}\right) \qquad \text{Eq. (H.9)}$$

Equilibrium phytoplankton biomass

The differential equation for phytoplankton biomass growth (mg chl-*a* m^{-3}) is:

$$\frac{dw}{dt} = \frac{P}{z} - l \times w \qquad \text{Eq. (H.10)}$$

The equilibrium phytoplankton biomass W^* (or w in the model of Huisman and Weissing) is derived by making this equation equal to zero:

$$\frac{P}{z} - l \times W^*\ = 0 \qquad \text{Eq. (H.11a)}$$

$$W^*\ = \frac{P}{l \times z} \qquad \text{Eq. (H.11b)}$$

Substituting Equation H.9 and assuming that I_{out} is zero gives the GPLake Equation H.1a:

$$W^* = \frac{p_{max}}{z \times k \times l} LN\left(\frac{I_{in}+H}{H}\right) \qquad \text{Eq. (H.12a)}$$

and the GPLake-M Equation H1.b:

$$Plateau_{phyt} = c\ \times \frac{p_{max}}{k \times l} \times LN\left(\frac{I_{in}+H}{H}\right) \qquad \text{Eq. (H.12b)}$$

References

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Supplementary material I: Differential equations and equilibrium solutions of GPLake-M

The macrophyte and phytoplankton equilibria of GPLake-M consist of four sets, based on combinations of the limitation-phases of macrophytes and phytoplankton in the graphical model (Roman numbers in Fig. 2). Here we present the ordinary differential equations and corresponding summer equilibria per set of GPLake-M, as well as the main model parameters. See Table B.1 for symbol descriptions and units (Supplementary material B).

Set I corresponds with loading levels at which both primary producers are potentially nutrient-limited whereas in set IV they are potentially light-limited. With macrophytes being the superior nutrient competitor and phytoplankton the superior light competitor, we assume that macrophytes will dominate in set I and phytoplankton will dominate in set IV. Sets II and III describe the situation where macrophytes are potentially light-limited and phytoplankton potentially nutrient-limited. In the overlap between both sets, we assume that the macrophyte dominance of set I will persist in set II during eutrophication, and the phytoplankton dominance of set IV will persist in set III during oligotrophication. We implemented this by given primacy to macrophytes in allocating nutrients in set II and only allocate those nutrients that macrophytes cannot absorb due to light limitation to phytoplankton. Likewise, we give phytoplankton primacy to allocating nutrients in set III, which leaves no nutrients available for macrophytes because phytoplankton is nutrient-limited in set III. According to the rules of GPLake-M, the switches between who has primacy to allocate nutrients occurs when the amount of phytoplankton crosses the critical turbidity, resulting in alternative stable states where sets II and III overlap.

These alternative stable states cannot be explained by the model of Huisman and Weissing (1994; 1995) for empirically relevant parameter settings (Supplementary material A). Actually, their model predicts a gradual replacement of light-limited macrophytes by nutrient-limited phytoplankton when both occur mixed throughout the water column (Supplementary material B). Moreover, the layered versions of the Huisman and Weissing (1994; 1995) model *sensu* van Gerven et al. (2015) show strong contrasts in the dominance of phytoplankton or macrophytes, depending on which group occurs above the other (Supplementary material B). GPLake-M combines elements of these different settings of the Huisman and Weissing (1994; 1995) model to capture the alternative stable states observed in nature and in PCLake output. Most importantly, we ignore the shading effect of phytoplankton on macrophytes in set II, resulting in a constant Plateau value for macrophytes during light-limitation.

Differential equations per set of GPLake-M

The differential equations per set of GPLake-M are:

Set I: Nutrient-limited macrophytes - Zero-biomass phytoplankton:

$$\frac{dPmacr}{dt} = p_{max,macr} \times \frac{Pwater}{Pwater + H_{nut,macr}} \times Pmacr - l_{macr} \times Pmacr \tag*{Eq. (I.1a)}$$

$$\frac{dP_{water}}{dt} = Pload - z \times D_{in} \times Pwater - p_{max,macr} \times \frac{Pwater}{Pwater + H_{nut,macr}} \times Pmacr \tag*{Eq. (I.1b)}$$

Set II: Light-limited macrophytes - Nutrient-limited phytoplankton:

$$\frac{dPphyt}{dt} = p_{max,phyt} \times \frac{Pwater}{Pwater + H_{nut,phyt}} \times Pphyt - l_{phyt} \times Pphyt \tag*{Eq. (I.2a)}$$

$$\begin{aligned} \frac{dPmacr}{dt} = p_{max,macr} \times \frac{1}{E_{macr}} \times LN\left(\frac{H_{light,macr} + I_{in,macr}}{H_{light,macr} + I_{in,macr} \times e^{-E_{macr}}}\right) \times Pmacr \\ - l_{macr} \times Pmacr \end{aligned} \tag*{Eq. (I.2b)}$$

$$\begin{aligned} \frac{dP_{water}}{dt} = Pload - z \times D_{in} \times Pwater - p_{max,phyt} \times \frac{Pwater}{Pwater + H_{nut,phyt}} \times Pphyt \\ - p_{max,macr} \times \frac{1}{E_{macr}} \times LN\left(\frac{H_{light,macr} + I_{in,macr}}{H_{light,macr} + I_{in,macr} \times e^{-E_{macr}}}\right) \times Pmacr \end{aligned} \tag*{Eq. (I.2c)}$$

$$E_{macr} = k_{macr} \times Pmacr + K_{bg} \times z \tag*{Eq. (I.2d)}$$

Set III: Zero-biomass macrophytes - Nutrient-limited phytoplankton:

$$\frac{dPphyt}{dt} = p_{max,phyt} \times \frac{Pwater}{Pwater + H_{nut,phyt}} \times Pphyt - l_{phyt} \times Pphyt \tag*{Eq. (I.3a)}$$

$$\begin{aligned} \frac{dP_{water}}{dt} = Pload - z \times D_{in} \times Pwater \\ - p_{max,phyt} \times \frac{Pwater}{Pwater + H_{nut,phyt}} \times Pphyt \end{aligned} \tag*{Eq. (I.3b)}$$

Set IV: Zero-biomass macrophytes - Light-limited phytoplankton:

$$\begin{aligned} \frac{dPphyt}{dt} = p_{max,phyt} \times \frac{1}{E_{phyt}} \times LN\left(\frac{H_{light,phyt} + I_{in,phyt}}{H_{light,phyt} + I_{in,phyt} \times e^{-E_{phyt}}}\right) \times Pphyt \\ - l_{phyt} \times Pphyt \end{aligned} \tag*{Eq. (I.4a)}$$

$$\begin{aligned} \frac{dPwater}{dt} = Pload - z \times D_{in} \times Pwater \\ - p_{max,phyt} \times \frac{1}{E_{phyt}} \times LN\left(\frac{H_{light,phyt} + I_{in,phyt}}{H_{light,phyt} + I_{in,phyt} \times e^{-E_{phyt}}}\right) \times Pphyt \end{aligned} \tag*{Eq. (I.4b)}$$

$$E_{phyt} = k_{phyt} \times Pphyt + K_{bg} \times z \tag*{Eq. (I.4c)}$$

Approximations to the equilibrium solutions per set of GPLake-M

The GPLake-M equilibrium solutions during summer can be derived from the four sets of differential equations under three assumptions. First, we assume that all the available light is used for biological production, hence I_{out} is assumed to approximate zero in terms of the model of Huisman and Weissing (1994; 1995). This is essential to provide explicit equilibrium solutions for the differential equations that include light limitation (i.e., sets II and IV). Second, while the equilibria for free nutrients ($Pwater^*$) play an important role in resource competition theory, they can be neglected when compared to the amount of nutrients stored in the biota (here phytoplankton and macrophytes). Hence, the minimum nutrient concentration needed by primary producers, R^* in the model of Tilman (1982), is assumed to approximate zero. Last, to ease understanding of the concept of critical turbidity, we assume that there is no background extinction (K_{bg}). This results in the following GPLake-M equilibria sets with $Pmacr^*$ and $Pphyt^*$ in mg P m^{-2}, and $Pwater^*$ in mg P m^{-3}:

Set I: Nutrient-limited macrophytes - Zero-biomass phytoplankton:

$$Pmacr^* = \frac{1}{l_{macr}} \times Pload - \frac{z \times D_{in}}{l_{macr}} \times Pwater^* \approx \frac{1}{l_{macr}} \times Pload \tag*{Eq. (I.5a)}$$

$$Pphyt^* = 0 \tag*{Eq. (I.5b)}$$

$$Pwater^* = \frac{l_{macr} \times H_{nut,macr}}{p_{max,macr} - l_{macr}} \approx 0 \tag*{Eq. (I.5c)}$$

Set II: Light-limited macrophytes - Nutrient-limited phytoplankton:

$$Pmacr^* = \frac{p_{max,macr}}{k_{macr} \times l_{macr}} \times LN\left(\frac{H_{light,macr} + I_{in,macr}}{H_{light,macr}}\right) \tag*{Eq. (I.6a)}$$

$$Pphyt^* = \frac{1}{l_{phyt}} Pload - \frac{z \times D_{in}}{l_{phyt}} \times Pwater^* - \frac{l_{macr}}{l_{phyt}} \times Pmacr^*$$

$$\approx \frac{1}{l_{phyt}} Pload - \frac{l_{macr}}{l_{phyt}} \times Pmacr^* \tag*{Eq. (I.6b)}$$

$$Pwater^* = \frac{l_{phyt} \times H_{nut,phyt}}{p_{max,phyt} - l_{phyt}} \approx 0 \tag*{Eq. (I.6c)}$$

Set III: Zero-biomass macrophytes - Nutrient-limited phytoplankton:

$$Pmacr^* = 0 \tag*{Eq. (I.7a)}$$

$$Pphyt^* = \frac{1}{l_{phyt}} Pload - \frac{z \times D_{in}}{l_{phyt}} \times Pwater^* \approx \frac{1}{l_{phyt}} \times Pload \tag*{Eq. (I.7b)}$$

$$Pwater^* = \frac{l_{phyt} \times H_{nut,phyt}}{p_{max,phyt} - l_{phyt}} \approx 0 \tag*{Eq. (I.7c)}$$

Set IV: Zero-biomass macrophytes - Light-limited phytoplankton:

$$Pmacr^* = 0 \tag*{Eq. (I.8a)}$$

$$Pphyt^* = \frac{p_{max,phyt}}{k_{phyt} \times l_{phyt}} LN\left(\frac{H_{light,phyt} + I_{in,phyt}}{H_{light,phyt}}\right) \tag*{Eq. (I.8b)}$$

$$Pwater^* = \frac{1}{z \times D_{in}} Pload - \frac{l_{phyt}}{z \times D_{in}} \times Pphyt^* \tag*{Eq. (I.8c)}$$

Main GPLake-M model parameters

Slope and Plateau

From the Equations I.5a, I.6a, I.7b and I.8b for equilibrium areal nutrient contents we can derive the GPLake-M Slope (d) and Plateau (mg P m^{-2}) parameters:

$$Slope_{macr} = \frac{1}{l_{macr}} \tag{Eq. (I.9a)}$$

$$Plateau_{macr} = \frac{p_{max,macr}}{k_{macr} \times l_{macr}} \times LN\left(\frac{H_{light,macr} + I_{in,macr}}{H_{light,macr}}\right) \tag{Eq. (I.9b)}$$

$$Slope_{phyt} = \frac{1}{l_{phyt}} \tag{Eq. (I.9c)}$$

$$Plateau_{phyt} = \frac{p_{max,phyt}}{k_{phyt} \times l_{phyt}} LN\left(\frac{H_{light,phyt} + I_{in,phyt}}{H_{light,phyt}}\right) \tag{Eq. (I.9d)}$$

Switch points

The nutrient loading (Pload, mg P m^{-2} d^{-1}) at which a transition between nutrient and light limitation occurs is for macrophytes:

$$I \longleftrightarrow II = \frac{Plateau_{macr}}{Slope_{macr}} = \frac{p_{max,macr}}{k_{macr}} \times LN\left(\frac{H_{light,macr} + I_{in,macr}}{H_{light,macr}}\right) \tag{Eq. (I.10a)}$$

and for phytoplankton:

$$III \longleftrightarrow IV = \frac{Plateau_{phyt}}{Slope_{phyt}} = \frac{p_{max,phyt}}{k_{phyt}} LN\left(\frac{H_{light,phyt} + I_{in,phyt}}{H_{light,phyt}}\right) \tag{Eq. (I.10b)}$$

Furthermore, during eutrophication regime shifts occur at:

$$\begin{aligned} II \rightarrow III &= \frac{Plateau_{macr}}{Slope_{macr}} + \frac{Pcrit}{Slope_{phyt}} \\ &= \frac{p_{max,macr}}{k_{macr}} LN\left(\frac{H_{light,macr} + I_{in,macr}}{H_{light,macr}}\right) + l_{phyt} \times P_{crit} \end{aligned} \tag{Eq. (I.10c)}$$

and during oligotrophication at:

$$II \leftarrow III = \frac{Pcrit}{Slope_{phyt}} = l_{phyt} \times Pcrit \tag{Eq. (I.10d)}$$

With P_{crit} (mg P m^{-2}) being the critical turbidity.

References

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Supplementary materials of Chapter 4

Supplementary material A: Alternative notation for GPLake-M

Here, we provide an alternative mathematical notation of the original GPLake-M model (van Wijk et al. 2023) as a first step towards the development of GPLake-R and to ease the comparison between both models. Specifically, we reorganized the model into equations for each of the four GPLake-M equilibrium curves (one for macrophytes and one for phytoplankton for the initial clear state and a second pair for the initial turbid state) instead of per equilibrium set as was done in van Wijk et al. (2023). The equations link GPLake-M equilibrium sets I and II, and III and IV, respectively, by if-functions that incorporate the GPLake-M switch points into the original equations. These switch points are based on the areal P content of phytoplankton (Pphyt in mg P m^{-2}) relative to the critical turbidity (Pcrit in mg P m^{-2}) (van Wijk et al. 2023). Here we note the Slope of macrophytes or phytoplankton as S_{macr} and S_{phyt} and their Plateaus as as M_{macr} and M_{phyt}, respectively. Thereafter, we combined the equations for the initial clear and turbid state into one equation for the equilibrium abundance of macrophytes and one for the equilibrium abundance of phytoplankton using the auxiliary parameter $Init_{clear}$ with values 1 for the clear initial state and 0 for the turbid initial state. This results in the following GPLake-M equilibrium equations for areal P contents of macrophytes ($Pmacr^{*}$) and phytoplankton ($Pphyt^{*}$) assuming that M_{phyt} is larger than Pcrit:

$$Pmacr^{*}_{clear} = \begin{cases} MIN(S_{macr}\,Pload, M_{macr}),\ if\ S_{phyt}\left(Pload - \frac{M_{macr}}{S_{macr}}\right) \le Pcrit \\ 0,\ if\ S_{phyt}\left(Pload - \frac{M_{macr}}{S_{macr}}\right) > Pcrit \end{cases} \qquad \text{Eq. (A.1a)}$$

$$Pmacr^{*}_{turbid} = \begin{cases} MIN(S_{macr}\,Pload, M_{macr}),\ if\ S_{phyt}\,Pload \le Pcrit \\ 0,\ if\ S_{phyt}\,Pload > Pcrit \end{cases} \qquad \text{Eq. (A.1b)}$$

$$Pmacr^{*} = Init_{clear}\,Pmacr^{*}_{clear} + (1 - Init_{clear})\,Pmacr^{*}_{turbid} \qquad \text{Eq. (A.1c)}$$

$$Pphyt^{*}_{clear} = \begin{cases} S_{phyt}\left(Pload - \frac{M_{macr}}{S_{macr}}\right),\ if\ S_{phyt}\left(Pload - \frac{M_{macr}}{S_{macr}}\right) \le Pcrit \\ MIN\left(S_{phyt}Pload, M_{phyt}\right),\ if\ S_{phyt}\left(Pload - \frac{M_{macr}}{S_{macr}}\right) > Pcrit \end{cases} \qquad \text{Eq. (A.2a)}$$

$$Pphyt^{*}_{turbid} = \begin{cases} S_{phyt}\left(Pload - \frac{M_{macr}}{S_{macr}}\right),\ if\ S_{phyt}\,Pload \le Pcrit \\ MIN\left(S_{phyt}\,Pload, M_{phyt}\right),\ if\ S_{phyt}\,Pload > Pcrit \end{cases} \qquad \text{Eq. (A.2b)}$$

$$Pphyt^{*} = Init_{clear}\,Pphyt^{*}_{clear} + (1 - Init_{clear})\,Pphyt^{*}_{turbid} \qquad \text{Eq. (A.2b)}$$

References

van Wijk D, Chang M, Janssen ABG, Teurlincx S, Mooij WM. 2023. Regime shifts in shallow lakes explained by critical turbidity. Water Research. 119950.

Supplementary material B: Making retention explicit in GPLake-M

We made the nutrient retention that is implicit to GPLake-M explicit by rewriting the Slopes of macrophytes and phytoplankton as defined in GPLake-M (section 4.2.1). We explicitly included the fundamental difference in loss processes between rooting macrophytes and phytoplankton, with macrophytes being lost by biological processes such as mortality, and living phytoplankton by hydrological outflow as well (see Supplementary material F in van Wijk et al. 2023). For this, we replaced the Slopes from GPLake-M by their expression in terms of nutrient retention rates (R_{macr} and R_{phyt} in d^{-1}) and dilution rate (D in d^{-1}). To keep the mass balance simple, here we focused on shallow lakes with a point loading of nutrients, which is decoupled from the hydrological inflow (see Supplementary material F in van Wijk et al. 2023). In preparation for allowing for co-limitation, we generalized the function describing the response of macrophytes and phytoplankton to nutrient loading (i.e., the minimum function in GPLake-M) to a what we call a load-response (LR) curve. This results in the following equations:

$$LR_{macr} = MIN\left(\frac{Pload}{R_{macr}}, M_{macr}\right) \tag*{Eq. (B.1a)}$$

$$LR_{phyt} = MIN\left(\frac{Pload}{R_{phyt}+D}, M_{phyt}\right) \tag*{Eq. (B.1b)}$$

$$Pmacr^{*}_{clear} = \begin{cases} LR_{macr}, \ if \ \frac{Pload-R_{macr}\,LR_{macr}}{R_{phyt}+D} \leq Pcrit \\ 0, \ if \ \frac{Pload-R_{macr}\,LR_{macr}}{R_{phyt}+D} > Pcrit \end{cases} \tag*{Eq. (B.2a)}$$

$$Pmacr^{*}_{turbid} = \begin{cases} LR_{macr}, \ if \ LR_{phyt} \leq Pcrit \\ 0, \ if \ LR_{phyt} > Pcrit \end{cases} \tag*{Eq. (B.2b)}$$

$$Pmacr^{*} = Init_{clear}Pmacr^{*}_{clear} + (1 - Init_{clear})Pmacr^{*}_{turbid} \tag*{Eq. (B.2c)}$$

$$Pphyt^{*}_{clear} = \begin{cases} \frac{Pload-R_{macr}\,LR_{macr}}{R_{phyt}+D}, \ if \ \frac{Pload-R_{macr}\,LR_{macr}}{R_{phyt}+D} \leq Pcrit \\ LR_{phyt}, \ if \ \frac{Pload-R_{macr}\,LR_{macr}}{R_{phyt}+D} > Pcrit \end{cases} \tag*{Eq. (B.3a)}$$

$$Pphyt^{*}_{turbid} = \begin{cases} \frac{Pload-R_{macr}\,LR_{macr}}{R_{phyt}+D}, \ if \ LR_{phyt} \leq Pcrit \\ LR_{phyt}, \ if \ LR_{phyt} > Pcrit \end{cases} \tag*{Eq. (B.3b)}$$

$$Pphyt^{*} = Init_{clear}\ Pphyt^{*}_{clear} + (1 - Init_{clear})\ Pphyt^{*}_{turbid} \tag*{Eq. (B.3c)}$$

$$Pwater^{*}_{clear} = \begin{cases} 0, \ if \ \frac{Pload-R_{macr}\,LR_{macr}}{R_{phyt}+D} \leq Pcrit \\ \frac{Pload-R_{phyt}\,LR_{phyt}}{z\,D}, \ if \ \frac{Pload-R_{macr}\,LR_{macr}}{R_{phyt}+D} > Pcrit \end{cases} \tag*{Eq. (B.4a)}$$

$$Pwater^*_{turbid} = \begin{cases} 0, \; if \; LR_{phyt} \leq Pcrit \\ \frac{Pload - R_{phyt} \, LR_{phyt}}{z \, D}, \; if \; LR_{phyt} > Pcrit \end{cases} \qquad \text{Eq. (B.4b)}$$

$$Pwater^* = Init_{clear} \, Pwater^*_{clear} + (1 - Init_{clear}) \, Pwater^*_{turbid} \qquad \text{Eq. (B.4c)}$$

$$Pret^* = R_{macr} \, Pmacr^* + R_{phyt} \, Pphyt^* \qquad \text{Eq. (B.5a)}$$

$$Pdil^* = D \, Pphyt^* + z \, D \, Pwater^* \qquad \text{Eq. (B.5b)}$$

$$Pload - Pret^* - Pdil^* = 0 \qquad \text{Eq. (B.5c)}$$

References

van Wijk D, Chang M, Janssen ABG, Teurlincx S, Mooij WM. 2023. Regime shifts in shallow lakes explained by critical turbidity. Water Research. 119950.

Supplementary material C: Allowing for co-limitation at the transition between nutrient and light limitation

We explored multiple mathematical functions that could describe co-limitation during the transition from nutrient limitation to light limitation with increasing nutrient load. In particular we were looking for functions that 1) go through the origin of the load-response curves (Fig. C.1), 2) have a linear asymptote for low nutrient loadings mimicking the Slope of GPLake-M, 3) have a horizontal asymptote for high nutrient loadings mimicking the Plateau of GPLake-M and 4) show co-limitation at intermediate nutrient loadings and 5) are differentiable for all nutrient loadings. The min-function employed in GPLake-M satisfies specifications 1-3 but not specifications 4-5:

$$LR_{macr}(Pload) = MIN(S_{macr}\, Pload, M_{macr}) = MIN\left(\frac{Pload}{R_{macr}}, M_{macr}\right) \qquad \text{Eq. (C.1a)}$$

$$LR_{phyt}(Pload) = MIN\left(S_{phyt}\, Pload, M_{phyt}\right) = MIN\left(\frac{Pload}{R_{phyt}+D}, M_{phyt}\right) \qquad \text{Eq. (C.1b)}$$

We first explored two well-known functions, the Monod function and the Von Bertalanffy function, that satisfy specifications 1-5 and parameterized them in terms of Pload, R_{macr}, M_{macr}, R_{phyt}, M_{phyt} and D.

For the Monod function we then get:

$$LR_{macr}(Pload) = \frac{S_{macr}\, Pload}{1+\frac{S_{macr}\, Pload}{M_{macr}}} = \frac{\frac{Pload}{R_{macr}}}{1+\frac{Pload}{R_{macr}}\cdot\frac{1}{M_{macr}}} \qquad \text{Eq. (C.2a)}$$

$$LR_{phyt}(Pload) = \frac{S_{phyt}\, Pload}{1+\frac{S_{phyt}\, Pload}{M_{phyt}}} = \frac{\frac{Pload}{R_{phyt}+D}}{1+\frac{Pload}{R_{phyt}+D}\cdot\frac{1}{M_{phyt}}} \qquad \text{Eq. (C.2b)}$$

And for the Von Bertalanffy function we then get:

$$LR_{macr}(Pload) = M_{macr}\left(1-e^{-\frac{S_{macr}\, Pload}{M_{macr}}}\right) =$$

$$M_{macr}\left(1-e^{-\frac{Pload}{R_{macr}}\cdot\frac{1}{M_{macr}}}\right) \qquad \text{Eq. (C.3a)}$$

$$LR_{phyt}(Pload) = M_{phyt}\left(1-e^{-\frac{S_{phyt}\, Pload}{M_{phyt}}}\right) =$$

$$M_{phyt}\left(1-e^{-\frac{Pload}{R_{phyt}+D}\cdot\frac{1}{M_{phyt}}}\right) \qquad \text{Eq. (C.3b)}$$

Note that in accordance to specifications 1-3, these Monod and Von Bertalanffy functions mathematically equal zero and approach the same linear slope when the loading is zero, and approach the same horizontal asymptote at high loadings (with the apostrophes indicating derivatives):

$$LR_{macr}(0) = 0 \qquad \text{Eq. (C.4a)}$$

$$LR_{phyt}(0) = 0 \qquad \text{Eq. (C.4b)}$$

$$LR_{macr}{}'(0) = S_{macr} \qquad \text{Eq. (C.4c)}$$

$$LR_{phyt}{}'(0) = S_{phyt} \qquad \text{Eq. (C.4d)}$$

$$\lim_{Pload \to \infty} LR_{macr}(Pload) = M_{macr} \qquad \text{Eq. (C.4e)}$$

$$\lim_{Pload \to \infty} LR_{phyt}(Pload) = M_{phyt} \qquad \text{Eq. (C.4f)}$$

$$\lim_{Pload \to \infty} LR_{macr}{}'(Pload) = 0 \qquad \text{Eq. (C.4g)}$$

$$\lim_{Pload \to \infty} LR_{phyt}{}'(Pload) = 0 \qquad \text{Eq. (C.4h)}$$

We were not satisfied with both functions, however, because the extent of co-limitation is a fixed attribute of these functions and quite strong, especially for the Monod function (Fig. C.1). We therefore developed a new function (in the sense we have not encountered it before) in which 6) the extent of co-limitation is determined by a parameter. Ideally, this parameter would also allow 7) to minimize co-limitation so the load-response curve approaches the min-function employed in GPLake-M. We found a function that satisfies all specifications 1-7 using the integral of the logistic equation as a starting point:

$$\int \frac{1}{1+e^{-x}}\,dx = LN(e^{x} + 1) + C \qquad \text{Eq. (C.5)}$$

This resulted in the following load-response curve that we refer to as the "intlog" function:

$$LR_{macr}(Pload) = M_{macr}\left(1 - \frac{LN\left(\mathrm{e}^{n_{intlog}\left(1-\frac{S_{macr}\,Pload}{M_{macr}}\right)}+1\right)}{LN\left(e^{n_{intlog}}+1\right)}\right) =$$

$$M_{macr}\left(1 - \frac{LN\left(\mathrm{e}^{n_{intlog}\left(1-\frac{Pload}{R_{macr}}\cdot\frac{1}{M_{macr}}\right)}+1\right)}{LN\left(e^{n_{intlog}}+1\right)}\right) \qquad \text{Eq. (C.6a)}$$

$$LR_{phyt}(Pload) = M_{phyt}\left(1 - \frac{LN\left(\mathrm{e}^{n_{intlog}\left(1-\frac{S_{phyt}\,Pload}{M_{phyt}}\right)}+1\right)}{LN\left(e^{n_{intlog}}+1\right)}\right) =$$

$$M_{phyt}\left(1 - \frac{LN\left(\mathrm{e}^{n_{intlog}\left(1-\frac{Pload}{R_{phyt}+D}\cdot\frac{1}{M_{phyt}}\right)}+1\right)}{LN\left(e^{n_{intlog}}+1\right)}\right) \qquad \text{Eq. (C.6b)}$$

For high values of parameter n_{intlog}, the intlog load-response curve resembles the minimum function of GPLake-M with a sharp transition between Slope and Plateau, whilst still being differentiable (Fig. C.1). For details on the development and analysis of the intlog function see Supplementary material H.

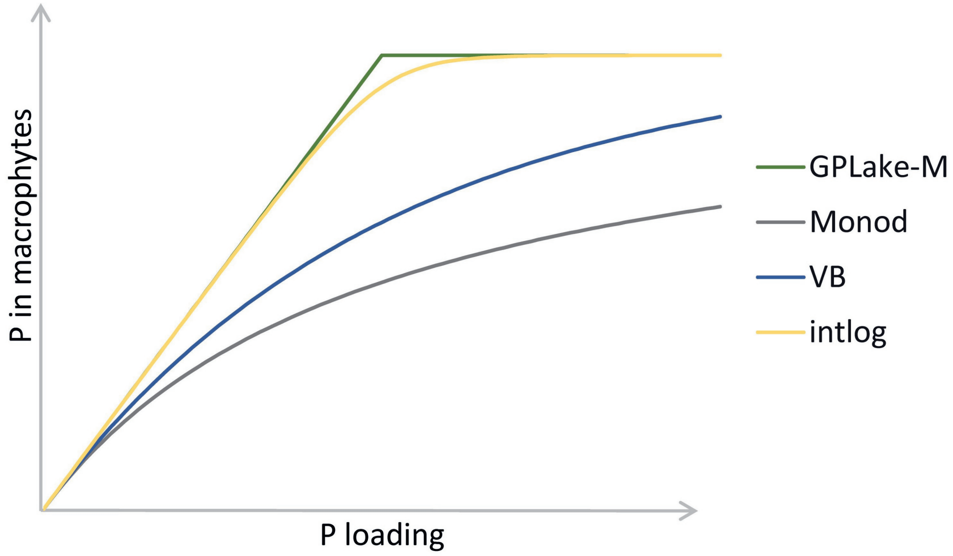

Figure C.1. Example of possible mathematical load-response curves for P in macrophytes: the minimum function following Liebig's law of GPLake-M (green), the Monod function (gray), the Von Bertalanffy function (VB, blue), and intlog function with n_{intlog} = 8 (yellow). See Supplementary material I for the fit of these four LR functions to the Vollenweider data.

Supplementary material D: Equilibrium version of GPLake-R allowing for macrophyte and phytoplankton coexistence around critical nutrient loadings

As a next step we implemented the possibility of coexistence between macrophytes and phytoplankton around critical nutrient loadings. We did so using a Hill function:

$$y(x) = \frac{c^n}{c^n + x^n} \qquad \text{Eq. (D.1)}$$

where c represents the critical turbidity, x the equilibrium turbidity of phytoplankton resulting from eutrophication or oligotrophication, and y is a variable between 0 and 1 representing the resulting ecosystem state with values ≪0.5 indicating phytoplankton dominance, values ≫0.5 indicating macrophyte dominance and a value of 0.5 indicating that the turbidity of phytoplankton matches the critical turbidity. As can be seen in Fig. 2 of van Wijk et al. (2023) the loading levels at which the phytoplankton induced turbidity matches the critical turbidity also define the critical nutrient loading during eutrophication (i.e., the transition from the clear to the turbid state) and oligotrophication (i.e., the transition from the turbid to the clear state). In GPLake-R we therefore refer to y in the above Hill-function as $State_{clear}$ and $State_{turbid}$. The power of the Hill function n_{Hill} determines the steepness of the transition. When n_{Hill} goes to infinity, the Hill function approaches a block function resulting in the catastrophic regime shift of GPLake-M. For lower values of n_{Hill}, however, a more gradual replacement of macrophytes by phytoplankton, and vice versa, takes place, thus resulting in macrophyte and phytoplankton coexistence around critical nutrient loadings.

This results in the following equations which constitute the equilibrium version of GPLake-R:

$$LR_{macr}(Pload) = M_{macr}\left(1 - \frac{LN\left(e^{n_{intlog}\left(1 - \frac{Pload}{R_{macr}} \cdot \frac{1}{M_{macr}}\right)} + 1\right)}{LN\left(e^{n_{intlog}} + 1\right)}\right) \qquad \text{Eq. (D.2a)}$$

$$LR_{phyt}(Pload) = M_{phyt}\left(1 - \frac{LN\left(e^{n_{intlog}\left(1 - \frac{Pload}{R_{phyt}+D} \cdot \frac{1}{M_{phyt}}\right)} + 1\right)}{LN\left(e^{n_{intlog}} + 1\right)}\right) \qquad \text{Eq. (D.2b)}$$

$$State_{clear} = \frac{Pcrit^{n_{Hill}}}{Pcrit^{n_{Hill}} + \left(\frac{Pload - R_{macr}\, LR_{macr}}{R_{phyt} + D}\right)^{n_{Hill}}} \qquad \text{Eq. (D.2c)}$$

$$State_{turbid} = \frac{Pcrit^{n_{Hill}}}{Pcrit^{n_{Hill}} + LR_{phyt}^{\ n_{Hill}}} \qquad \text{Eq. (D.2d)}$$

$$Pmacr^*_{clear} = LR_{macr}\, State_{clear} \qquad \text{Eq. (D.3a)}$$

$$Pmacr^*_{turbid} = LR_{macr}\, State_{turbid} \qquad \text{Eq. (D.3b)}$$

$$Pmacr^* = Init_{clear}\, Pmacr^*_{clear} + (1 - Init_{clear})\, Pmacr^*_{turbid} \qquad \text{Eq. (D.3c)}$$

$$Pphyt^*_{clear} = \frac{Pload - R_{macr}\, LR_{macr}}{R_{phyt} + D} State_{clear} + LR_{phyt}\,(1 - State_{clear}) \qquad \text{Eq. (D.4a)}$$

$$Pphyt^*_{turbid} = \frac{Pload - R_{macr}\, LR_{macr}}{R_{phyt} + D} State_{turbid} + LR_{phyt}\,(1 - State_{turbid}) \qquad \text{Eq. (D.4b)}$$

$$Pphyt^* = Init_{clear}\, Pphyt^*_{clear} + (1 - Init_{clear})\, Pphyt^*_{turbid} \qquad \text{Eq. (D.4c)}$$

$$Pwater^*_{clear} = \frac{Pload - (R_{phyt} + D)\, LR_{phyt}}{z\, D}\,(1 - State_{clear}) \qquad \text{Eq. (D.5a)}$$

$$Pwater^*_{turbid} = \frac{Pload - (R_{phyt} + D)\, LR_{phyt}}{z\, D}\,(1 - State_{turbid}) \qquad \text{Eq. (D.5b)}$$

$$Pwater^* = Init_{clear}\, Pwater^*_{clear} + (1 - Init_{clear})\, Pwater^*_{turbid} \qquad \text{Eq. (D.5c)}$$

$$Pret^* = R_{macr} Pmacr^* + R_{phyt} Pphyt^* \qquad \text{Eq. (D.6a)}$$

$$Pdil^* = D\, Pphyt^* + z\, D\, Pwater^* \qquad \text{Eq. (D.6b)}$$

$$Pload - Pret^* - Pdil^* = 0 \qquad \text{Eq. (D.6c)}$$

References

van Wijk D, Chang M, Janssen ABG, Teurlincx S, Mooij WM. 2023. Regime shifts in shallow lakes explained by critical turbidity. Water Research. 119950

Supplementary material E: Dynamical implementation of GPLake-R

Finally, we developed a dynamic version of the GPLake-R that leads to the equilibrium solutions as shown in Supplementary material D. To start with the differential equations, these consist of proportional growth terms $GR_{macr,t}$ and $GR_{phyt,t}$ and proportional loss terms R_{macr} and (R_{phyt} + D) for macrophytes and phytoplankton, respectively. The differential equation for water includes the P loading as a gain term and uptake by macrophytes and phytoplankton and dilution by the outflowing water as loss terms. The proportional growth terms for macrophytes and phytoplankton each have a Monod term that guarantees that no growth can take place when there are no nutrients available in the water. This Monod term is multiplied by a second term that guarantees that when the actual macrophyte and phytoplankton abundance reaches the equilibrium abundance of GPLake-R, the proportional growth terms of macrophytes and phytoplankton become equal to their respective loss terms. Instead of using the contrasting states $State_{clear}$ and $State_{turbid}$ of the equilibrium version of GPLake-R, the dynamic version uses the actual state $State_t$ at time t. This results in the following equations which constitute the dynamic version of GPLake-R:

$$LR_{macr}(Pload) = M_{macr}\left(1 - \frac{LN\left(e^{n_{intlog}\left(1-\frac{Pload_t}{R_{macr}}\cdot\frac{1}{M_{macr}}\right)}+1\right)}{LN\left(e^{n_{intlog}}+1\right)}\right) \qquad \text{Eq. (E.1a)}$$

$$LR_{phyt}(Pload) = M_{phyt}\left(1 - \frac{LN\left(e^{n_{intlog}\left(1-\frac{Pload_t}{R_{phyt}+D}\cdot\frac{1}{M_{phyt}}\right)}+1\right)}{LN\left(e^{n_{intlog}}+1\right)}\right) \qquad \text{Eq. (E.1b)}$$

$$State_t = \frac{Pcrit^{n_{Hill}}}{Pcrit^{n_{Hill}}+Pphyt_t^{\,n_{Hill}}} \qquad \text{Eq. (E.1c)}$$

$$Pmacr^* = LR_{macr}\,State_t \qquad \text{Eq. (E.2a)}$$

$$Pphyt^* = \frac{Pload_t - R_{macr}\,LR_{macr}}{R_{phyt}+D}\,State_t + LR_{phyt}\,(1 - State_t) \qquad \text{Eq. (E.2b)}$$

$$Pwater^* = \frac{Pload_t - (R_{phyt}+D)\,LR_{phyt}}{z\,D}\,(1 - State_t) \qquad \text{Eq. (E.2c)}$$

$$GR_{macr,t} = G_{macr}\left(\frac{Pwater_t}{H_{macr}+Pwater_t}\right)\left(1 - \left(1 - \frac{R_{macr}}{G_{macr}}\right)\frac{Pmacr_t}{Pmacr^*}\right) \qquad \text{Eq. (E.3a)}$$

$$GR_{phyt,t} = G_{phyt}\left(\frac{Pwater_t}{H_{phyt}+Pwater_t}\right)\left(1 - \left(1 - \frac{(R_{phyt}+D)}{G_{phyt}}\right)\frac{Pphyt_t}{Pphyt^*}\right) \qquad \text{Eq. (E.3b)}$$

$$\frac{dPmacr}{dt} = GR_{macr,t}\ Pmacr_t - R_{macr}\ Pmacr_t \qquad \text{Eq. (E.4a)}$$

$$\frac{dPphyt}{dt} = GR_{phyt,t}\ Pphyt_t - \left(R_{phyt} + D\right) Pphyt_t \qquad \text{Eq. (E.4b)}$$

$$\frac{dPwater}{dt} = \frac{Pload_t - GR_{macr,t}\ Pmacr_t - GR_{phyt,t}\ Pphyt_t}{z} - D\ Pwater_t \qquad \text{Eq. (E.4c)}$$

$$Pret_t = R_{macr} Pmacr_t + R_{phyt} Pphyt_t \qquad \text{Eq. (E.5a)}$$

$$Pdil_t = D\ P_{phyt,t} + z\ D\ Pwater_t \qquad \text{Eq. (E.5b)}$$

$$Pload_t - \frac{dPmacr}{dt} - \frac{dPphyt}{dt} - z\frac{dPwater}{dt} - Pret_t - Pdil_t = 0 \qquad \text{Eq. (E.5c)}$$

Supplementary material F: Network perspective for GPLake-R

The differential equations of GPLake-R can also be applied to networks of lakes. For this, first, we define the P loading entering the lake as the nutrient outflow of the upstream lake (Pupstream). Next, we distinguish the P that is actively involved in the biological interactions (Pactive) from the P that is retained in the lake (Pretained). Finally, the part of the nutrients that is neither active nor retained, constitutes the nutrient flow out of the lake which serves as the nutrient loading into the next downstream lake (Pdownstream). This logic leads to the following set of differential equations for the dynamical network version of GPLake R:

$$Pactive_t = \; Pmacr_t + Pphyt_t + \; z\,Pwater_t \qquad \text{Eq. (F.1a)}$$

$$Ptotal_t = Pupstream_t + Pactive_t + Pretained_t + Pdownstream_t \qquad \text{Eq. (F.1b)}$$

$$\frac{dPupstream}{dt} = -Pload \qquad \text{Eq. (F.1c)}$$

$$\frac{dPactive}{dt} = \frac{dPmacr}{dt} + \frac{dPphyt}{dt} + z\frac{dPwater}{dt} =$$

$$Pload - R_{macr}\,Pmacr_t - R_{phyt}\,Pphyt_t - D\,Pphyt_t \; - z\,D\,Pwater_t \qquad \text{Eq. (F.1d)}$$

$$\frac{dPretained}{dt} = R_{macr}Pmacr_t + R_{phyt}Pphyt_t \qquad \text{Eq. (F.1e)}$$

$$\frac{dPdownstream}{dt} = D\,Pphyt_t + z\,D\,Pwater_t \qquad \text{Eq. (F.1f)}$$

$$\frac{dPtotal}{dt} = \frac{dPupstream}{dt} + \frac{dPactive}{dt} + \frac{dPretained}{dt} + \frac{dPdownstream}{dt} =$$

$$-Pload + Pload - R_{macr}\,Pmacr_t - R_{phyt}\,Pphyt_t - D\,Pphyt_t \; - z\,D\,Pwater_t +$$

$$R_{macr}\,Pmacr_t + R_{phyt}\,Pphyt_t + D\,Pphyt_t + z\,D\,Pwater_t = 0 \qquad \text{Eq. (F.1g)}$$

Supplementary material G: Comparison between GPLake-R and the Huisman-Weissing resource competition model and layered extensions thereof

We examined the consequences of changing the minimum resource requirement assumption (i.e., Liebig's law) employed in the analysis of the combined Tillman resource competition and Huisman-Weissing light competition model presented in Supplementary material B in van Wijk et al. (2023) with the resource co-limitation assumption of the original model (Huisman and Weissing 1994; 1995). For co-limitation, the equations of the Huisman-Weissing model become:

$$\frac{dPphyt}{dt} = p_{max,phyt} \times \frac{Pwater}{H_{nut,phyt}+Pwater} \times \frac{1}{E_{phyt}} \times LN\left(\frac{H_{light,phyt}+I_{in,phyt}}{H_{light,phyt}+I_{in,phyt} \times e^{-E_{phyt}}}\right) \times Pphyt$$

$$-l_{phyt} \times Pphyt \qquad \text{Eq. (G.1a)}$$

$$\frac{dPmacr}{dt} = p_{max,macr} \times \frac{Pwater}{H_{nut,macr}+Pwater} \times \frac{1}{E_{macr}} \times LN\left(\frac{H_{light,macr}+I_{in,macr}}{H_{light,macr}+I_{in,macr} \times e^{-E_{macr}}}\right)$$

$$\times Pmacr - l_{macr} \times Pmacr \qquad \text{Eq. (G.1b)}$$

$$\frac{dPwater}{dt} = Pload - z \times D_{in} \times Pwater -$$

$$p_{max,phyt} \times \frac{Pwater}{H_{nut,phyt}+Pwater} \times \frac{1}{E_{phyt}} \times LN\left(\frac{H_{light,phyt}+I_{in,phyt}}{H_{light,phyt}+I_{in,phyt} \times e^{-E_{phyt}}}\right) \times Pphyt -$$

$$p_{max,macr} \times \frac{Pwater}{H_{nut,macr}+Pwater} \times \frac{1}{E_{macr}} \times LN\left(\frac{H_{light,macr}+I_{in,macr}}{H_{light,macr}+I_{in,macr} \times e^{-E_{macr}}}\right)$$

$$\times Pmacr \qquad \text{Eq. (G.1c)}$$

with mass balance:

$$Pload - l_{macr} \times Pmacr - l_{phyt} \times Pphyt - z \times D_{in} \times Pwater = 0 \qquad \text{Eq. (G.2)}$$

For the version of the model in which macrophytes and phytoplankton are mixed over the water column we get:

$$I_{in,phyt} = I_{in,macr} = I_{in} \qquad \text{Eq. (G.3a)}$$

$$E_{phyt} = E_{macr} = k_{phyt} \times Pphyt + k_{macr} \times Pmacr + K_{bg} \times z \qquad \text{Eq. (G.3b)}$$

For the situation in which macrophytes are in a layer above phytoplankton we get:

$$I_{in,phyt} = I_{in} \qquad \text{Eq. (G.4a)}$$

$$E_{phyt} = k_{phyt} \times Pphyt + K_{bg} \times z \qquad \text{Eq. (G.4b)}$$

$$I_{in,macr} = I_{in,phyt} \times e^{-E_{phyt}} \qquad \text{Eq. (G.4c)}$$

$$E_{macr} = k_{macr} \times Pmacr \qquad \text{Eq. (G.4d)}$$

And for the reverse situation in which phytoplankton are in a layer above macrophytes we get:

$$I_{in,macr} = I_{in} \qquad \text{Eq. (G.5a)}$$

$$E_{macr} = k_{macr} \times Pmacr \qquad \text{Eq. (G.5b)}$$

$$I_{in,phyt} = I_{in,macr} \times e^{-E_{macr}} \qquad \text{Eq. (G.5c)}$$

$$E_{phyt} = k_{phyt} \times Pphyt + K_{bg} \times z \qquad \text{Eq. (G.5d)}$$

In all of the analysis we performed, we used the parameters of the Huisman-Weissing model as specified in Supplementary material B in van Wijk et al. (2023) except for parameter $H_{nut,macr}$ that we set here to a value of 0.117 to give macrophytes a stronger competitive advantage for nutrients over phytoplankton.

Comparison of the results for the resource co-limitation assumption presented here against the results for the minimum resource requirement assumption used in Supplementary material B in van Wijk et al. (2023) shows that for the parameters used in our analyses the differences are quite modest. For the case where macrophytes are on top of phytoplankton the difference is limited to a narrow zone of loadings around the point where nutrient-limitation of macrophytes turns into light-limitation (Fig. G.1a). For the mixed case where macrophytes and phytoplankton occur together throughout the water column, differences in the abundance of phytoplankton around the point where nutrient-limitation of phytoplankton turns into light-limitation are more pronounced than they are for macrophytes (Fig. G.1b). This is due to the fact that the minimum required nutrient concentration (R*) for phytoplankton is set to a higher value than for macrophytes in accordance with the empirical observation that macrophytes are superior competitors for nutrients compared to phytoplankton. In the case in which phytoplankton are above macrophytes, a third difference appears, namely that co-limitation gives macrophytes a small competitive disadvantage at their maximum density compared to the minimum function (Fig. G.1c).

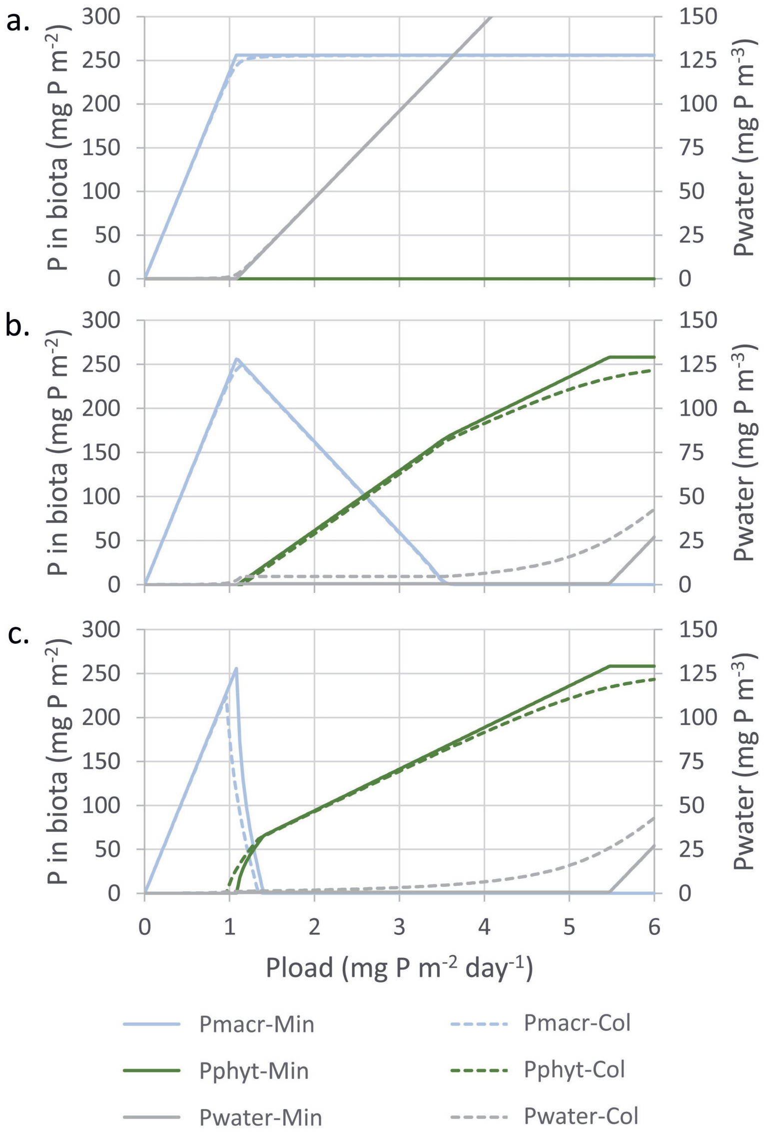

Figure G.1. Comparison between the equilibrium abundance of macrophytes (Pmacr), phytoplankton (Pphyt), and water (Pwater) with a minimum resource requirement (Min) and a resource co-limitation (Col) version of the (layered extension of the) Huisman-Weissing model with a) macrophytes above phytoplankton, b) vertically mixed communities, and c) phytoplankton above macrophytes.

Having obtained these results we checked the suitability of the intlog function that we developed for GPLake-R to capture the load-response curves that follow from the co-limitation version of the Huisman-Weissing model. For this purpose, we ran mono-culture simulations of macrophytes and phytoplankton and fitted the intlog function to the resulting equilibria by calibrating the n_{intlog} parameter. The results show that the intlog function with the appropriate parameter captures the load-response co-limitation curves of the Huisman-Weissing model well for both macrophytes (blue lines in Fig. G.2) and phytoplankton (green lines in Fig. G.2).

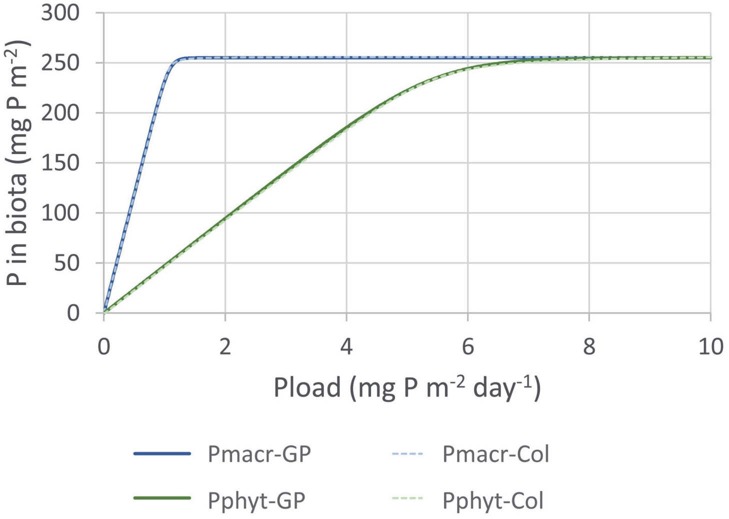

Figure G.2. Comparison between GPLake-R intlog load-response curves (GP, example with S_{macr} = 237 d, S_{phyt} = 47.4 d, M_{macr} = M_{phyt} = 255 mg P m^{-2}, $n_{intlog,macr}$ = 14, and $n_{intlog,phyt}$ = 8) and the co-limitation version of the Huisman-Weissing model (Col), with only macrophytes (blue) or only phytoplankton (green).

Having found parameters of the intlog load-response curve employed in GPLake-R that matches the patterns resulting from co-limitation in the Huisman-Weissing model for mono-cultures of macrophytes and phytoplankton, we proceeded with searching for parameters of the Hill function employed in GPLake-R that match the patterns of coexistence of macrophytes and phytoplankton shown by the mixed version of the Huisman-Weissing model and the layered version with phytoplankton on top of macrophytes (Supplementary material B in van Wijk et al. (2023)). For the mixed version (Fig. G.3a), the replacement of macrophytes by phytoplankton is more gradual than for the layered version with phytoplankton on top of macrophytes (Fig. G.3b) resulting in estimates of n_{Hill} of 2.5 and 15, respectively. For these n_{Hill} values, patterns from GPLake-R are comparable to the Huisman-Weissing model for the specific vertical organizations during eutrophication and oligotrophication (Fig. G.3).

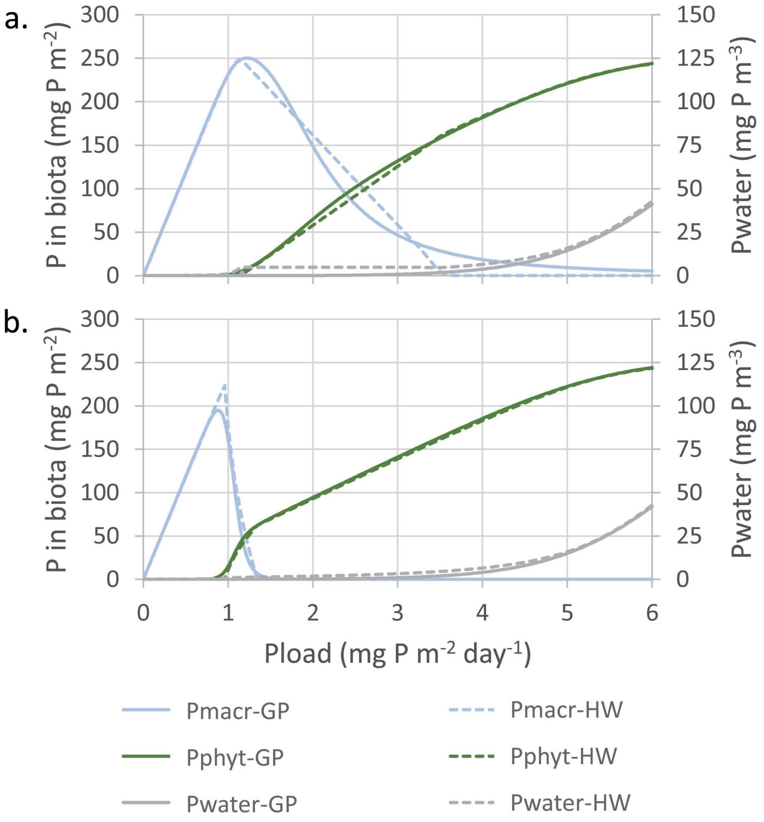

Figure G.3. Comparison between GPLake-R intlog load-response curves (GP) during a) eutrophication or b) oligotrophication, and the Huisman-Weissing (HW) model with a) macrophytes and phytoplankton mixed over the water column or b) phytoplankton above macrophytes. With GPLake-R parameter values of: S_{macr} = 237 d, S_{phyt} = 47.4 d, M_{macr} = M_{phyt} = 255 mg P m^{-2}, $n_{intlog,macr}$ = 14, $n_{intlog,phyt}$ = 8, and Pcrit = 50 mg P m^{-2}. Additionally, separate n_{Hill} parameter values were used for eutrophication (2.5) and oligotrophication (15).

Combining both versions of the Huisman-Weissing model in one graph (Fig. G.4a) and doing the same for GPLake-R (Fig. G.4b) shows contrasting states that we interpret for the Huisman-Weissing model as resulting from the vertical organization of the macrophyte-phytoplankton community and that we interpret for GPLake-R as patterns that represent alternative stable states during eutrophication and oligotrophication. More specifically, for the parameters analyzed here, the mixed version of the Huisman-Weissing model matches the patterns obtained during eutrophication with GPLake-R and the version of the Huisman-Weissing model with phytoplankton on top matches the pattern obtained during oligotrophication of GPLake-R. Moreover, it shows that GPLake-R is in fact a model of alternative stable states of coexistence of macrophytes and phytoplankton as opposed to the classical view on alternative stable states of monocultures of either macrophytes or phytoplankton.

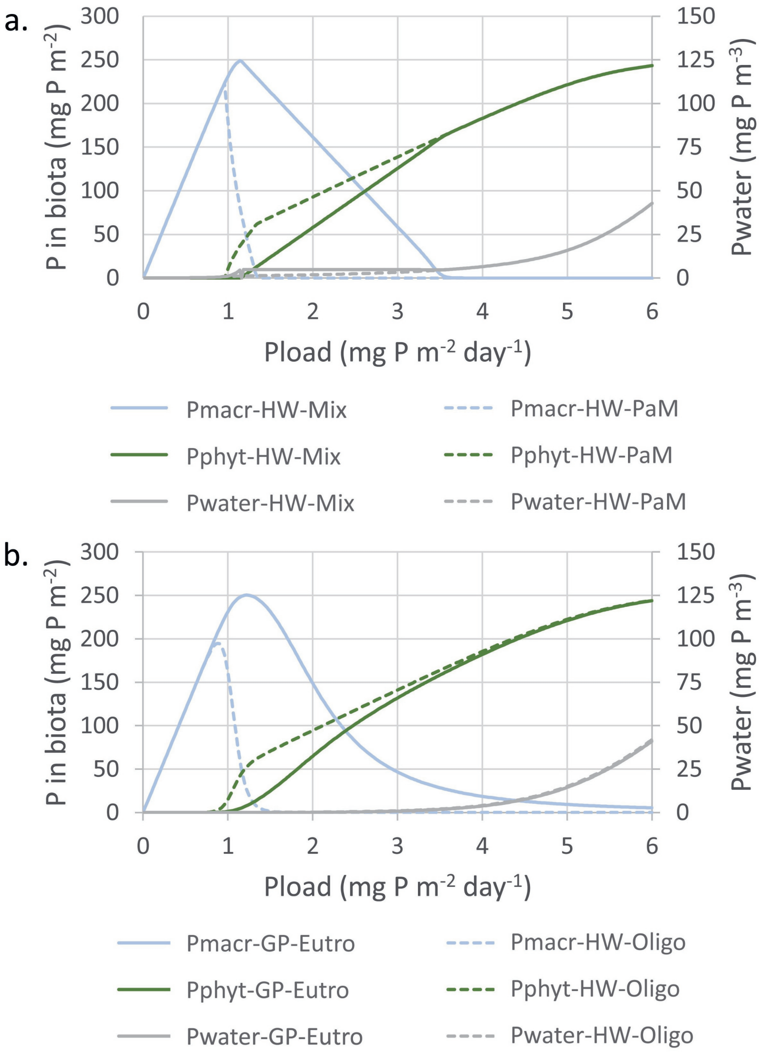

Figure G.4. Different levels of coexistence between macrophytes and phytoplankton a) by contrasting the outcomes of the Huisman-Weissing (HW) model for macrophytes and phytoplankton mixed over the water column (Mix) or phytoplankton above macrophytes (PaM), and b) according to GPLake-R (GP) during eutrophication (Eutro) and oligotrophication (Oligo). With GPLake-R parameter values of: S_{macr} = 237 d, S_{phyt} = 47.4 d, M_{macr} = M_{phyt} = 255 mg P m^{-2}, $n_{intlog,macr}$ = 14, $n_{intlog,phyt}$ = 8, and Pcrit = 50 mg P m^{-2}. Additionally, separate n_{Hill} parameter values were used for eutrophication (2.5) and oligotrophication (15).

The standard version of GPLake-R does not allow for making a distinction between the value of n_{intlog} for macrophytes and phytoplankton and between the value of n_{Hill} for the clear and the turbid state that we employ in our comparison between GPLake-R and the Huisman-Weissing including layered versions thereof. Implementing these distinctions in the equilibrium version of GPLake-R (presented in Supplementary material D) would be straightforward. This holds also for specific values of n_{intlog} in the specific functions for macrophytes and phytoplankton but the difference in values of n_{Hill} cannot be implemented directly in the single Hill function in the dynamic version of GPLake-R (presented in Supplementary material E). To implement specific values for n_{Hill} that represent the clear and the turbid state we therefore would need an additional equation with an extra parameter n_{Aux} in the dynamic version of GPLake-R that could look like:

$$n_{Hill,t} = n_{Hill,clear} - (n_{Hill,clear} - n_{Hill,turbid}) \frac{Pphyt_t^{\,n_{Aux}}}{Pcrit^{n_{Aux}} + Pphyt_t^{\,n_{Aux}}} \qquad \text{Eq. (G.6)}$$

and replace the existing formula (see Supplementary material E)

$$State_t = \frac{Pcrit^{n_{Hill}}}{Pcrit^{n_{Hill}} + Pphyt_t^{\,n_{Hill}}} \qquad \text{Eq. (G.7a)}$$

by

$$State_t = \frac{Pcrit^{n_{Hill,t}}}{Pcrit^{n_{Hill,t}} + Pphyt_t^{\,n_{Hill,t}}} \qquad \text{Eq. (G.7b)}$$

By means of these changes, the steepness of the Hill function in the $State_t$ variable of the model would become dependent on the abundance of phytoplankton relative to the critical turbidity.

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Supplementary material H: Development and analysis of the intlog function

We developed a versatile mathematical function that could describe co-limitation during the transition from nutrient limitation to light limitation with increasing nutrient load that complies with the following seven specifications. The function should 1) go through the origin of the load-response curves (Fig. C.1), 2) have a linear asymptote for low nutrient loadings mimicking the Slope of GPLake-M, 3) have a horizontal asymptote for high nutrient loadings mimicking the Plateau of GPLake-M and 4) show co-limitation at intermediate nutrient loadings, 5) be differentiable for all nutrient loadings, 6) have a parameter that determines the extent of co-limitation and 7) allow to mimic the absence of co-limitation in GPLake-M by means of this parameter (i.e., making GPLake-R backward compatible with GPLake-M).

The min-function employed in GPLake-M satisfies specifications 1-3 but not specifications 4-7. The Monod function and the Von Bertalanffy function that are discussed in Supplementary material C satisfy specifications 1-5 but not specifications 6-7. Having no knowledge of functions that meet all seven specifications, we developed a new function that does satisfy specifications 1 and 3-7 and approaches specification 2.

Because we focus here on the mathematical aspects, we use the standard notation of y = f(x) with y being either Pmacr or Pphyt and x being Pload. As parameters for function f(x) we used s for $\mathrm{Slope}_{\mathrm{macr}} = 1/R_{\mathrm{macr}}$ or $\mathrm{Slope}_{\mathrm{Phyt}} = 1/(D+R_{\mathrm{phyt}})$, m for M_{macr} or M_{phyt}, and n for the specific n_{intlog} parameter mentioned in specifications 6-7.

Not knowing any existing functions that meet the above specifications and not knowing where to start with developing the function directly we first focused on its derivative. The derivative of the min-function of GPLake-M (Fig. H.1, left panel) is a step function with value s at loadings below the threshold loading x = m / s (van Wijk et al. 2023) that separates nutrient limitation and light limitation and value 0 above this threshold (Fig. H.1, right panel).

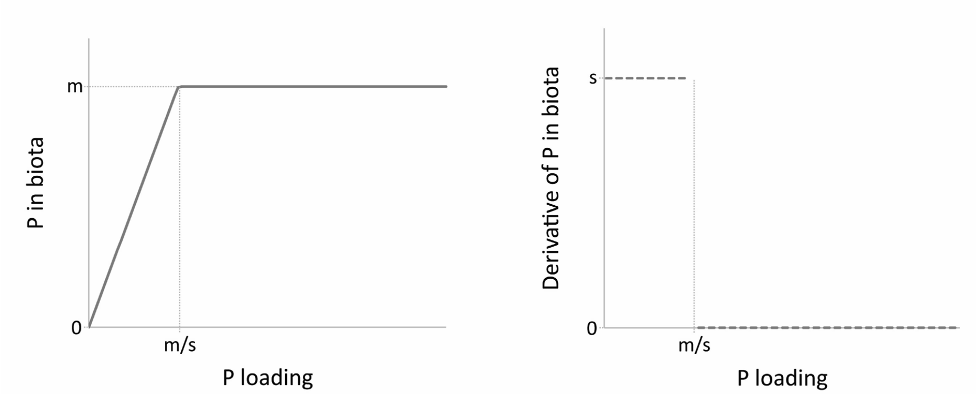

Figure H.1. The response of P in macrophytes or phytoplankton to P loading in GPLake-M (left panel) and its derivative (right panel).

To make the transition from nutrient to light limitation differentiable we replaced the step function in the derivative of GPLake-M (Fig. H1, right panel) with a logistic function in the derivative of GPLake-R (Fig. H.2, left panel).

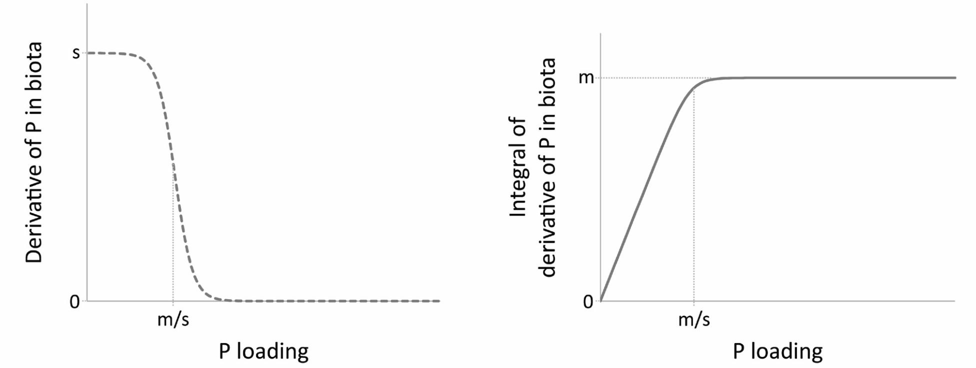

Figure H.2. A logistic function that represents the derivative of the load-response curve (left panel) and its integral, the intlog-function (right panel).

More specifically we used a logistic function (Fig. H.2, left panel) that a) that s has an asymptote for x goes to minus infinity, b) has zero as an asymptote for for x goes to infinity c) has its inflection point at x = m / s and d) has a parameter n that modifies the steepness of the logistic curve at the inflection point. As first trial we used the following function:

$$y'(x) = s\frac{e^{n\left(1-\frac{s}{m}x\right)}}{\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right)} = s\frac{1}{\left(1+e^{n\left(\frac{s}{m}x-1\right)}\right)} \qquad \text{Eq. (H.1a)}$$

with characteristics:

$$y'(0) = s\frac{1}{(1+e^{-n})} \qquad \text{Eq. (H.1b)}$$

$$\lim_{n\to\infty} y'(0) = s \qquad \text{Eq. (H.1c)}$$

$$\lim_{x\to\infty} y'(x) = 0 \qquad \text{Eq. (H.1d)}$$

Integration of this logistic function leads to either a function that has the light limited abundance m as its positive term:

$$y(x) = m - \frac{m\,LN\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right)}{\mathrm{n}} \qquad \text{Eq. (H.2a)}$$

with characteristics:

$$y(0) = \; m - \frac{m\,LN(e^{n}+1)}{\mathrm{n}} \qquad \text{Eq. (H.2b)}$$

$$\lim_{n\to\infty} y(0) = 0 \qquad \text{Eq. (H.2c)}$$

$$\lim_{x\to\infty} y(x) = m \qquad \text{Eq. (H.2d)}$$

or a function that has the nutrient limited abundance s x as its positive term:

$$y(x) = s\,x - \frac{m\,LN\left(e^{n\left(\frac{s}{m}x-1\right)}+1\right)}{n} \qquad \text{Eq. (H.3a)}$$

with characteristics:

$$y(0) = \frac{-m\,LN(e^{-n}+1)}{n} \qquad \text{Eq. (H.3b)}$$

$$\lim_{n\to\infty} y(0) = 0 \qquad \text{Eq. (H.3c)}$$

$$\lim_{x\to\infty} y(x) = m \qquad \text{Eq. (H.3d)}$$

To understand why both results for y(x) are identical it is useful to first understand the following equality:

$$LN(e^{c}+1) - LN(e^{-c}+1) = LN\left(\frac{e^{c}+1}{e^{-c}+1}\right) = LN\left(\frac{e^{c}+1}{\frac{1}{e^{c}}+1}\right) = LN\left(\frac{e^{c}+1}{\frac{1}{e^{c}}+\frac{e^{c}}{e^{c}}}\right) = LN\left(\frac{e^{c}+1}{\frac{1+e^{c}}{e^{c}}}\right)$$

$$= LN(e^{c}) = c \qquad \text{Eq. (H.4)}$$

with c being an arbitrary number, variable or function. Applying this knowledge we can now prove that:

$$y(x) = s\,x - \frac{m\,LN\left(e^{n\left(\frac{s}{m}x-1\right)}+1\right)}{n} = m - \frac{m\,LN\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right)}{n} \Rightarrow$$

$$\frac{n\,s\,x - m\,LN\left(e^{n\left(\frac{s}{m}x-1\right)}+1\right)}{n} = \frac{m\,n - m\,LN\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right)}{n} \Rightarrow$$

$$n\,\frac{s}{m}\,x - LN\left(e^{n\left(\frac{s}{m}x-1\right)}+1\right) = n - LN\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right) \Rightarrow$$

$$LN\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right) - LN\left(e^{n\left(\frac{s}{m}x-1\right)}+1\right) = n\left(1-\frac{s}{m}\,x\right) \qquad \text{Eq. (H.5)}$$

The latter expression being an instance of the earlier expression with:

$$c = n\left(1-\frac{s}{m}\,x\right) \qquad \text{Eq. (H.6)}$$

Along the same lines we can prove that:

$$y(0) = \frac{-m\,LN(e^{-n}+1)}{n} = m - \frac{m\,LN(e^{n}+1)}{n} \Rightarrow$$

$$\frac{-m\,LN(e^{-n}+1)}{n} = \frac{m\,n - m\,LN(e^{n}+1)}{n} \Rightarrow$$

$$LN(e^{n}+1) - LN(e^{-n}+1) = n \qquad \text{Eq. (H.7)}$$

Having proven that both expressions for y(x) and y(0) are identical we proceeded with the more simple version that has the light-limited maximum abundance at high nutrient loadings as its positive term:

$$y(x) = m\left(1 - \frac{LN\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right)}{n}\right) \qquad \text{Eq. (H.8)}$$

When reformulated in terms of the parameters of GPLake-R this function meets specifications 3-7 and approaches specification 2 for larger values of n but fails to meet specification 1 that the function should go through the origin of the load-response curves because:

$$y(0) = m\left(1 - \frac{LN(e^{n}+1)}{n}\right) \qquad \text{Eq. (H.9)}$$

Because $\ln(e^{n}+1)/n$ is always larger than 1 for positive values of n, y(x) will become negative at low nutrient loadings, particularly when n is small. As these negative values of n are biologically infeasible and can cause technical problems in implementations of the model we made a correction to y(x) to ensure that we also meet specification 1:

$$y(0) = 0 \qquad \text{Eq. (H.10)}$$

while still meeting all the other specifications. This resulted in a new function:

$$y(x) = m\left(1 - \frac{LN\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right)}{LN(e^{n}+1)}\right) = \frac{m\ LN(e^{n}+1) - m\ LN\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right)}{LN(e^{n}+1)} \qquad \text{Eq. (H.11a)}$$

with characteristics:

$$y(0) = 0 \qquad \text{Eq. (H.11b)}$$

$$\lim_{x\to\infty} y(x) = m \qquad \text{Eq. (H.11c)}$$

Differentiating this new function we get the following logistic equation:

$$y'(x) = s\,\frac{e^{n\left(1-\frac{s}{m}x\right)}}{\left(e^{n\left(1-\frac{s}{m}x\right)}+1\right)}\,\frac{n}{LN(e^{n}+1)} = s\,\frac{1}{\left(1+e^{n\left(\frac{s}{m}x-1\right)}\right)}\,\frac{n}{LN(e^{n}+1)} \qquad \text{Eq. (H.12a)}$$

with characteristics:

$$y'(0) = s\,\frac{1}{(1+e^{-n})}\,\frac{n}{LN(e^{n}+1)} \qquad \text{Eq. (H.12b)}$$

$$\lim_{n\to\infty} y'(0) = s \qquad \text{Eq. (H.12c)}$$

$$\lim_{x\to\infty} y'(x) = 0 \qquad \text{Eq. (H.12d)}$$

Reformulating this new function, that we call the intlog function, in terms of the parameters of GPLake-R we get:

$$LR_{macr}(Pload) = M_{macr}\left(1 - \frac{LN\left(\mathrm{e}^{n_{intlog}\left(1-\frac{S_{macr}}{M_{macr}}Pload\right)}+1\right)}{LN\left(\mathrm{e}^{n_{intlog}}+1\right)}\right) \qquad \text{Eq. (H.13a)}$$

$$LR_{macr}{}'(Pload) = S_{macr}\,\frac{1}{\left(1+e^{n_{intlog}\left(\frac{S_{macr}}{M_{macr}}Pload-1\right)}\right)}\,\frac{n_{intlog}}{LN\left(e^{n_{intlog}}+1\right)} \qquad \text{Eq. (H.13b)}$$

$$LR_{phyt}(Pload) = M_{phyt}\left(1 - \frac{LN\left(\mathrm{e}^{n_{intlog}\left(1-\frac{S_{phyt}}{M_{phyt}}Pload\right)}+1\right)}{LN\left(\mathrm{e}^{n_{intlog}}+1\right)}\right) \qquad \text{Eq. (H.13c)}$$

$$LR_{phyt}{}'(Pload) = S_{phyt}\frac{1}{\left(1+e^{n_{intlog}\left(\frac{S_{phyt}}{M_{phyt}}Pload-1\right)}\right)}\frac{n_{intlog}}{LN\left(e^{n_{intlog}}+1\right)} \quad \text{Eq. (H.13d)}$$

with characteristics:

$$LR_{macr}(0) = 0 \quad \text{Eq. (H.14a)}$$

$$\lim_{Pload\to\infty} LR_{macr}(Pload) = M_{macr} \quad \text{Eq. (H.14b)}$$

$$LR_{macr}{}'(0) = S_{macr}\frac{1}{\left(1+e^{-n_{intlog}}\right)}\frac{n_{intlog}}{\ln\left(e^{n_{intlog}}+1\right)} \quad \text{Eq. (H.14c)}$$

$$\lim_{n_{intlog}\to\infty} LR_{macr}{}'(0) = S_{macr} \quad \text{Eq. (H.14d)}$$

$$\lim_{Pload\to\infty} LR_{macr}{}'(Pload) = 0 \quad \text{Eq. (H.14e)}$$

$$LR_{phyt}(0) = 0 \quad \text{Eq. (H.14f)}$$

$$\lim_{Pload\to\infty} LR_{phyt}(Pload) = M_{phyt} \quad \text{Eq. (H.14g)}$$

$$LR_{phyt}{}'(0) = S_{phyt}\frac{1}{\left(1+e^{-n_{intlog}}\right)}\frac{n_{intlog}}{\ln\left(e^{n_{intlog}}+1\right)} \quad \text{Eq. (H.14h)}$$

$$\lim_{n_{intlog}\to\infty} LR_{phyt}{}'(0) = S_{phyt} \quad \text{Eq. (H.14i)}$$

$$\lim_{Pload\to\infty} LR_{phyt}{}'(Pload) = 0 \quad \text{Eq. (H.14j)}$$

Hence, the intlog function meets specifications 1 and 3-7 for all values of n and additionally approaches specification 2 for larger values of n.

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Supplementary material I: Fit of load-response curves to the Vollenweider data

We tested the four load-response curves of Supplementary material C (min, Monod, Von Bertalanffy and intlog) for phytoplankton against a field data set of >300 waterbodies compiled by Vollenweider (referred to in Jones and Lee, 1986). This dataset contains chlorophyll concentrations per normalized P loading for numerous deep lakes around the world. Both the original power function (i.e., a linear regression in log-log space) and the four load-response-curves examined in Supplementary material C, result in a good fit to the updated Vollenweider data (R^2: 0.71-0.74) (Fig. I.1).

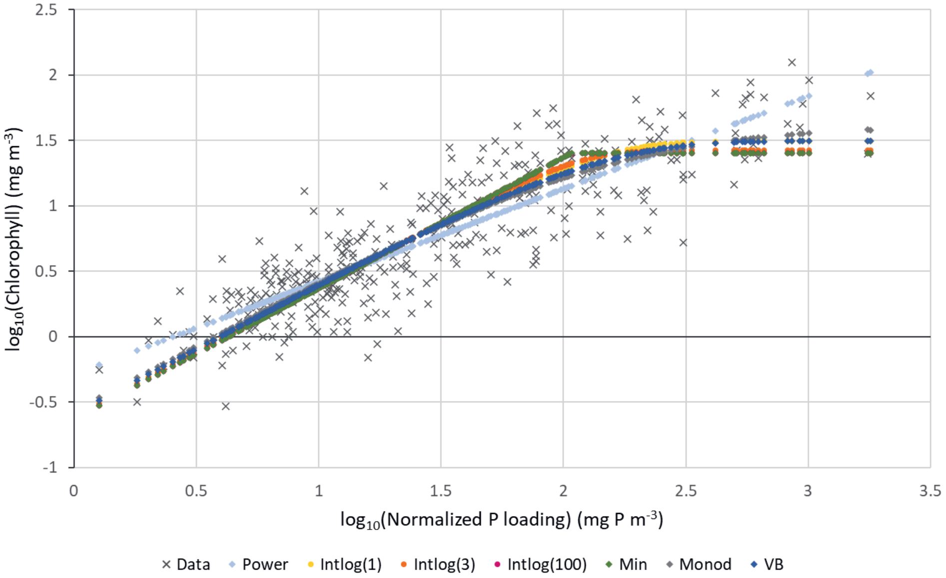

Figure I.1. Fitting a range of load-response curves to the updated Vollenweider data for >300 waterbodies (Jones and Lee, 1986). Different lines refer to the power (i.e., linear regression in log-log space) function of the original Vollenweider model and the minimum (Min), Monod, Von Bertalanffy (VB) and intlog (with an n_{intlog} of 1, 3, and 100) functions discussed in Supplementary material C. The resulting R^2 values are: 0.74; 0.71; 0.74; 0.73, 0.72; 0.71; 0.71, respectively. This analysis therefore provided no guidance on which load-response curve to use in GPLake-R.

References

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Supplementary materials of Chapter 5

Supplementary material A: Equilibrium ecosystem state as water quality indicator

In alternative stable states theory of shallow lakes, ecological water quality is defined by a turbid, phytoplankton-dominated versus clear, macrophyte-dominated state (Scheffer et al. 1993). The essence of alternative stable states is that two ecosystem states are possible at equilibrium, depending on the stressor level (e.g., nutrient loading) and – in case of hysteresis – the initial ecosystem state (May 1977). In PCLake+, an initial turbid ecosystem state is characterized by low macrophyte and high chlorophyll-*a* (chl-*a*) levels, and an initial clear ecosystem state by high macrophyte and low chl-*a* levels (Janssen et al. 2019). We use this clear versus turbid initial state definition to analyze the effect of our scenarios on the ecological water quality at equilibrium. The equilibrium ecosystem state, we here define as macrophyte or phytoplankton dominance based on a threshold macrophyte:phytoplankton ratio of 1.75 g DW m^{-2} per mg chl-*a* m^{-3}. (Fig. A.1). This ratio correspond with the high-end values at the lower critical nutrient loading for an average Dutch shallow lake for macrophyte (aDVeg >70 g DW m^{-2}) and phytoplankton dominance (oChlaT <40 mg chl-*a* m^{-3}), respectively (Janse et al. 2008).

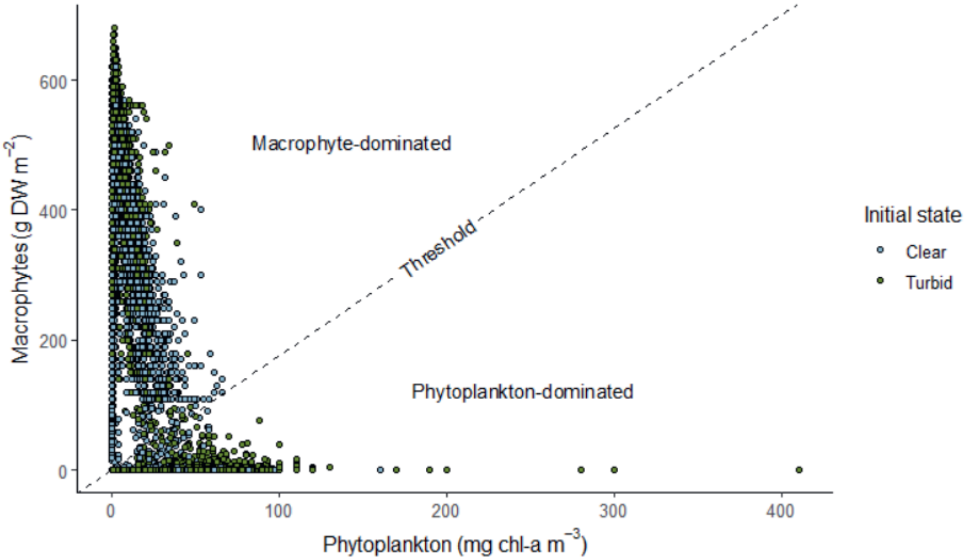

Figure A.1. Spread of macrophyte (g DW m^{-2}) and phytoplankton levels (mg chl-*a* m^{-3}) per initial state and dashed threshold line for the definition of macrophyte- and phytoplankton-dominated equilibrium ecosystem states in this study. Initial clear and turbid states are indicated by blue and green dots, respectively.

Table A.1. Number of lakes per scenario, equilibrium ecosystem state (macrophyte- or phytoplankton-dominated) and initial state (clear or turbid).

Scenario	Total number of lakes (#)	Macrophyte-dominated lakes (#) (initial state clear, turbid)	Phytoplankton-dominated lakes (#) (initial state clear, turbid)	% of lakes macrophyte-dominated
2012	6964	1237 (951, 286)	5727 (2531, 3196)	17.7
Sustainability-focused 2050	6964	3115 (1812, 1303)	3849 (1670, 2179)	44.7
Economy-focused 2050	6964	1653 (1204, 449)	5311 (2278, 3033)	23.7
Total	20892	6005 (3967, 2038)	14887 (6479, 8408)	28.7

References

Janse JH, de Senerpont Domis LN, Scheffer M, Lijklema L, Van Liere L, Klinge M, Mooij WM. 2008. Critical phosphorus loading of different types of shallow lakes and the consequences for management estimated with the ecosystem model PCLake. Limnologica. 38(3-4):203-219.

Janssen ABG, Teurlincx S, Beusen AHW, Huijbregts MAJ, Rost J, Schipper AM, Seelen LMS, Mooij WM, Janse JH. 2019. PCLake+: A process-based ecological model to assess the trophic state of stratified and non-stratified freshwater lakes worldwide. Ecological modelling. 396:23-32.

May RM. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature. 269(5628):471-477.

Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E. 1993. Alternative equilibria in shallow lakes. Trends in Ecology & Evolution. 8(8):275-279.

Supplementary material B: Water inflow and nutrient loading calculation

Water inflow

In PCLake+ we defined the total surface water inflow (mQin, Supplementary material C) as inflow from the river plus precipitation. This water inflow per lake was derived from water outflow at the lake pour point from the HydroLAKES database (Messager et al. 2016), and evaporation data from ISIMIP (Inter-Sectoral Impact Model Intercomparison Project) (Golub et al. 2022), assuming a constant lake water depth (Δz = 0) (Figure B.1).

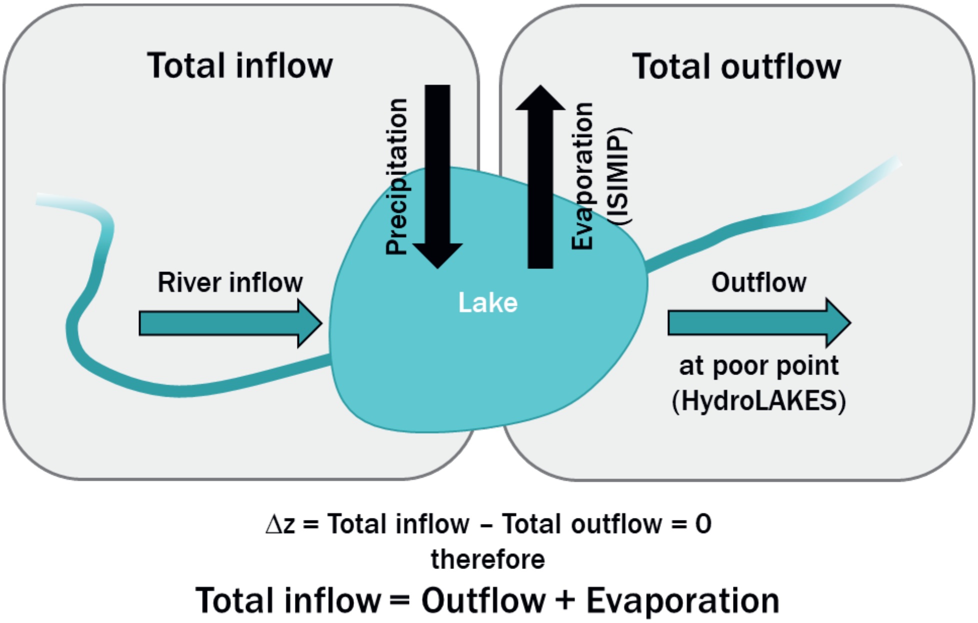

Figure B.1. Schematic of lake water balance with a constant lake water depth (z). Data for the outflow at the lake pour point and evaporation originate from the HydroLAKES (Messager et al. 2016) and ISIMIP database (Golub et al. 2022), respectively.

Nutrient loading to lakes

The nutrient loadings to lakes were calculated according to the scheme in Fig. B.2. Total dissolved N and P missions from anthropogenic sources (E_{grid}, kg yr^{-1}) based on the NUFER model (Wang et al. 2020) were obtained from the grid cell that contains the lake (outlet) coordinates from HydroLAKES (Messager et al. 2016). This total nutrient input was converted to an area averaged total nutrient loading per 0.5° × 0.5° grid cell (L_{grid}, kg km^{-2} yr^{-1}):

$$L_{grid} = \frac{E_{grid}}{A_{grid}} \qquad \text{Eq. (B.1)}$$

Here A_{grid} is the surface area of the grid (km^2).

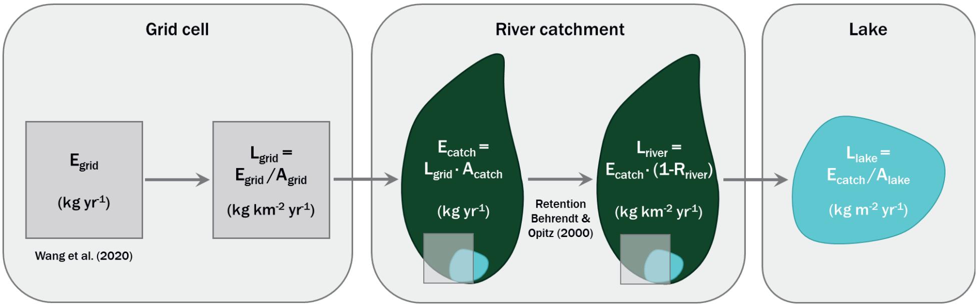

Figure B.2. Schematic of lake nutrient loading calculations with emissions (E) and loading (L) in the grid cell, river catchment (catch), river or lake as indicated by the corresponding subscript. A is the corresponding surface area from HydroLAKES (Messager et al. 2016) and R_{river} the nutrient retention in the river system according to Behrendt and Opitz (2000).

The catchment draining into the lake was assumed to have the same area-averaged nutrient loading (L_{catch}, kg km^{-2} yr^{-1}) as the grid cell containing the lake, leading to a total nutrient emission to the catchment E_{catch} (kg yr^{-1}):

$$E_{catch} = L_{grid} \times A_{catch} \qquad \text{Eq. (B.3)}$$

Here A_{catch} is the catchment surface area (km^2) from HydroLAKES (Messager et al. 2016).

Next, nutrient loading of the river transporting nutrients from the catchment to the lake (L_{river}, kg km^{-2} yr^{-1}) was calculated, accounting for nutrient retention in the river system:

$$L_{river} = E_{catch} \times (1 - R_{river}) \qquad \text{Eq. (B.4)}$$

Retention fraction (R_{river}, unitless) is based on the formula by Behrendt and Opitz (2000) with nutrient specific retention coefficients a (6.9 for N and 26.6 for P, unitless) and b (-1.10 for N and -1.71 for P, unitless), and catchment specific runoff q (l km^{-2} s^{-1}) from HydroLAKES (Messager et al. 2016):

$$R_{river} = a \times q^{b} \qquad \text{Eq. (B.5)}$$

Thereafter, the remaining nutrient loading from the river into the lake was expressed per lake surface area (A_{lake}, m^{-2}), being the lake nutrient loading (L_{lake}, g m^{-2} yr^{-1}) used as input in PCLake+:

$$L_{lake} = \frac{L_{river}}{A_{lake}} \qquad \text{Eq. (B.6)}$$

To compare the simulated nutrient loadings against in-lake nutrient concentrations from 96 lakes (Tong et al. 2020), we converted these concentrations to a proxy nutrient loading according to Reckhow (1988). The linear regression in log-log space shows a good fit (Table B.1), especially given the uncertainty regarding the proxy and simulated nutrient loadings.

Table B.1. Statistics of linear regression in log-log space between simulated nutrient loading against proxy nutrient loading for 96 lakes.

Nutrient	Simulated intercept	Simulated slope	R^2_{adj}
N	-0.55	0.9	0.74
P	-1.12	0.77	0.55

References

Behrendt H, Opitz D. 2000. Retention of nutrients in river systems: Dependence on specific runoff and hydraulic load. Hydrobiologia. 410:111-122.

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Wang M, Kroeze C, Strokal M, van Vliet MT, Ma L. 2020. Global change can make coastal eutrophication control in China more difficult. Earth's Future. 8(4):e2019EF001280.

Supplementary material C: PCLake+ parameter description

Table C.1. Input parameters of PCLake+ with their description, unit and source according to their use (i.e., as constant, for 2012, 2050 SSP scenarios and/or 2050 RCP scenarios). With DW being dry weight.

PCLake+ input parameter	Description	Unit	Source
Constants			
cDepthWInit0	Initial water depth	m	HydroLAKES
cFetch	Fetch	m	HydroLAKES; square root of area
cLAT	Latitude	Degrees	HydroLAKES
fDOrgS0	Initial organic fraction of sediment DW	g DW g DW^{-1}	Harmonized World Soil Database according to Janssen et al. (2021)
fDTotS0	Initial dry-weight fraction of sediment	g DW g DW^{-1}	Harmonized World Soil Database according to Janssen et al. (2021)
fLutum	Lutum fraction of inorganic matter	-	Harmonized World Soil Database according to Janssen et al. (2021)
fFeDIM	Iron content of inorganic matter	g Fe g DW^{-1}	Harmonized World Soil Database according to Janssen et al. (2021)
fAlDIM	Aluminum content of inorganic matter	g Al g DW^{-1}	Harmonized World Soil Database according to Janssen et al. (2021)
mQIn	Water inflow	mm d^{-1}	HydroLAKES
mQEv	Evaporation	mm d^{-1}	VIC-LAKE
2012 and 2050 RCP scenarios			
mTempEpi	Epilimnion temperature	°C	VIC-LAKE
mTempHyp	Hypolimnion temperature	°C	VIC-LAKE
mStrat	Stratification switch (0 = mixed, 1 = stratified)	-	VIC-LAKE according to Janssen et al. (2021)

mMixDepth	Mixing depth between epilimnion and hypolimnion	m	VIC-LAKE according to Janssen et al. (2021)
mVWind	Wind speed	$m\ s^{-1}$	VIC-LAKE
fRefl	Fraction photosynthetically active radiation reflected at the surface (i.e., albedo)	-	VIC-LAKE
mLOut	Average light intensity during daytime	$J\ s^{-1}\ m^{-2}$	VIC-LAKE
2012 and SSP scenarios			
mNLoad	N loading to lake	$g\ N\ m^{-2}\ d^{-1}$	NUFER
mPLoad	P loading to lake	$g\ P\ m^{-2}\ d^{-1}$	NUFER

Table C.2. New parameters of PCLake+ in this study with their description and unit.

Symbol (this study)	Symbol (PCLake+)	Description	Unit
$\mathbf{L_{out,i}}$ with i = N or P	tPOutflTotTW; tNOutflTotTW	Outflow of nutrient i	$g\ m^{-2}\ d^{-1}$
$\mathbf{[i]_{out,j}}$ with i = N or P and j = epi or hyp	wPOutflTotEpi; wNOutflTotEpi; wPOutflTotHyp; wNOutflTotHyp	Concentration of nutrient i in outflow from water layer j (epilimnion or hypolimnion)	$g\ m^{-3}\ d^{-1}$
$\mathbf{z_j}$ with j = epi or hyp	uDepthWEpi; uDepthWHyp	Depth of water layer j (epilimnion or hypolimnion)	m
$\mathbf{aR_i}$ with i = N or P	tPRet; tNRet	Absolute amount of nutrients (i) retained	$g\ m^{-2}\ d^{-1}$
$\mathbf{L_{lake,i}}$ with i = N or P	uPLoadTotTW; uNLoadTotTW	Total external loading of nutrient i into the lake	$g\ m^{-2}\ d^{-1}$
$\mathbf{R_i}$ with i = N or P	afPRet; afNRet	Retention fraction of nutrient i	-

References

Janssen ABG, Droppers B, Kong X, Teurlincx S, Tong Y, Kroeze C. 2021. Characterizing 19 thousand Chinese lakes, ponds and reservoirs by morphometric, climate and sediment characteristics. Water Research. 202:117427.

Supplementary material D: Scenario density plots

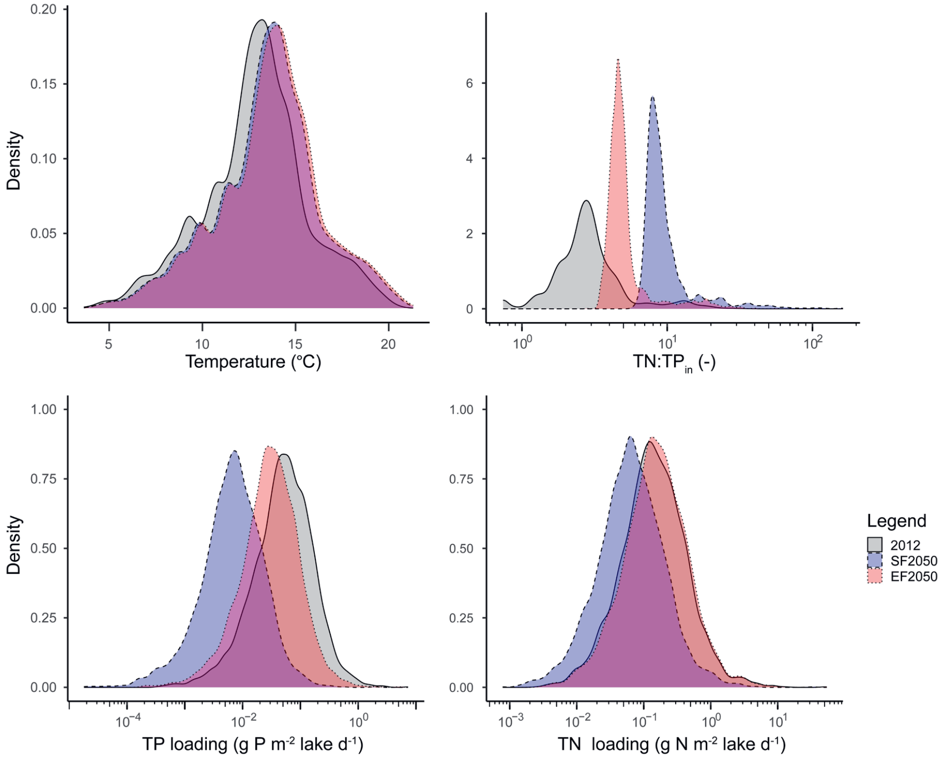

Figure D.1. Kernel density plots of scenario epilimnion temperature (°C), TP and TN loading from the socio-economic development scenarios input (g nutrient m^{-2} lake d^{-1}), and TN:TP ratio of the inflow (unitless). Lines (gray filling) indicate 2012, dashes (blue filling) the sustainability-focused scenario (SF2050), and dots (red filling) the economy-focused scenario (EF2050). The TN:TP plot has 1.5 times the standard band width.

Supplementary material E: Absolute amount of nutrients retained

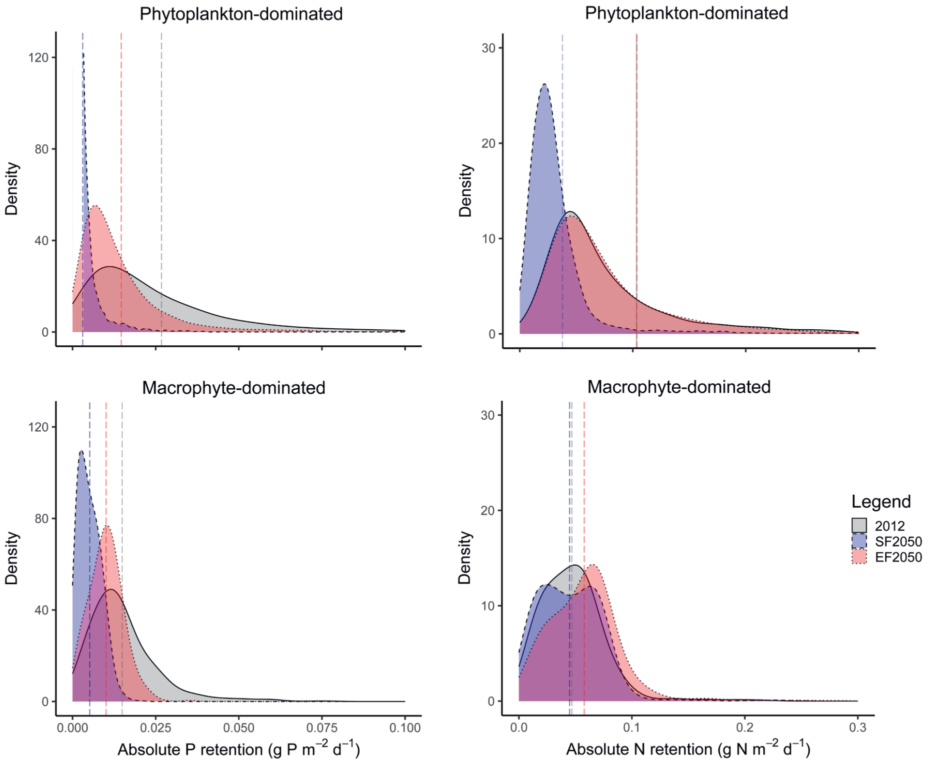

Figure E.1. Absolute nutrient retention (g Nutrient m^{-2} d^{-1}) of P (left) and N (right) for phytoplankton- (top panels) and macrophyte-dominated (bottom panels) equilibrium ecosystem states. Lines (gray filling) indicate 2012, dashes (blue filling) the sustainability-focused scenario (SF2050), and dots (red filling) the economy-focused scenario (EF2050). Some extreme data points were omitted for phytoplankton-dominated lakes. Note the difference in the axes scales of P (left) and N (right) and that 2 times the standard band width was applied.

Supplementary material F: Nutrient ratios per depth and hydraulic residence time

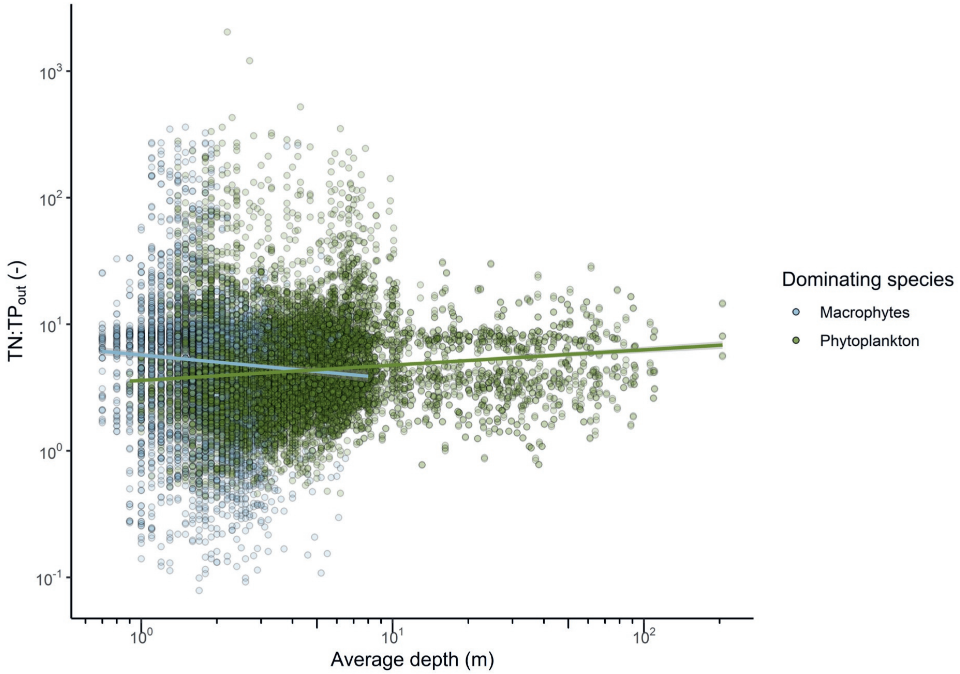

Figure F.1. TN:TP ratios of the outflow (unitless) per ecosystem state against average lake depth (m). The light blue and dark green lines are the linear regression lines in log-log space (i.e., power functions in non-log space) for macrophyte- and phytoplankton-dominated lakes, respectively.

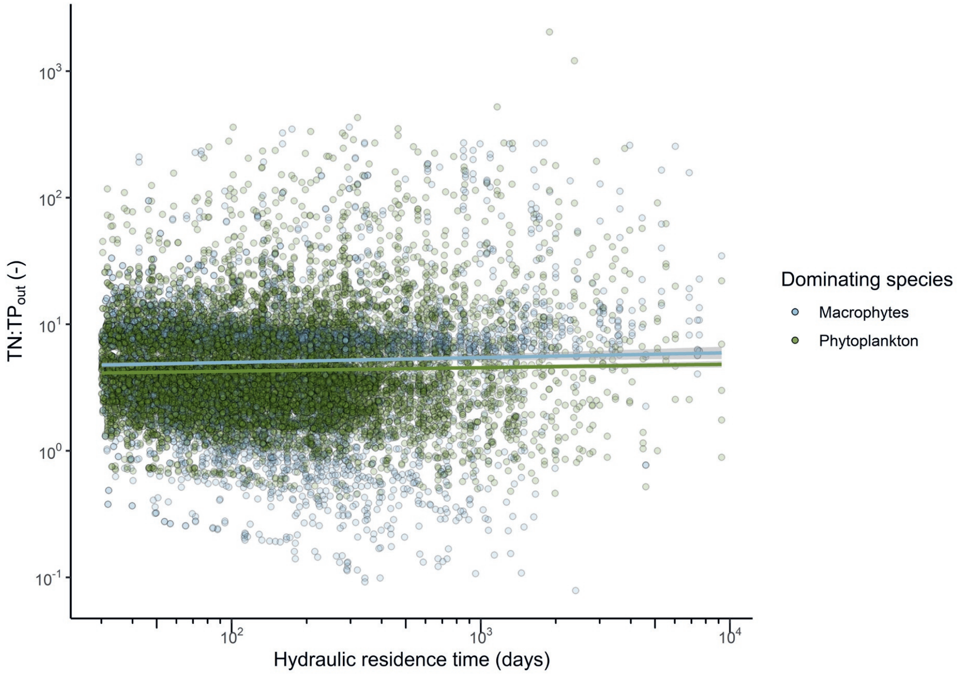

Figure F.2. TN:TP ratios of the outflow (unitless) per ecosystem state against hydraulic residence time (days). The light blue and dark green lines are the linear regression lines in log-log space (i.e., power functions in non-log space) for macrophyte- and phytoplankton-dominated lakes, respectively.

Supplementary materials of Chapter 6

Supplementary material A: Creating a digital Escape Room

The digital EscapeBLOOM game was created in Microsoft Excel in such a way that new challenges, additional background information, and clues appear when players provide correct answers. In brief, the game consists of 4 challenges, each with their own sheet. After clicking on the “Start” button in the “Introduction” sheet, the challenge sheets will appear. Each challenge sheet contains colored cells where players can provide answers, either by filling in a number (within a certain range) or by choosing from a list of answers from a drop-down menu. Once a correct answer is provided, the new text will appear in the next challenge and players can continue their quest. In case a wrong answer is provided, the text in the next challenge will indicate that the previous challenge is still to be solved or even provides some clues on how to solve it. In addition to the challenge sheets, there are sheets related to the storyline which also contain some instructions on how to play the game, a “Notebook” sheet for players to make their own notes and calculations, and sheets with more background information needed to solve the challenges (Table A.1). Some of the additional sheets only appear when a challenge is completed, to prevent an initial information overload or giving clues too early on. Here we will first explain how the layout of the EscapeBLOOM game was created and, next, how the answer-dependent dynamics were implemented. Thereafter, the addition of the timer, and the formatting of an editor versus a player version is described. Together with the dummy and player version of the game (available through https://doi.org/10.5281/zenodo.8116796 upon publication), this allows anyone to adjust the game to their own needs, for example, to adjust the difficulty of the game, to apply it to another case study, or to create a new serious game using the same techniques.

Layout

Microsoft Excel was used to create the game because this software is generally known, runs on the majority of computers, and is relatively easy to edit without programming knowledge. We adjusted the formatting in Microsoft Excel to make it look smoother than a regular spreadsheet. For this, the first row and column were kept blank to create white space, which is especially relevant when removing column and row headers in the final editing of the player version (see below). Moreover, grid lines were removed by unchecking the “Gridlines” box under View -> Show. A coherent layout was used throughout the game, with cell B1 containing the sheet name and cell C1 the title of the sheet (e.g., the title of challenge 2 is “Diving into the lake”). Below this, the second column (B) states who is “talking” (i.e., the instructor “Prof. Clear water” or the player “You”) to indicate where information on the assignment is provided and where answers can be given. The third column (C) displays the actual text of the storyline with instructions, clues, and

Table A.1. Overview of sheets in the EscapeBLOOM game in Microsoft Excel.

Sheet #	Sheet name	Content	Availability
1	Instructions	Instructions on how to save the document and how to enable macros	Always
2	Introduction	Introduction of storyline and "Start" button	Always
3	Challenge 1	Challenge to find out which lake has to be saved	After clicking "Start" button
4	Table 1	Background information for Challenge 1	After clicking "Start" button
5	Table 2	Background information for Challenge 1	After clicking "Start" button; content after solving the first question in Challenge 1
6	Challenge 2	Challenge to increase insight in lake dynamics by applying models	After clicking "Start" button; content after solving Challenge 1
7	Challenge 3	Challenge to find best nutrient load reduction measure	After clicking "Start" button; content after solving Challenge 2
8	Background report	Background information for Challenge 3	After solving Challenge 2
9	Challenge 4	Challenge to find two additional measures	After clicking "Start" button; content after solving Challenge 3
10	Decision Tree	Background information for Challenge 4	After solving Challenge 3
11	The grand finale	Finalization of storyline and "Stop the time" button	After clicking "Start" button; content after solving Challenge 4
12	Notebook	Space for notes and calculations by players	Always
13	Unit conversion table	Background information	Always
14	Hints	Place where automatically timed hints will be stored as background information	Always
15	X	Sheet with buttons for moderators to interfere with the timer	Always

assignments through an IF function referring to columns (E and further) with text to be hidden in the player version. The fourth column (D) provides answer cells and figures. Alternatively, some sheets only contain a picture with a header whilst maintaining the blank first row and column.

The text and figures were created in Microsoft Word (because of grammar and spell check functions) and Microsoft PowerPoint, respectively, and pasted into the relevant Microsoft Excel cells. Depending on the paragraph length, single or multiple paragraphs were pasted into individual cells and formatted to fit the cell using the “wrap text” function via Home -> Alignment. Column and row sizes were manually adjusted to create a layout that fits on computer screens of varying sizes and is consistent throughout the game. Here we paid attention to the use of white space between paragraphs to ease reading. When inserting a single large figure into a sheet (i.e., in the sheets “Background report” and “Decision Tree”), the original row size was maintained to ease scrolling through the sheet.

Answer-dependent dynamics

Dynamics

Answer-dependent dynamics (i.e., certain information only appears when a correct answer is provided) were implemented by IF functions and Microsoft Excel macros. An example of the simplest IF function in the game is used in cell C3 in sheet “Table 2”:

=IF('Challenge 1'!D$5='Challenge 1'!E$5, D3,E3) (Function 1)

This function refers to the cell where an answer has to be provided in challenge 1 ('Challenge 1'!D$5) and checks whether this equals the hidden real answer ('Challenge 1'!E$5). Depending on whether the answer is correct or incorrect, the cell returns the textual content of cell D3 or E3, respectively. Here, cell D3 contains text that is needed to continue playing the game and E3 contains an explanation that an earlier answer still has to be found. In multiple places more complex functions with a similar structure and functionality are applied, with the most complex one in cell C3 in sheet “Challenge 3” being:

=IF(AND('Challenge 2'!D$10='Challenge 2'!E$10,'Challenge 2'!D$9='Challenge 2'!E$9),E3, IF('Challenge 2'!D$10='Challenge 2'!E$10,G3, IF('Challenge 2'!D$9='Challenge 2'!E$9,H3,F3))) (Function 2)

Here the AND function ensures that two correct answers have to be provided in sheet “Challenge 2” before being able to continue playing the game (i.e., getting the textual content of cell E3). Multiple IF functions are used to allow clues to appear (cell F3-H3), depending on whether one or multiple answers are incorrect.

Next, similar to IF functions for individual cells, macros were used to make whole sheets with large figures appear when correct answers are provided. We applied macros to create code. This was done by right-clicking on the sheet that contains the relevant answer cells

(“Challenge 2” or “Challenge 3”) and then “View code”. Next, in a pop-up window “Microsoft Visual Basic for Applications” (VBA) code was added in the sub-window of the selected sheet (details in Supplementary material B). Here an IF-ELSE function was inserted that refers to the answer-provision and real answer cells to determine whether the next sheet (“Background report” or “Decision Tree”) should be visible or not (Table A.1). Please note that these macros will only work when the file is saved in .xls format on a Microsoft device.

Formatting of answer cells

In the EscapeBLOOM we implemented multiple types of answers: a specific number, a number within a certain range, and a list of answers using a drop-down menu. For answer cells where a specific number (with decimals) has to be provided, the formatting has to be set as "Text" to avoid issues with decimal formatting on personal computer devices. For this, first format the cell as "Text", then type the numerical answer. When an error warning (green triangle on top left cell corner) appears: place the cursor on the warning symbol and select "Ignore error" from the drop-down menu. Now the error message will disappear. These warning messages may still appear in the answer cells in the editable version, but this will disappear once formatted into a protected player version. To make content of the Microsoft Excel sheets dependent on numerical answer ranges, we use >= and <= signs in IF functions. Additionally, to make whole sheets dependent on numerical answer ranges, we applied a similar approach in the VBA code (Supplementary material B).

Lastly, drop-down lists with warning messages were added to answer cells that would otherwise be spelling sensitive or have too many answer options (e.g., due to rounding, calculation, or interpretation issues). For this first, a list of answer options was created in cells that will be hidden in the player version. Next, the answer cell was selected and the drop-down list was added via Data -> Data Tools -> Data Validation -> Settings. For this “List” was selected under “Allow” and under “Source” we referred to the cells containing the answers options (e.g., =$E$11:$E$17 for the answer options regarding stratification in cell D9 of sheet “Challenge 2”). Moreover, in the tab “Error Alert” we activated the option to “show error alert after invalid data is entered”. We selected a warning icon under “Style” and entered a warning message related to the storyline under “Error message”.

Timer

A timer was added as a game element to help to moderate the game by 1) keeping track of the time that groups have spent on playing the game (i.e., to decide on a winner, being the group that solves the game the fastest), 2) automatically giving an end-signal after one hour of game play and 3) automatically providing hints at certain time intervals. The timer counts down from the starting time of one hour to zero in steps of one second and is visible in a movable pop-up. This allows the players to see the remaining time they have to complete the EscapeBLOOM challenges. The timer is made in a 1) VBA user form, containing the pop-up format and the underlying code of the timer, and 2) a VBA module, containing the code for the macros to manage the timer from the worksheet (details in Supplementary material B).

The timer is initialized by pressing the "Start" button on the "Introduction" sheet. When the timer is started, the sheets with the challenges appear as well. When Challenge 4 is completed successfully, a button "Stop the time" will appear in the sheet "The grand finale". Pressing this button notes down the current time which can be used to determine the winner. Sheet "X" contains a "Stop timer and quit" and "Pause" button for the moderator in case the game needs to be stopped and reset or paused respectively. Both buttons can only be activated by filling out a password to limit the ability of the individual player to stop the timer. If the pause button is pressed when the timer is running, a "Continue" button appears to continue the game.

The timer is used to supply hints at given intervals. The hints appear as pop-ups and are written down in the sheet "Hints". This happens regardless of whether the user already managed to continue past the point at which the respective hint is needed. Alternatively, game moderators can themselves provide the hints at certain time intervals to all teams at the same time.

Editor versus player version

Once all the answer-dependent dynamics and the timer were implemented, the editable game was converted into a player version where the technical details are invisible and un-editable. First, the font of the text that should not be visible in the player version (column E and further) was set to match the fill color (i.e., white). Next, all cells except answer cells (and the "Notebook" sheet which should remain editable for the players) were set to be locked and hidden when protecting sheets. Locking prevents unwanted edits to the cells and hiding makes the content of the equation bar invisible to users once the sheets are protected. This was done per sheet by selecting the whole sheet and deselecting the exceptions using the short key Crtl+A. Consecutively, the options to lock and hide the cells were activated by right-clicking the selected group of cells and then selecting Format Cells -> Protection. Next, each sheet was protected by twice entering a single password via Review -> Protect -> Protect Sheet. Please note that "Protect Workbook" was not applied since that would disturb the macros controlling the answer-dependent visibility of entire sheets. Before saving the Microsoft Excel file, in each sheet, the zoom level was set at 100% and the top left cell was selected. Lastly, the first sheet of the game was opened when saving the document to ensure that players open the game on this sheet.

Supplementary material B: VBA codes

Here we provide the VBA codes that are used in the EscapeBLOOM in MS Excel. The VBA codes are used to create buttons to control a timer for automated hints, and to make sheets (dis)appear based on whether correct answers are provided in the game.

modUserFormTimer (code) module

Description: Contains code for the macros related to the buttons in the MS Excel workbook.

Important code:

- Public Const timerDuration = "01:00:00": the time of the countdown
- Public Sub btnStartTimer_Click(): connected to the “Start” button on the sheet “Introduction”. Starts countdown and calls the timer pop-up
- Sub WriteTimerValueToWorksheet(): connected to the button "Stop the time" on the sheet "The grand finale". Writes down time in certain cell
- Sub btnPauseButton_Click(): connected to the button "Pause" on the sheet "X". Writes down time in certain cell
- Public Sub testRestartButton_Click(): connected to the button "Continue" on the sheet "X". Continues time based on time written down by btnPauseButton_Click()

```
Option Explicit 'modUserFormTimer
Public Const showTimerForm = True 'timer runs with/without the
userform showing
Public Const playTickSound = True 'tick tock (a WAV sounds could be
embedded: `https:// goo.gl/ ReuUyd`)
Public Const timerDuration = "01:00:00" 'countdown time
Public timerDurationRestart As Date
Public remainingTime As Date
Public Const onTimerStart_MaximizeExcel = True
'timer could be on top of other applications; instructions here:
`https:// goo.gl/ AgmWrM`
'safe for 32 or 64 bit Office:
Private Declare PtrSafe Function SetTimer Lib "user32" (ByVal hWnd As
Long, ByVal nIDEvent As Long, _
ByVal uElapse As Long, ByVal lpTimerFunc As LongPtr) As Long
Private Declare PtrSafe Function KillTimer Lib "user32" (ByVal hWnd As
Long, ByVal nIDEvent As Long) As Long
Public schedTime As Date 'this is the "major" timer set date
Private m_TimerID As Long

Public Sub OnTimerTask()
'The procedure that runs on completion of the "major timer" (timer
won't reschedule)
    Unload frmTimer
```

```
    'MsgBox "Time's up!"
   End Sub

'For the "Start" button on the sheet "Introduction". Calls the
userform and starts the countdown
Public Sub btnStartTimer_Click()
    schedTime = Now() + TimeValue(timerDuration)
    InitTimerForm
    Worksheets("Introduction").Activate
End Sub

'Initializes timer (called by btnStartTimer_Click())
Public Sub InitTimerForm()
'Run this procedure to start the timer
    frmTimer.OnTimer
    Load frmTimer
    If showTimerForm Then

        frmTimer.Show
    End If
End Sub

'Starts timer
Public Sub StartTimer(ByVal Duration As Long)
    'Begin Millisecond Timer using Windows API (called by UserForm)
    If m_TimerID = 0 Then
        If Duration > 0 Then
            m_TimerID = SetTimer(0, 0, Duration, AddressOf TimerEvent)
            If m_TimerID = 0 Then
                MsgBox "Timer initialization failed!", vbCritical,
"Timer"
            End If
        Else
            MsgBox "The duration must be greater than zero.",
vbCritical, "Timer"
        End If
    Else
        MsgBox "Timer already started.", vbInformation, "Timer"
    End If
End Sub


'For the "Stop timer and quit" button on the sheet "X". Closes the
timer and removes some values.
Public Sub btnStopTimer_Click()
    'Prompt user to enter password
    Dim password As String
    password = InputBox("Enter password to stop timer")
```

```
    'Check if password is correct
    If password = "your_password_here" Then
        'Password is correct, end timer
        schedTime = 0
        frmTimer.UserForm_Terminate
        'Values in the following cells are removed. This allows e.g.
the "Start" button of the sheet "Introduction" to re-appear
        ThisWorkbook.Worksheets("Introduction").Range("C6").Value = "
"  'This makes the “Start” button appear, and all sheets disappear
        ThisWorkbook.Worksheets("X").Range("H12").Value = " "
        ThisWorkbook.Worksheets("X").Range("H11").Value = " " 'Removes
the time when "Pause" is clicked, needed to press continue, and see
the continue button
        ThisWorkbook.Worksheets("The grand finale").Range("C8").Value
= " " 'Removes the time of completion in "the grand finale"
    Else
        'Password is incorrect, do nothing
        MsgBox "Incorrect password. Timer not stopped."
    End If
End Sub

Public Sub StopTimer()
    If m_TimerID <> 0 Then 'check if timer is active
        KillTimer 0, m_TimerID 'it's active, so kill it
        m_TimerID = 0
    End If
End Sub

Private Sub TimerEvent()
'The API calls this procedure
    frmTimer.OnTimer
End Sub

'For the button "Stop the time" on the sheet "The grand finale".
Writes down time in certain cell (for rest of the code see the
userform "frmTimer")
Sub WriteTimerValueToWorksheet()
    frmTimer.StopTimerAndWriteValueToWorksheet
End Sub

'For the button "Pause" on the sheet "X". Writes down time in certain
cell (for rest of the code see the userform "frmTimer")
Sub btnPauseButton_Click()
    frmTimer.StopTimerAndWriteValueToWorksheetForPause
End Sub

'For the button "Continue" on the sheet "X". Continues time based on
time written down by btnPauseButton_Click()
```

```
Public Sub testRestartButton_Click()
    timerDurationRestart =
Format(ThisWorkbook.Worksheets("X").Range("K12").Value, "hh:mm:ss")
    schedTime = Now() + TimeValue(timerDurationRestart)
    InitTimerForm
    Worksheets("X").Activate
    ThisWorkbook.Worksheets("X").Range("H11").Value = " " 'removes the
value in H11, causing the continue button to disappear
End Sub

'for the button "Show Hints" on the sheet "Hints". Writes down the
time in a certain cell to assess which hints the player should see
Sub btnShowHints_Click()
    frmTimer.TimerValueToWorksheet
End Sub
```

frmTimer (code) userform

Description: The pop-up containing the timer (the object).

Important code:

- Public Sub OnTimer(): the format of the timer and how it counts down. Also contains the time when a hint is given
- Private Sub ScheduleNextTrigger(): defines that the countdown step is one second
- Code to write down the time of the timer in MS Excel (for time notation, and for the pause/continue button)
    - Public Function GetCountdownValue() As String
    - Public Sub StopTimerAndWriteValueToWorksheet()
    - Public Sub StopTimerAndWriteValueToWorksheetForPause()

```
Option Explicit 'code for userform "frmTimer"
'Requires a textbox named "txtCountdown" and "ShowModal" set to False.
Dim nextTriggerTime As Date
Dim secLeft As Long
Dim currentSecLeft As Long

'This sub prevents the user from being able to close the timer by
pressing the close button (disables close button)
Private Sub UserForm_QueryClose(Cancel As Integer, CloseMode As
Integer)
    If CloseMode = vbFormControlMenu Then
        Cancel = True 'Prevents the close button from closing the
UserForm
```

```
    End If
End Sub

'This sub defines that the userform continues running the time
Private Sub UserForm_Initialize()
    ScheduleNextTrigger
End Sub

'This sub sets up the timer in seconds (1000 miliseconds)
Private Sub ScheduleNextTrigger() 'sets the "minor" timer (for the
countdown)
    StartTimer (1000) 'one second
End Sub

Public Sub UserForm_Terminate()
    StopTimer
    If schedTime > 0 Then
        schedTime = 0
    End If
    If onTimerStart_MaximizeExcel Then Application.WindowState =
xlMaximized 'maximize Excel window
    Unload Me
End Sub

'This sub contains the timer countdown and the format and the hints at
certain intervals (in seconds from 0)
Public Sub OnTimer()
    'Either update the countdown or fire the "major" timer task
    Dim secLeft As Long
    Static hint1Shown As Boolean 'Variable to track if hint 1 has been
shown
    Static hint2Shown As Boolean 'Variable to track if hint 2 has been
shown
    Static hint3aShown As Boolean 'Variable to track if hint 3a has
been shown
    Static hint3bShown As Boolean 'Variable to track if hint 3b has
been shown
    Static hint4Shown As Boolean 'Variable to track if hint 4 has been
shown
    Static dropDownClosedTime As Date 'Variable to store the time when
the drop-down menu was closed

    If Now >= schedTime Then
        OnTimerTask 'Run "major" timer task
        Unload Me  'Close userForm (won't schedule)
    Else
        secLeft = CLng((schedTime - Now) * 60 * 60 * 24)
```

```
        If secLeft < 60 Then 'Under 1 minute (don't show mm:ss)
            txtCountdown = secLeft & " sec"
        Else
            'Update time remaining in textbox on userform
            If secLeft > 60 * 60 Then
                txtCountdown = Format(secLeft / 60 / 60 / 24,
"hh:mm:ss")
            Else 'Between 59 and 1 minutes remain
                txtCountdown = Right(Format(secLeft / 60 / 60 / 24,
"hh:mm:ss"), 5)
            End If
        End If

        'The hints at certain times (Seconds from 0)
        If secLeft = 3600 Then
            ThisWorkbook.Worksheets("Introduction").Range("C6").Value
= "Yes" 'This makes the start button disappear, and all sheets appear
        End If

        'Check if the drop-down menu is active
        Dim isDropDownActive As Boolean
        On Error Resume Next
        isDropDownActive = Application.Selection.Validation.Type =
xlValidateList
        On Error GoTo 0

        'Check if the specified time has passed
        If secLeft = 3000 Then
            If Not isDropDownActive Then
                If Not hint1Shown Then
                    MsgBox "Hint Challenge 1: Which lake in Table 2 of
Janse et al. 2008 matches with what the person in the picture is
trying to calculate? The final sheet 'Unit conversion table' might
help with unit conversions. Once you know the name of the lake, you
can find the coordinates in Table 1."
                    ThisWorkbook.Worksheets("Hints").Range("C3").Value
= "Hint challenge 1: Which lake in Table 2 of Janse et al. 2008
matches with what the person in the picture is trying to calculate?
The final sheet 'Unit conversion table' might help with unit
conversions. Once you know the name of the lake, you can find the
coordinates in Table 1."
                    hint1Shown = True ' Mark hint as shown
                End If
            End If
            If dropDownClosedTime <> 0 Then
                ThisWorkbook.Worksheets("Hints").Range("C3").Value =
"Hint challenge 1: Which lake in Table 2 of Janse et al. 2008 matches
with what the person in the picture is trying to calculate? The final
```

```
sheet 'Unit conversion table' might help with unit conversions. Once
you know the name of the lake, you can find the coordinates in Table
1."
            End If
        End If

        If secLeft = 2400 Then
            If Not isDropDownActive Then
                If Not hint2Shown Then
                    MsgBox "Hint Challenge 2: To run iGOTM the
coordinates from Table 1 are needed. All other information to run the
models (depth, hydraulic residence time being the retention time, and
current P loading being the observed P load) can be found in Table 2
in Janse et al. 2008 (note that there is a scroll bar at the bottom of
the Table)."
                    ThisWorkbook.Worksheets("Hints").Range("C4").Value
= "Hint challenge 2: To run iGOTM the coordinates from Table 1 are
needed. All other information to run the models (depth, hydraulic
residence time being the retention time, and current P loading being
the observed P load) can be found in Table 2 in Janse et al. 2008
(note that there is a scroll bar at the bottom of the Table)."
                    hint2Shown = True ' Mark hint as shown
                End If
            End If
            If dropDownClosedTime <> 0 Then
                ThisWorkbook.Worksheets("Hints").Range("C4").Value =
"Hint challenge 2: To run iGOTM the coordinates from Table 1 are
needed. All other information to run the models (depth, hydraulic
residence time being the retention time, and current P loading being
the observed P load) can be found in Table 2 in Janse et al. 2008
(note that there is a scroll bar at the bottom of the Table)."
            End If
        End If

        If secLeft = 1500 Then
            If Not isDropDownActive Then
                If Not hint3aShown Then
                    MsgBox "Hint Challenge 3a: PCLake output shows
that the low critical nutrient load is about 0.0012 g P/m2/d. How much
is this in g P/m2/y? The total current nutrient loading is the sum of
all loadings into the lake that can be found in the Background report
in g P/m2/y."
                    ThisWorkbook.Worksheets("Hints").Range("C5").Value
= "Hint Challenge 3a: PCLake output shows that the low critical
nutrient load is about 0.0012 g P/m2/d. How much is this in g P/m2/y?
The total current nutrient loading is the sum of all loadings into the
lake that can be found in the Background report in g P/m2/y."
                    hint3aShown = True ' Mark hint as shown
```

```
                End If
            End If
            If dropDownClosedTime <> 0 Then
                ThisWorkbook.Worksheets("Hints").Range("C5").Value =
"Hint Challenge 3a: PCLake output shows that the low critical nutrient
load is about 0.0012 g P/m2/d. How much is this in g P/m2/y? The total
current nutrient loading is the sum of all loadings into the lake that
can be found in the Background report in g P/m2/y."
            End If
        End If

        If secLeft = 600 Then
            If Not isDropDownActive Then
                If Not hint3bShown Then
                    MsgBox "Hint Challenge 3b (follow up): Using the
Background report, for each management option the nutrient load
reduction can be calculated in g P/m2/y. Which two options are most
effective? Similarly, the eventual nutrient loading after these two
measures can be calculated."
                    ThisWorkbook.Worksheets("Hints").Range("C6").Value
= "Hint Challenge 3b (follow up): Using the Background report, for
each management option the nutrient load reduction can be calculated
in g P/m2/y. Which two options are most effective? Similarly, the
eventual nutrient loading after these two measures can be calculated."
                    hint3bShown = True ' Mark hint as shown
                End If
            End If
            If dropDownClosedTime <> 0 Then
                ThisWorkbook.Worksheets("Hints").Range("C6").Value =
"Hint Challenge 3b (follow up): Using the Background report, for each
management option the nutrient load reduction can be calculated in g
P/m2/y. Which two options are most effective? Similarly, the eventual
nutrient loading after these two measures can be calculated."
            End If
        End If

        If secLeft = 300 Then
            If Not isDropDownActive Then
                If Not hint4Shown Then
                    MsgBox "Hint Challenge 4: Follow the questions in
the Decision Tree to find or cancel out measures. When combining
information provided by Prof. Clearwater and the Background report,
only two measures should remain."
                    ThisWorkbook.Worksheets("Hints").Range("C7").Value
= "Hint challenge 4: Follow the questions in the Decision Tree to find
or cancel out measures. When combining information provided by Prof.
Clearwater and the Background report, only two measures should
remain."
```

```
                    hint4Shown = True ' Mark hint as shown
                End If
            End If
            If dropDownClosedTime <> 0 Then
                ThisWorkbook.Worksheets("Hints").Range("C7").Value =
"Hint challenge 4: Follow the questions in the Decision Tree to find
or cancel out measures. When combining information provided by Prof.
Clearwater and the Background report, only two measures should
remain."
            End If
        End If

        'Record the time when the drop-down menu was closed
        If isDropDownActive Then
            dropDownClosedTime = 0 'Reset the drop-down closed time if
it is open
        Else
            dropDownClosedTime = Now 'Record the time when the drop-
down menu was closed
        End If

        'Check if time is up
        If secLeft = 0 Then
            ThisWorkbook.Worksheets("The grand finale").Range("C9") =
"Oh no, time is up!"
        End If
    End If
    currentSecLeft = secLeft

End Sub

'this function checks if a drop-down menu is active
Function isDropDownActive() As Boolean
    On Error Resume Next
    isDropDownActive = Application.Selection.Validation.Type =
xlValidateList
    On Error GoTo 0
End Function
```

Sheet1 (Introduction)

Description: Contains code for Sheet1, the “Introduction” sheet of the workbook

Important code:

- Private Sub Worksheet_Change(ByVal Target As Range): this code makes the challenges and other sheets appear when the “Start” button is pressed. Additionally, the “Start” button disappears.

```
'This sub lets the worksheets appear when the “Start” button is
pressed
Private Sub Worksheet_Change(ByVal Target As Range)
If [D9] = [E9] And [D10] = [E10] Then
Sheets("Background report").Visible = True
Else
Sheets("Background report").Visible = False
End If
'Makes sure the time is started before beginning with challenge 1
If [C6] = [D6] Then
Sheets("Challenge 1").Visible = True
Else
Sheets("Challenge 1").Visible = False
End If
If [C6] = [D6] Then
Sheets("Challenge 2").Visible = True
Else
Sheets("Challenge 2").Visible = False
End If
If [C6] = [D6] Then
Sheets("Challenge 3").Visible = True
Else
Sheets("Challenge 3").Visible = False
End If
If [C6] = [D6] Then
Sheets("Challenge 4").Visible = True
Else
Sheets("Challenge 4").Visible = False
End If
If [C6] = [D6] Then
Sheets("Table 1").Visible = True
Else
Sheets("Table 1").Visible = False
End If
If [C6] = [D6] Then
Sheets("Table 2").Visible = True
Else
Sheets("Table 2").Visible = False
End If
If [C6] = [D6] Then
Sheets("Background report").Visible = False
Else
Sheets("Background report").Visible = False
End If
If [C6] = [D6] Then
Sheets("Decision Tree").Visible = False
Else
Sheets("Decision Tree").Visible = False
```

```
End If
If [C6] = [D6] Then
Sheets("The grand finale").Visible = True
Else
Sheets("The grand finale").Visible = False
End If
If [C6] = [D6] Then
'If the condition is met, show “Start” on Sheet1
Shapes("Oval 4").Visible = False
Else
'If the condition is not met, hide “Start” on Sheet1
Shapes("Oval 4").Visible = True
End If
End Sub
```

Sheet5 (Challenge 2)

Description: Contains code for Sheet5, the “Challenge 2” sheet of the workbook

Important code:

- Private Sub Worksheet_Change(ByVal Target As Range): this code makes the “Background report” sheet appear when the questions in challenge 2 are answered correctly

```
Private Sub Worksheet_Change(ByVal Target As Range)
If [D9] = [E9] And [D10] = [E10] Then
Sheets("Background report").Visible = True
Else
Sheets("Background report").Visible = False
End If
End Sub
```

Sheet6 (Challenge 3)

Description: Contains code for Sheet6, the “Challenge 3” sheet of the workbook

Important code:

- Private Sub Worksheet_Change(ByVal Target As Range): this code makes the “Decision Tree” sheet appear when the last question of the challenge is correctly answered (0.39 >= answer <= 0.49)

```
Private Sub Worksheet_Change(ByVal Target As Range)
    If [D22] >= 0.39 And [D22] <= 0.49 Then
        Sheets("Decision Tree").Visible = True
    Else
        Sheets("Decision Tree").Visible = False
```

```
    End If
End Sub
```

Sheet10 (The grand finale)

Description: Contains code for Sheet10, the “The grand finale” sheet of the workbook

Important code:

- Private Sub Worksheet_Calculate(): this code shows or hides the “Stop the time” button on this sheet dependent whether or not “Challenge 4” has been completed directly.

```
'This sub makes the button “Stop timer” appear
Private Sub Worksheet_Calculate()
    'Check if the condition is met
    If Me.Range("C3").Value = Me.Range("D3").Value Then
        'If the condition is met, show “Stop the time” on Sheet10
        ThisWorkbook.Worksheets("The grand finale").Shapes("Rectangle
6").Visible = True
    Else
        'If the condition is not met, hide “Stop the time” on Sheet10
        ThisWorkbook.Worksheets("The grand finale").Shapes("Rectangle
6").Visible = False
    End If
End Sub
```

Sheet14 (Hints)

Description: Contains code for Sheet14, the “Hints” sheet of the workbook

Important code:

- Private Sub Worksheet_Calculate(): this codes checks the value in cell B10 where the seconds left from 0 are written down when the “Show hints” button is pushed. Based on this the appropriate hints are shown.

```
'This sub makes the hints appear when the “Show hints” button is
pushed
Private Sub Worksheet_Calculate()
    Dim cellB10Value As Variant
    cellB10Value = ThisWorkbook.Worksheets("Hints").Range("B10").Value

    If cellB10Value > 0 And cellB10Value <= 3000 Then
        ThisWorkbook.Worksheets("Hints").Range("C3").Value = "Hint
Challenge 1: Which lake in Table 2 of Janse et al. 2008 matches with
what the person in the picture is trying to calculate? The final sheet
```

```
'Unit conversion table' might help with unit conversions. Once you
know the name of the lake, you can find the coordinates in Table 1."
    End If
    If cellB10Value > 0 And cellB10Value <= 2400 Then
        ThisWorkbook.Worksheets("Hints").Range("C4").Value = "Hint
Challenge 2: To run iGOTM the coordinates from Table 1 are needed. All
other information to run the models (depth, hydraulic residence time
being the retention time, and current P loading being the observed P
load) can be found in Table 2 in Janse et al. 2008 (note that there is
a scroll bar at the bottom of the Table)."
    End If
    If cellB10Value > 0 And cellB10Value <= 1500 Then
        ThisWorkbook.Worksheets("Hints").Range("C5").Value = "Hint
Challenge 3a: PCLake output shows that the low critical nutrient load
is about 0.0012 g P/m2/d. How much is this in g P/m2/y? The total
current nutrient loading is the sum of all loadings into the lake that
can be found in the Background report in g P/m2/y."
    End If
    If cellB10Value > 0 And cellB10Value <= 600 Then
        ThisWorkbook.Worksheets("Hints").Range("C6").Value = "Hint
Challenge 3b (follow up): Using the Background report, for each
management option the nutrient load reduction can be calculated in g
P/m2/y. Which two options are most effective? Similarly, the eventual
nutrient loading after these two measures can be calculated."
    End If
    If cellB10Value > 0 And cellB10Value <= 300 Then
        ThisWorkbook.Worksheets("Hints").Range("C7").Value = "Hint
Challenge 4: Follow the questions in the Decision Tree to find or
cancel out measures. When combining information provided by Prof.
Clearwater and the Background report, only two measures should
remain."
    End If

End Sub
```

Sheet15 (X)

Description: Contains code for Sheet15, the “X” sheet of the workbook

Important code:

- Private Sub Worksheet_Change(ByVal Target As Range): this code makes sure there is a calculation in the worksheet (to trigger the next Private Sub), and copies the value of cell H12 to Cell I12.
- Private Sub Worksheet_Calculate(): this code shows or hides the continue button dependent on whether or not the pause button has been pressed.

```
Private Sub Worksheet_Change(ByVal Target As Range)
    If Target.Address = "$H$12" Then 'Change H12 to the cell with the
time duration
        Range("I12").Value = Target.Value 'Change B1 to the cell where
you want to copy the value
    End If
End Sub

Private Sub Worksheet_Calculate()
    'Check if the condition is met
    If Me.Range("I11").Value = "X" Then
        'If the condition is met, show “Continue” on Sheet15
        ThisWorkbook.Worksheets("X").Shapes("Rectangle 10").Visible =
True
    Else
         'If the condition is not met, hide the Continue on Sheet15
        ThisWorkbook.Worksheets("X").Shapes("Rectangle 10").Visible =
False
    End If
End Sub
```

Supplementary material C: Questionnaire concepts

The concepts as included in the questionnaires before and after playing the game are listed below. Control concepts are indicated by an asterisk in this overview but were not marked in the actual questionnaire.

1. Water quantity models*
2. Water quality models
3. Lake models
4. Nutrient load reduction
5. Hydrological regulation
6. Lake restoration
7. Ecological engineering
8. Lake characteristics
9. Lake morphology
10. Hydraulic residence time
11. Lake stratification
12. Water quality indicators
13. Water quality standards
14. Macroinvertebrates*
15. Harmful algal blooms
16. Alternative stable states
17. Critical nutrient loading
18. Tipping points
19. Water turbidity
20. Ecosystem services*
21. Nutrient sources
22. Nutrient release from sediment
23. Point/Non-point sources of nutrients
24. Bird feces as nutrient source*
25. Water quality stressors
26. Impact of climate change on water quality*
27. Impact of nutrient loading on water quality
28. Impact of fishery on water quality
29. Water balance calculation*
30. Nutrient balance calculation
31. Literature search
32. Analytical thinking

Supplementary material D: Insignificant perceived learning

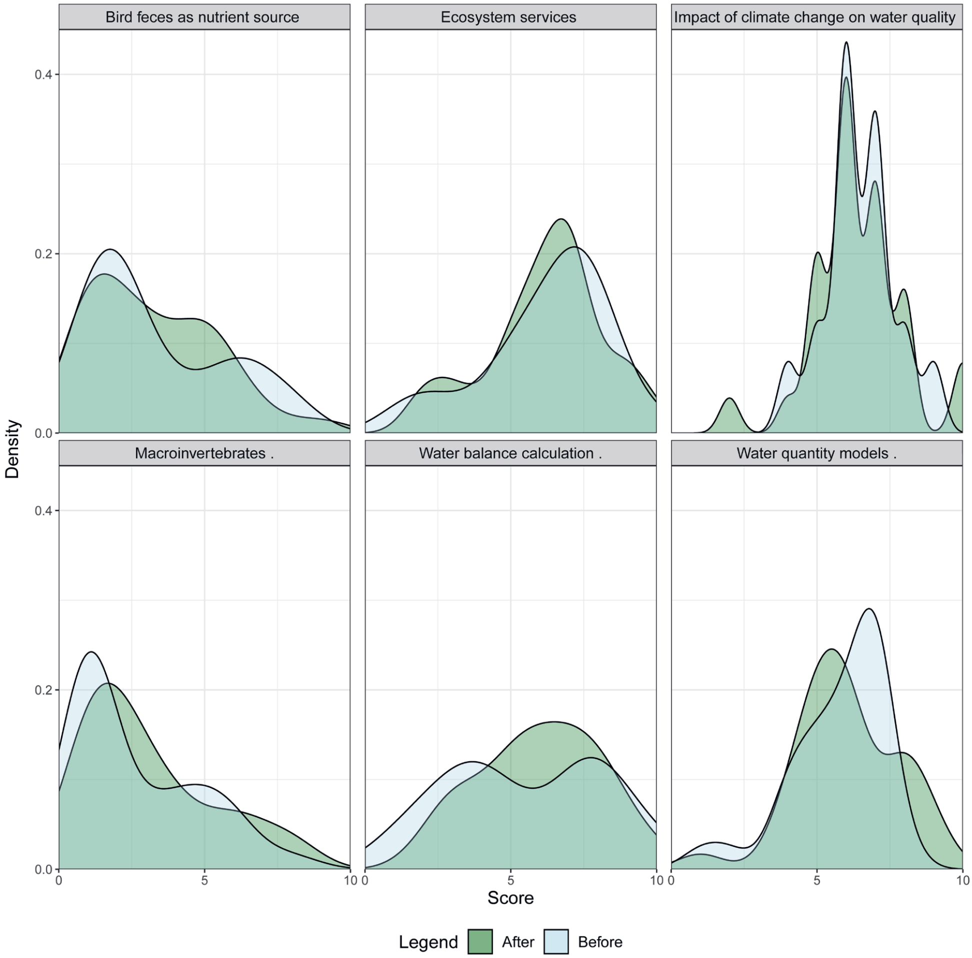

Figure D.1. Distribution of perceived learning scores (*n* = 30) for control concepts before (light blue) and after (dark green) playing the game. The scores (x-axis) range between 0 (not familiar with the concept) to 10 (expert on the concept) and the y axis gives the cumulative probability density (fraction of participants) based on the kernel density estimation method of Sheather and Jones (1991). The results of the students' scores were analyzed using a paired Two-sample Fisher-Pitman permutation test. A dot indicates insignificance with 0.05<P<0.1, and absence of a dot P>0.1.

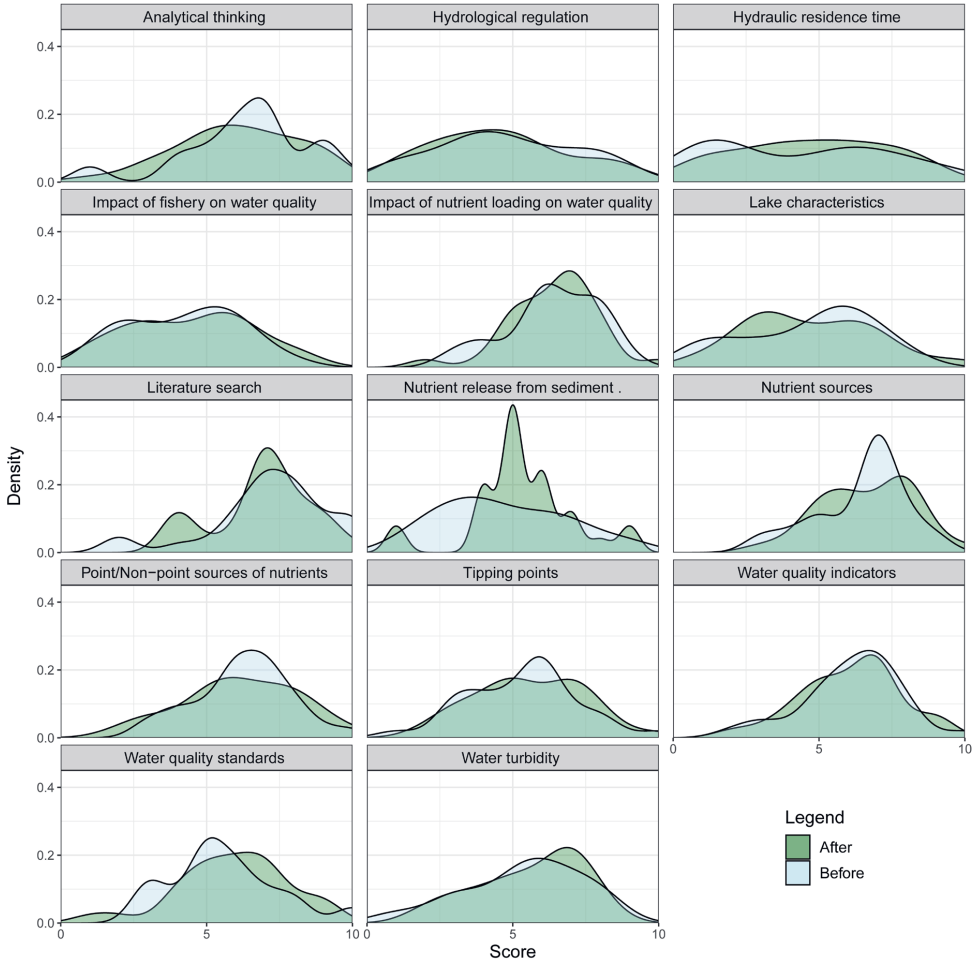

Figure D.2. Distribution of perceived learning scores (*n* = 30) with insignificant differences between scores before (light blue) and after (dark green) playing the game (P>0.1). The scores (x-axis) range between 0 (not familiar with the concept) to 10 (expert on the concept) and the y axis gives the cumulative probability density (fraction of participants) based on the kernel density estimation method of Sheather and Jones (1991). The results of the students' scores were analyzed using a paired Two-sample Fisher-Pitman permutation test.

Supplementary material E: The use of macros

The use of Microsoft Excel macros is desirable to hide figures or whole sheets until certain progress in the game is made. We included instructions on two ways to enable macros in the EscapeBLOOM game. Still, macros cannot be enabled on every computer. Therefore, it is recommended to test each computer beforehand. When this is not possible (e.g., due to online setting of bring-your-own device policies in education), ways to deal with this are to a) have players working together on those PCs that do support macros (e.g., MSc course at Wageningen University & Research) or b) actively provide print-outs of separate documents of the pages controlled by macros (e.g., Department Christmas Party at IGB Berlin).

Summary (English)

Water and nutrients are essential to life and wellbeing, however, excess nutrients also pollute surface waters. These excess nutrients threaten human and natural health through eutrophication problems such as potentially toxic algal blooms and oxygen depletion, and affect services that surface waters provide. Still, nutrients are valuable resources for food production, but a large part is transported through surface waters and eventually lost into the deep oceans. Despite attempts to increase nutrient use efficiency on land, nutrient pollution of surface waters appears inevitable. Moreover, in spite of incentives to benefit from large scale water quality improvements, water quality management approaches are generally focused on individual waterbodies. Alternatively, here, I focus on nutrient retention in interconnected aquatic ecosystems as a novel direction for water quality management. By this, I hope to stimulate more sustainable management of water and nutrients.

In this thesis, I develop and present the novel “Smart Nutrient Retention Networks” (SNRNs) concept as a concrete direction for water quality management aimed at enhanced nutrient conservation by retention and consecutive reuse. The development of this concept required a compilation of the existing knowledge on nutrient retention in surface waters. Next, models are promising tools to support the development of SNRN management strategies. However, simple, mass-balanced, and process-based lake models are missing that include the interactions between nutrient retention, ecosystem state and nutrient loading which are a key aspect of SNRNs. The development of such models calls for an understanding of ecological mechanisms underlaying transitions in lake ecosystem state (i.e., macrophyte versus phytoplankton dominance) and the associated nutrient retention.

Additionally, it is important to consider alterations in nutrient ratios and how to communicate scientific findings in the light of SNRNs. First, changes in ratios of the nutrients nitrogen (N) and phosphorus (P) influence ecological

water quality. Nevertheless, only a few studies assessed the relative retention of N and P in waterbodies and its implication for downstream water quality. Increased insights in how N:P ratios of in- and outflows of waterbodies will develop in the future may advance water quality management strategies for connected waterbodies. Second, it would be useful to have tools to bridge the gap between modelers and non-modelers in the field of nutrient and water quality management, and to inform them on new insights, management perspectives, modeling tools and their results.

Therefore, in this PhD thesis I aim *to increase our understanding of nutrient retention in connected surface waters*. I build on existing — and develop novel — *perspectives*, *theories*, and *tools* to support water quality management with the objective to:

1) Develop the SNRN concept based on existing knowledge of nutrient retention in surface waters (Chapter 2).
2) Support the development of SNRNs through relatively simple and versatile dynamic models that are rooted in resource competition *theory* (Chapter 3 and 4).
3) Increase understanding of how nutrient retention may influence nutrient ratios and their transport to downstream systems (Chapter 5).
4) Develop a *tool* to interactively increase the non-modelers' understanding of concepts and results that arise from a lake modeling exercise (Chapter 6).

First, I developed and presented the Smart Nutrient Retention Networks (SNRNs) concept as a novel *perspective* to focus water quality management on nutrient retention in networks of surface waters to support nutrient conservation (Chapter 2). For this, I compiled existing literature on nutrient retention processes in inland waters, water quality management options for nutrient retention and nutrient retention models. With the development of the SNRN concept, also a new spatial feedback *theory* emerged for potential cascades of water quality improvement when regime shifts in lake ecosystem state occur by nutrient load reduction. The *theory* is that with improved ecosystem state, nutrient retention will increase, leading to reduced nutrient loading to downstream systems, where it may trigger consecutive regime shifts. To support system understanding and the development of SNRN management strategies, I identified a lack of nutrient retention models that include this spatial feedback in networks of inland waters in relation to management options.

Therefore, I aimed to fill this gap through the development of two modeling *tools*: GPLake-M and GPLake-R (Chapter 3 and 4). First, I developed the graphical and mathematical GPLake-M model as a novel approach to describe regime shifts in shallow lakes that is rooted in resource competition *theory* and the critical turbidity concept (Chapter 3). Second, I further developed this approach, leading to the GPLake-R model as the first versatile process-based, mass-balanced model of nutrient retention in relation to ecosystem state in shallow lakes (Chapter 4). GPLake-R dynamically captures the hysteretic pattern from the more complex PCLake model, with macrophyte-dominated lakes having higher P retention than phytoplankton-dominated lakes. I believe the GPLake-R model is a major step towards a model *tool* to support development of SNRNs as it includes the spatial feedback presented in Chapter 2.

Next, I exemplified the use of models to inform management *perspectives* by increasing *theoretical* insight in how nutrient retention may influence nutrient ratios and their transport to downstream systems (Chapter 5). Here, I performed a scenario analysis of 3482 Chinese lakes under a low climate change and sustainability-focused, and a high climate change and economy-focused scenario for 2050 using the relatively complex lake ecosystem model PCLake+. This study confirmed the spatial feedback *theory* introduced in Chapter 2, illustrating that water quality management could benefit even more from nutrient pollution reduction than one would expect at first sight. Moreover, I found that TN:TP ratios in lake outflows depend on lake ecosystem state and inflow TN:TP ratios, which may be explained *theoretically* by nutrient limitation and nutrient retention processes.

Thereafter, I developed the "EscapeBLOOM" serious game to interactively introduce water quality management concepts and freely available lake models (Chapter 6). This science communication *tool* presents a historic lake management case through multiple challenges involving different modeling steps. The game significantly contributed to perceived learning on lake modeling and concepts that lay at the core of this thesis and the SNRN concept, such as critical nutrient loading (i.e., the nutrient loading at which regime shifts occur). Based on the positive feedback on applications of the game in different countries and cultures, I envision that this serious game approach can be applied, modified, or serve as inspiration for others to create their own "Escape-game" to aid the communication of water quality management — or other environmental — modeling cases.

Lastly, I discussed the implications of my findings in a broader context (Chapter 7). First, I addressed nutrient retention *theories* and *perspectives*, demonstrating the novelties of the SNRN *perspective*, and lessons from nutrient retention models regarding hydrological assumptions that may ease the first modeling efforts of nutrient retention and transport in lake networks. Second, I discussed the mechanistic, *theoretical* background of the newly developed model *tools*, concluding that the relatively simple GPLake-type models are promising building blocks to model SNRNs in the future. Third, based on my scenario analysis, the *theoretical* insights regarding the spatial feedback *theory* of SNRNs and the effect of lake ecosystem state and nutrient retention on downstream N:P ratios are discussed, as well as the lessons for future scenario analyses. Finally, I broadened the scope by discussing the availability and development of serious games as a science communication *tool*, with lessons for the development of an SNRN serious game inspired by the EscapeBLOOM.

I hope this thesis will serve as an inspiration for (collaborations with) water quality mangers, to start designing management strategies based on lessons from the SNRN *perspective*. I believe the relatively simple, but mechanistically understandable GPLake-type models presented in this thesis may form the basis of a future SNRN *tool* that can be applied in by water quality managers and scientist to explore future management scenarios that consider the core principles of SNRNs. In the future, serious games may also be applied as *tools* to introduce and stimulate the uptake of the SNRN approach. In the end, I hope this PhD thesis increases understanding of nutrient retention in connected surface waters to contribute to more sustainable management of water and nutrients, and therewith to the UN Sustainable Development Goals (SDGs) of zero hunger (SDG 2), clean water and sanitation (SDG 6), and responsible consumption and production (SDG 12).

Summary (Nederlands)

Summary (Nederlands)

Water en voedingsstoffen (d.w.z. nutriënten of meststoffen) zijn essentieel voor het leven en welzijn, maar tegelijkertijd vervuilt een overschot aan voedingstoffen het oppervlaktewater. Dit nutriëntenoverschot bedreigt de gezondheid van mens en natuur door eutrofiëringsproblemen (d.w.z. vermesting) zoals massale groei van potentieel giftige algen en zuurstofuitputting in oppervlaktewateren. Bovendien beïnvloedt het de diensten die oppervlaktewateren leveren. Hoewel nutriënten waardevolle hulpbronnen voor voedselproductie zijn, verplaats een groot deel zich via oppervlaktewater en gaat uiteindelijk verloren in de diepte van de oceanen. Ondanks pogingen om het gebruik van meststoffen op land efficiënter te maken, lijkt vermesting van oppervlaktewater onvermijdelijk. Bovendien is waterkwaliteitsbeheer, ondanks aansporingen om waterkwaliteits-verbeteringen op grote schaal te benutten, over het algemeen gericht op individuele waterlichamen. Als een nieuwe richting voor waterkwaliteitsbeheer, focus ik mij hier op het vasthouden van voedingsstoffen (d.w.z. nutriëntenretentie) in aquatische ecosystemen die onderling met elkaar verbonden zijn. Hiermee hoop ik duurzamer water- en voedingsstoffenbeheer te stimuleren.

In dit proefschrift ontwikkel en presenteer ik het nieuwe “Smart Nutrient Retention Networks” (SNRN’s) concept als een concrete richting voor waterkwaliteitsbeheer, met als doel het behoud van nutriënten te vergroten dankzij retentie gevolgd door hergebruik. Om dit concept te ontwikkelen, was het nodig bestaande kennis over nutriëntenretentie in oppervlaktewater te verzamelen. Vervolgens zijn modellen veelbelovende instrumenten ter ondersteuning van de ontwikkeling van SNRN-managementstrategieën. Er ontbreken echter eenvoudige, massa-gebalanceerde en procesmatige modellen van meren die een belangrijk aspect van SNRN’s omvatten: de interacties tussen nutriëntenretentie, de ecosysteemtoestand en de nutriëntenbelasting. De ontwikkeling van dergelijke modellen vereist inzicht in de ecologische mechanismen die ten grondslag liggen aan omslagen in de ecosysteemtoestand van meren (d.w.z. dominantie van macrofyten versus fytoplankton) en de nutriëntenretentie die daarmee samenhangt.

In het licht van SNRN's is het daarnaast belangrijk om rekening te houden met veranderingen in de nutriëntenverhoudingen en hoe wetenschappelijke inzichten met een breder publiek te delen. Ten eerste wordt ecologische waterkwaliteit beïnvloed door veranderingen in de verhoudingen van de nutriënten stikstof (N) en fosfor (P). Er zijn echter slechts enkele studies die de verhouding tussen retentie van N en P in waterlichamen en de gevolgen daarvan voor de benedenstroomse waterkwaliteit beoordeeld hebben. Met vergroot inzicht in de toekomstige ontwikkeling van de N:P-verhoudingen in het in- en uitstromende water van waterlichamen zouden de waterkwaliteitsbeheerstrategieën voor verbonden waterlichamen verbeterd kunnen worden. Ten tweede zouden communicatie-instrumenten van pas komen om de kloof tussen modelleurs en niet-modelleurs op het gebied van nutriënten- en waterkwaliteitsbeheer te overbruggen, en hen te informeren over nieuwe inzichten, managementperspectieven, modelleringsinstrumenten en modelresultaten.

Daarom is mijn streven in dit proefschrift om *ons begrip van de nutriëntenretentie in verbonden oppervlaktewateren te vergroten*. Ik bouw voort op bestaande – en ontwikkel nieuwe – *perspectieven*, *theorieën* en *instrumenten* (d.w.z. *hulpmiddelen*) ter ondersteuning van waterkwaliteitsbeheer met als doel om:

1) Het SNRN-concept te ontwikkelen op basis van bestaande kennis over nutriëntenretentie in oppervlaktewater (hoofdstuk 2).

2) De ontwikkeling van SNRN's te ondersteunen door middel van relatief eenvoudige en veelzijdige dynamische modellen die geworteld zijn in "resource competition *theory*" (hoofdstuk 3 en 4).

3) Het inzicht te vergroten in hoe nutriëntenretentie invloed kan hebben op de nutriëntenverhoudingen en -transport naar benedenstroomse systemen (hoofdstuk 5).

4) Een *hulpmiddel* te ontwikkelen om op interactieve wijze het begrip van niet-modelleurs te vergroten met betrekking tot concepten en resultaten die voortkomen uit een modelexercitie voor meren (hoofdstuk 6).

Ten eerste heb ik het Smart Nutrient Retention Networks (SNRN's) concept ontwikkeld en gepresenteerd als een nieuw *perspectief* om het waterkwaliteitsbeheer te richten op nutriëntenretentie in netwerken van oppervlaktewateren ter ondersteuning van het behoud van nutriënten (hoofdstuk 2). Hiervoor heb ik bestaande literatuur verzameld over nutriëntenretentieprocessen in binnenwateren en daaraan gerelateerde waterkwaliteitsbeheeropties en modellen. Met de ontwikkeling van het SNRN-concept ontstond ook een nieuwe ruimtelijke feedback*theorie* voor potentiële reeksen van verbeterde waterkwaliteit wanneer door vermindering van de nutriëntenbelasting de ecosysteemtoestand van meren omslaat. De *theorie* is dat met een verbeterde toestand van het ecosysteem de retentie van nutriënten zal toenemen, wat zal leiden tot een verminderde nutriëntenbelasting naar benedenstroomse systemen, waar dit opeenvolgende omslagen in ecosysteemtoestand kan veroorzaken. Ik constateerde een lacune in nutriëntenretentiemodellen over deze ruimtelijke feedback in oppervlaktewaternetwerken in relatie tot beheeropties terwijl die zouden kunnen helpen bij het systeembegrip en de ontwikkeling van SNRN-beheerstrategieën.

Zodoende beoogde ik deze leemte op te vullen door de ontwikkeling van twee modellerings*instrumenten*: GPLake-M en GPLake-R (hoofdstuk 3 en 4). Eerst heb ik het grafische en wiskundige GPLake-M-model ontwikkeld als een nieuwe aanpak om omslagen in ecosysteemtoestand in ondiepe meren te beschrijven. Dit is gebaseerd op "resource competition *theory*" en het "critical turbidity" concept (hoofdstuk 3). Ten tweede heb ik deze aanpak verder ontwikkeld, wat heeft geleid tot het GPLake-R-model. Dit is het eerste veelzijdige procesmatige, massa-gebalanceerde model van nutriëntenretentie in relatie tot ecosysteemtoestand in ondiepe meren (hoofdstuk 4). GPLake-R vangt op dynamische wijze het hysteretische patroon van het complexere PCLake-model, waarbij door macrofyten gedomineerde meren een hogere P-retentie hebben dan door fytoplankton gedomineerde meren. Ik geloof dat het GPLake-R-model een belangrijke stap vormt in de richting van een model*instrument* om de ontwikkeling van SNRN's te ondersteunen, omdat het de ruimtelijke feedback (van hoofdstuk 2) bevat.

Vervolgens illustreerde ik hoe modellen gebruikt kunnen worden om management*perspectieven* te informeren door *theoretische* inzicht te vergroten over de potentiële invloed van nutriëntenretentie op de nutriëntenverhoudingen en -transport naar benedenstroomse systemen (hoofdstuk 5). Met het relatief complexe meer-ecosysteemmodel PCLake+ heb ik voor 3482 Chinese meren een scenarioanalyse voor 2050 uitgevoerd met een lage klimaatverandering en duurzaamheids-gefocust scenario, en een hoge klimaatverandering en een economisch-gefocust scenario. Deze studie bevestigde de ruimtelijke feedback*theorie* die in hoofdstuk 2 geïntroduceerd werd en illustreert dat het waterkwaliteitsbeheer nog meer zou kunnen profiteren van de vermindering van nutriëntenvervuiling dan je op het eerste gezicht zou verwachten. Bovendien ontdekte ik dat de N:P-verhoudingen van het water dat uit meren stroomt, afhankelijk zijn van de ecosysteemtoestand van het meer en de N:P-verhoudingen van de instroom. Dit kan *theoretisch* verklaard worden door nutriëntlimitatie en nutriëntenretentie processen.

Daarna heb ik het “EscapeBLOOM” spel ontwikkeld als “serious game” om op interactieve wijze concepten voor waterkwaliteitsbeheer en gratis beschikbare modellen van meren te introduceren (hoofdstuk 6). Via meerdere uitdagingen met verschillende modelleringsstappen presenteert dit wetenschapscommunicatie-*instrument* een geschiedkundig voorbeeld van het beheer van een meer. Het spel heeft aanzienlijk bijgedragen aan de leerervaring met betrekking tot het modelleren van meren en kernconcepten van dit proefschrift en het SNRN-concept, zoals de kritische nutriëntenbelasting (d.w.z. de nutriëntenbelasting waarbij omslagen in ecosysteemtoestand optreden). Gebaseerd op de positieve reacties op toepassingen van het spel in verschillende landen en culturen, stel ik me voor dat deze serious game-aanpak kan worden toegepast, aangepast of als inspiratie kan dienen voor anderen om hun eigen "Escape-game" te creëren om zo de communicatie van waterkwaliteitsbeheer- en andere milieumodelleringscasussen te ondersteunen.

Ten slotte besprak ik de implicaties van mijn bevindingen in een bredere context (hoofdstuk 7). Eerst beschouwde ik *theorieën* en *perspectieven* op het gebied van nutriëntenretentie, waarbij ik de vernieuwing van het SNRN-*perspectief* liet zien. Naar aanleiding van bestaande nutriëntenretentie-modellen besprak ik lessen met betrekking tot hydrologische aannames die de eerste pogingen om nutriëntenretentie en -transport in netwerken van meren te modelleren kunnen vergemakkelijken. Ten tweede besprak ik de mechanistische en *theoretische* achtergrond van de nieuwe model-*instrumenten* die ik in dit proefschrift ontwikkeld heb. Hierbij concludeerde ik dat de relatief eenvoudige GPLake-achtige modellen veelbelovende bouwstenen zijn om in de toekomst SNRN's te modelleren. Ten derde besprak ik, op basis van mijn scenarioanalyse, de *theoretische* inzichten met betrekking tot de ruimtelijke feedback*theorie* van SNRN's en het effect van de ecosysteemtoestand van meren en nutriëntenretentie op benedenstroomse N:P-verhoudingen, evenals de lessen voor toekomstige scenarioanalyses. Ten slotte verbrede ik de blik door een discussie over de beschikbaarheid en ontwikkeling van serious games als *instrument* voor wetenschapscommunicatie, met lessen voor de ontwikkeling van een SNRN serious game geïnspireerd op de EscapeBLOOM.

Ik hoop dat dit proefschrift als inspiratie zal dienen voor (samenwerking met) waterkwaliteitsbeheerders om managementstrategieën te gaan creëren op basis van lessen uit het SNRN-*perspectief*. Ik geloof dat de relatief eenvoudige, maar mechanistisch begrijpelijke, GPLake-achtige modellen van dit proefschrift de basis kunnen vormen van een toekomstig SNRN-*instrument*. Een dergelijk *instrument* zou door waterkwaliteitsbeheerders en wetenschappers gebruikt kunnen worden om toekomstige managementscenario's te verkennen die rekening houden met de kernprincipes van SNRN's. In de toekomst kunnen serious games ook als *instrument* worden toegepast om de SNRN-aanpak te introduceren en de acceptatie ervan te stimuleren. Tenslotte hoop ik dat dit proefschrift inzicht in nutriëntenretentie in verbonden oppervlaktewateren vergroot en bijdraagt aan duurzamer beheer van water en voedingsstoffen, alsook de “Sustainable Development Goals” (SDG’s) van de VN met betrekking tot geen honger (SDG 2), schoon water en sanitair (SDG 6), en verantwoorde consumptie en productie (SDG 12).

Summary (Nederlands)

Acknowledgements

When I started studying in Wageningen in 2012, I could not have imagined pursuing a PhD in three inspiring departments with many lovely colleagues. I really enjoyed my PhD-time and would like to thank all those people that enriched this period in life.

First of all, I want to thank my wonderfully diverse supervisor team. Wolf, in hindsight, our first conversations might have set the scene for the special ways we have to interact. While I was enjoying my internship in Scotland, we had calls in which you directly showed your open and person-oriented attitude that you connected with scientific and philosophical concepts. Even after I concluded I did not want to work on models, you somehow convinced me to start working together with you at NIOO. I lively remember that we started off with two intense weeks together in one office to co-write a paper in google docs and a memorable frog-pond-break. I think this special start of my PhD proposal writing time at NIOO smoothened the transition to collaborative work from home during the COVID-19 pandemic. Although you sometimes push my boundaries, I appreciate your creative and coaching nature. It is really fun and inspiring to work together with you, and I notice a special synergy that goes beyond science.

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During my PhD, I enjoy collaborations with many people. First, the other members of the “PCLake-team” that I collaborated with the most: Manqi, Lilith and Sven. Manqi, I really enjoyed working and travelling together, no matter the weather conditions. You helped to widen my worldview by your stories and lovely philosophical inspiration. I feel I can always rely on your mental support and math skills, and hope we can continue to share our life and work. Lilith, I remember I spoke with you for the first time at a network event during my MSc, and now I feel you became my “big-network-sister”. Thank you for the nice lunch walks, GLEON trip to Canada, and your crash course in R. It is special how you use your own experience to give valuable advise whilst allowing others to grow. I believe you will be a great mother. Sven, it is miraculous that — no matter which issue — you always seem to have thought it through before. Whether it is about modeling, empirical work, administrative procedures, or construction work, I can always rely on your reflection, pragmatic advice, and dedication to help out where possible. That is worth treasuring.

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BSc and MSc, and always welcomed me during my PhD. NIOO-AqE colleagues, you formed the ecological seedbed for my PhD, with a welcoming vibe and great content-based discussions. I am pleased to make my next step in work-life together with you.

I am grateful for the nice friendships, deep conversations, and good times I had with many people and that enrich(ed) my life. I appreciate the relaxing times with lovely acrobats in Wageningen for so many years. De vele mensen van de GK en GGG in Rhenen, en de nieuwe opbouwende contacten in Zetten, bedankt voor het samen groeien en vergroenen. En bovenal, Angeline, Henriette, Laura, Lies, Lisanne en Marieke, bedankt voor jullie vriendschap.

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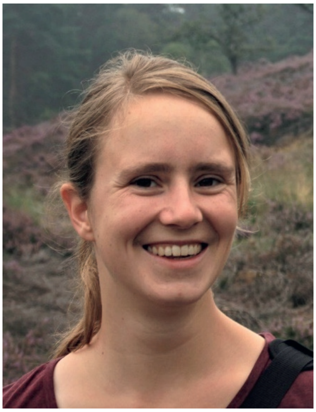
About the author



Dianneke van Wijk was born on 4 April 1994 in Geldermalsen, the Netherlands. After finishing secondary school in 2012 with a thesis for Rijkswaterstaat about fish migration, she moved to Wageningen to study Environmental Sciences. There she specialized in Aquatic Ecology and Water Quality Management with an MSc thesis about algae-zooplankton interactions under global warming. In 2017, she moved to Scotland for an internship at the Centre for Ecology & Hydrology (CEH) where she amongst others explored the potential reuse of waste materials to remove phosphorus from surface waters. Thereafter, she returned to Wageningen to start as a junior researcher at the Aquatic Ecology group of the Netherlands Institute for Ecology (NIOO-KNAW). During this period, she contributed to multiple research proposals and obtained a personal research grant from the Wageningen Institute for Environment and Climate Research (WIMEK) for her own PhD project at the Water Systems and Global Change group and the Aquatic Ecology and Water Quality Management group. In her PhD project she focused on nutrient retention in interconnected lakes as means to manage eutrophication and to contribute to sustainable use and conservation of nutrients. Moreover, she collaborated on publications about water quality modeling, nature futures, and sustainable development. In 2022, she developed the “EscapeBLOOM” serious game and applied it during workshops that she organized at scientific conferences and during an MSc course. She has presented her work on “Smart Nutrient Retention Networks” at various scientific conferences and now in this PhD thesis: “Towards Smart Nutrient Retention Networks to improve water quality: perspectives, theories and tools”.

Peer reviewed publications

Armstrong M, Kramer L, de Senerpont Domis LN, **van Wijk D**, Gsell AS, Mooij WM, Teurlincx S. 2021. Flipping lakes: Explaining concepts of catchment-scale water management through a serious game. Limnology and Oceanography: Methods. 19(7):443-456.

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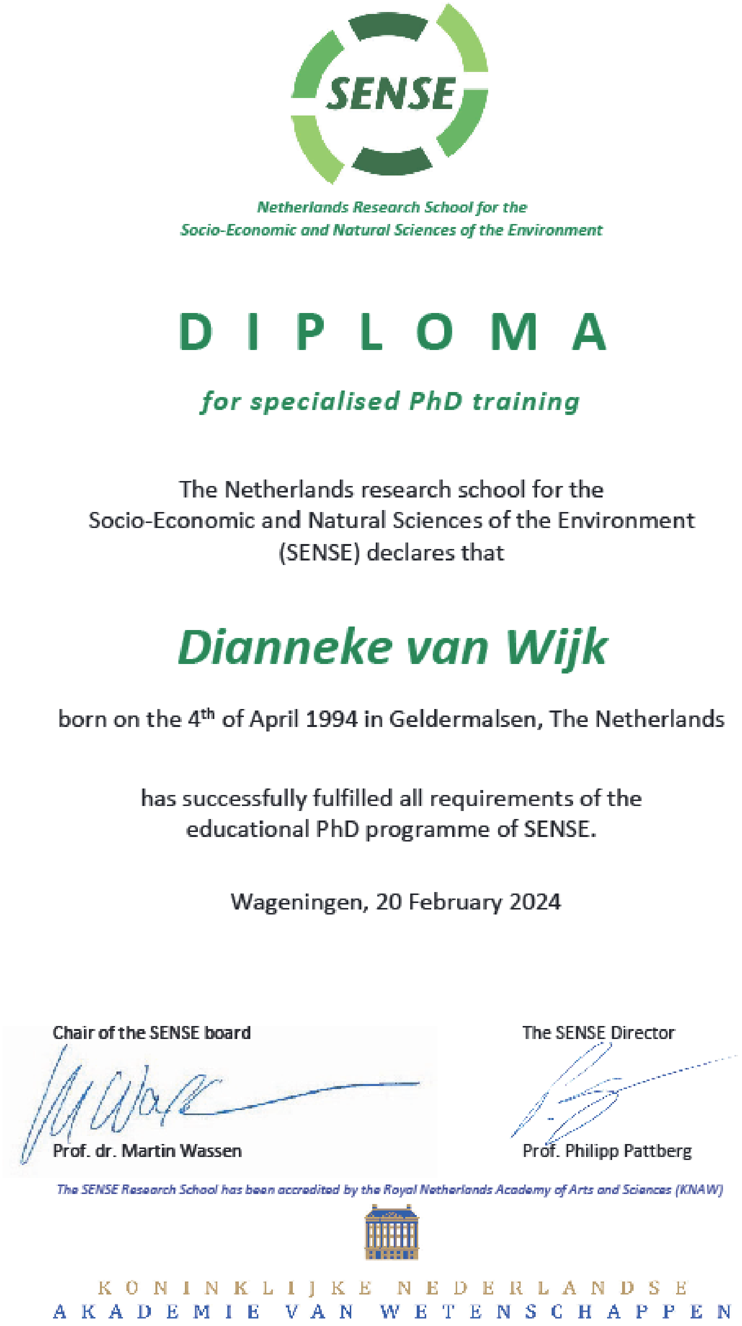
Honors and Awards

- Personal PhD Scholarship, call Open Round, Wageningen Institute for Environment and Climate Research (WIMEK) (2018)
- Presentation Price BSc Thesis Environmental Sciences (2015)
- Thesis award Koningin Wilhelmina College (2012)



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- Environmental research in context (2019)
- Research in context activity: EscapeBLOOM: 100 measures, but which to take? (Serious game development and workshop at SIL2022, Berlin, Germany) (2022)

Other PhD and Advanced MSc Courses

- Consumer-Resource Interactions in Times of Global Environmental Change, PE&RC graduate school (2018)
- Summer School "Ecology and society: frontiers and boundaries", University of Bordeaux, LabEx COTE, France (2019)
- Making an Impact! How to increase the societal relevance of your PhD research, Wageningen Graduate Schools (2019)
- Scientific Artwork, Data visualization and Infographics with Adobe Illustrator (2021)

Selection of Management and Didactic Skills Training

- Supervising two MSc students with thesis (2020-2021), and one with internship (2023)
- Assisting practicals of the MSc course "Models for Ecological Systems" (2021-2023)
- Teaching in MSc course "Modelling Future Water Stress" (2022) and BSc course "Disaster Risk Management and Nature Based Solutions" (2023)
- Organizing "EscapeBLOOM" workshop at GLEON, Ryn, Poland (2023)

Selection of Communicating your science

- Co-author of a box and spotlight in the Human Development Report (2020)
- Writing press release: "What ice cream, domino and water management have in common", WUR & Nature NatureToday (2022)
- Co-author of essay "Nationaal Park 3.0: Een welkome toevoeging aan de diversiteit van nationale parken?" Journal: Landschap (2022)
- Editor at Journal: Landschap (2023-present)

Selection of Oral Presentations

- *Smart Nutrient Retention Networks: how to benefit from cascading effects of water quality*. 10th Shallow Lakes International Conference 1-5 March 2021, Online
- *Smart Nutrient Retention Networks: a 21st Century approach for nutrient conservation through water quality management*. International Society of Limnology (SIL) 36th Congress, 7-10 August 2022, Berlin, Germany

SENSE coordinator PhD education

Dr. ir. Peter Vermeulen

Colophon

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