



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.

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; Janssen 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 northeast 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 (Compendium voor de Leefomgeving 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

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two critical stressor levels at which regime shift can occur, but the direction of change differs per critical stressor level (black arrows in Fig. 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).

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. 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 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

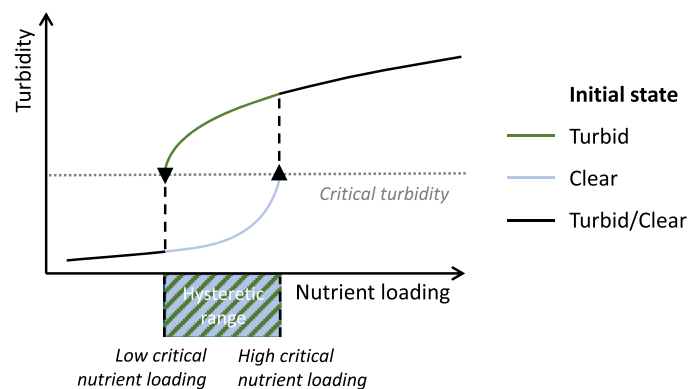


Fig. 1. Schematic of alternative stable states in shallow lakes with nutrient loading as a stressor (x-axis). In the hysteretic range between the low and high critical nutrient loading the equilibrium ecosystem state (y-axis) depends on the initial ecosystem state (i.e., historically turbid phytoplankton-dominated, 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.

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. (2019) 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.

1.2. A novel model of alternative stable 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.

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).

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., 2019a). 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. 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 $aExt_{Tot}$ (-) 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 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 Q_{in} ($mm\ d^{-1}$) (sets 2–11 in Table 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 Q_{in} . 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. Results

3.1. A graphical model of alternative stable states: GPLake-M

The GPLake-M model describes the amount of macrophytes and

Table 1

Sets of lake characteristics used as input in PCLake (depth z and hydrological loading Q_{in}) 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)	Q_{in} ($mm\ d^{-1}$)	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

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. 2).

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. 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 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. 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

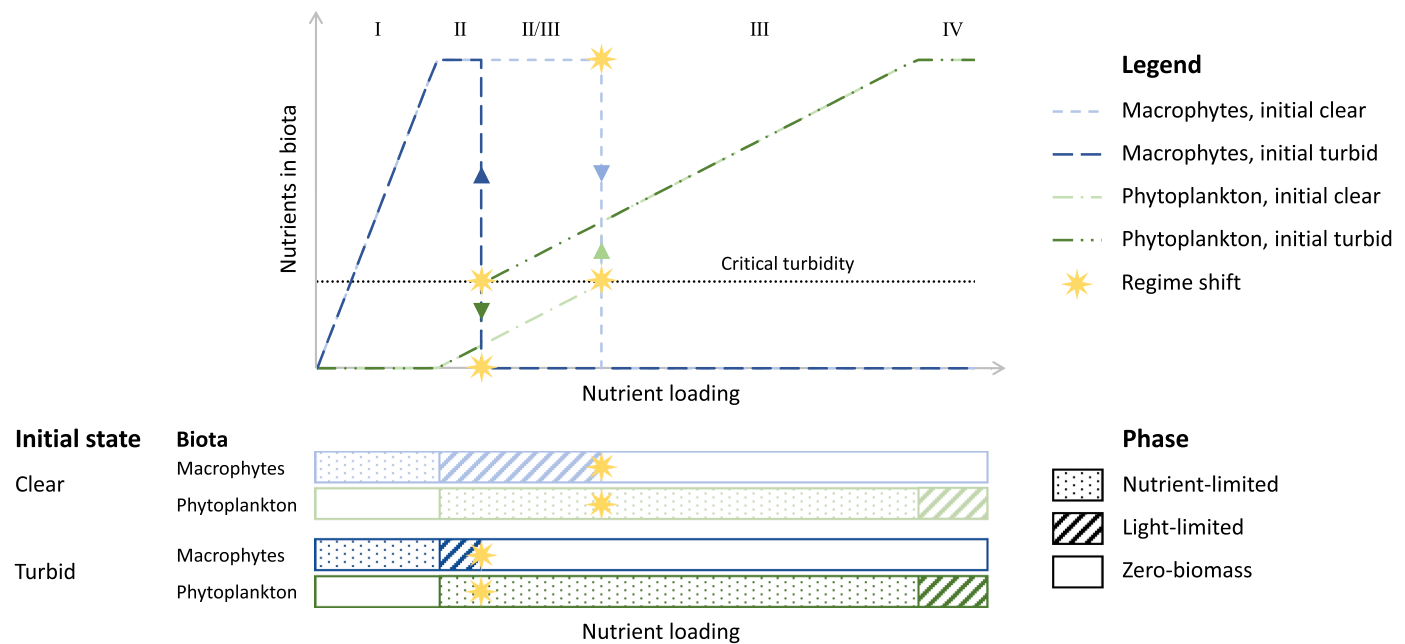


Fig. 2. Graphical GPLake-M model showing the four nutrient-response curves for macrophytes with an initial clear state (light blue) and initial turbid state (dark blue), and phytoplankton with an initial clear state (light green) and initial turbid state (dark green). The critical turbidity (black dashed 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.

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 out-competed 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.

3.1.2. 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. 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. 2). The same pattern is visible in PCLake output (Supplementary material C).

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

Table 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 and Jagtman 1990)
Loosdrecht Lakes	Turbid	2.0	<0.50	<1.0	>3.6	>7.2	(Hosper and Jagtman 1990)
Loosdrecht Lakes	Clear	2.0	2.0–2.5	4.1–5.1	0.72–0.90	1.4–1.8	(Hosper and 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 et al., 1999)
8 lakes	Clear	1.0–2.5	1.0–2.5	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.

explain both regime shifts. In GPLake-M the critical turbidity is expressed in areal phytoplankton P content (horizontal dotted line in Fig. 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 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 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 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 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.

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).

3.2.1. 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 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 Plateau 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.

3.2.2. 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. 2):

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

$$P_{macr}^* = Slope_{macr} \times P_{load} \quad \text{Eq. (1a)}$$

$$P_{phyt}^* = 0 \quad \text{Eq. (1b)}$$

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

$$P_{macr}^* = Plateau_{macr} \quad \text{Eq. (2a)}$$

Table 3
GPLake-M symbols with unit and description.

Symbol	Unit	Description	Category
P_{crit}	$g P m^{-2}$	Critical P content of phytoplankton (i.e., a measure of critical turbidity)	Biological parameter
P_i	$g P m^{-2}$	Areal P content of species i macrophytes (macr) or phytoplankton (phyt)	Output variable
P_{load}	$g P m^{-2} d^{-1}$	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

$$P_{phyt}^* = Slope_{phyt} \times \left(P_{load} - \frac{Plateau_{macr}}{Slope_{macr}} \right) \quad \text{Eq. (2b)}$$

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

$$P_{macr}^* = 0 \quad \text{Eq. (3a)}$$

$$P_{phyt}^* = Slope_{phyt} \times P_{load} \quad \text{Eq. (3b)}$$

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

$$P_{macr}^* = 0 \quad \text{Eq. (4a)}$$

$$P_{phyt}^* = Plateau_{phyt} \quad \text{Eq. (4b)}$$

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

$$I \leftrightarrow II = \frac{Plateau_{macr}}{Slope_{macr}} \quad \text{Eq. (5a)}$$

$$II \rightarrow III = \frac{Plateau_{macr}}{Slope_{macr}} + \frac{P_{crit}}{Slope_{phyt}} \quad \text{Eq. (5b)}$$

$$II \leftarrow III = \frac{P_{crit}}{Slope_{phyt}} \quad \text{Eq. (5c)}$$

$$III \leftarrow IV = \frac{Plateau_{phyt}}{Slope_{phyt}} \quad \text{Eq. (5d)}$$

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

Here P_{crit} , 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. 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 1). For GPLake-M, here we assumed the scenario of Vollenweider-type nutrient retention with s is 81 d, derived from a parameterized $Slope_{phyt}$ of 47.3 and a 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 (Figs. 3–6). 1) In the nutrient-limited phase, $Slope_{phyt}$ of both models increase with τ (Fig. 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 (Figs. 3–6). In GPLake-M the Plateau does not scale with τ and z , whereas it does in PCLake. Nevertheless, $Plateau_{phyt}$ 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). Moreover, $Plateau_{macr}$ from GPLake-M falls within the PCLake macrophyte P content peak at the hysteric phase for the tested range of τ (Fig. 5) and z 1.5–2.5 m (Fig. 6). At larger depths, GPLake-M somewhat overestimates the Plateaus relative to PCLake

(Figs. 4 and 6). 3) The nutrient loadings at which the regime shifts occur are comparable among both models for all tested τ 's (Figs. 3 and 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 (Figs. 4 and 6).

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.

4. Discussion

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 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

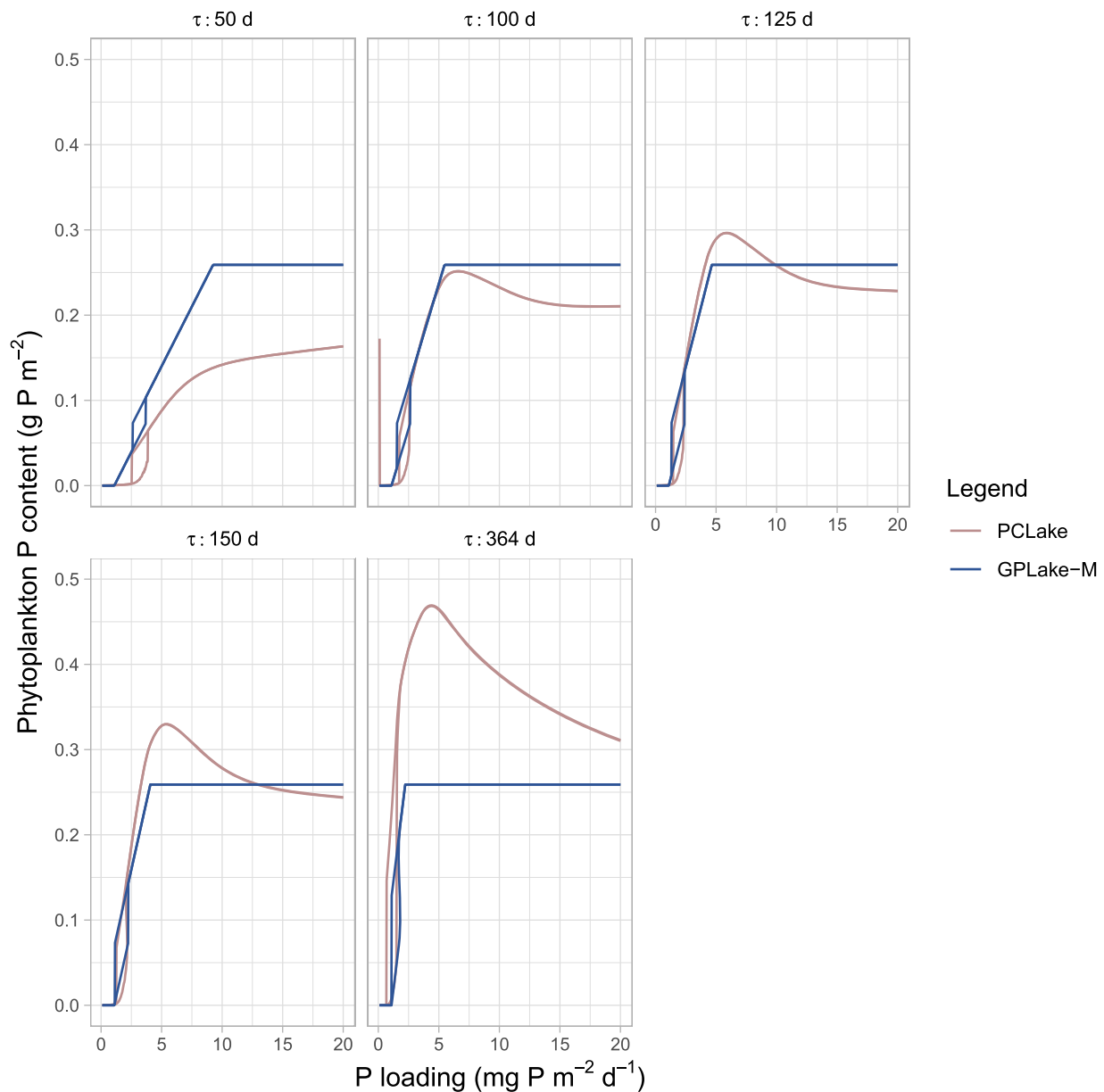


Fig. 3. Comparison of GPLake-M (blue) and PCLake (red) phytoplankton P content per residence time (τ : 50–364 d) for depth 2 m (set 1–5, Table 1), assuming the scenario in GPLake-M of Vollenweider-type nutrient retention. For a range of τ values, the models resemble each other in terms of Slope, P content at the Plateau, and critical nutrient loadings.

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.

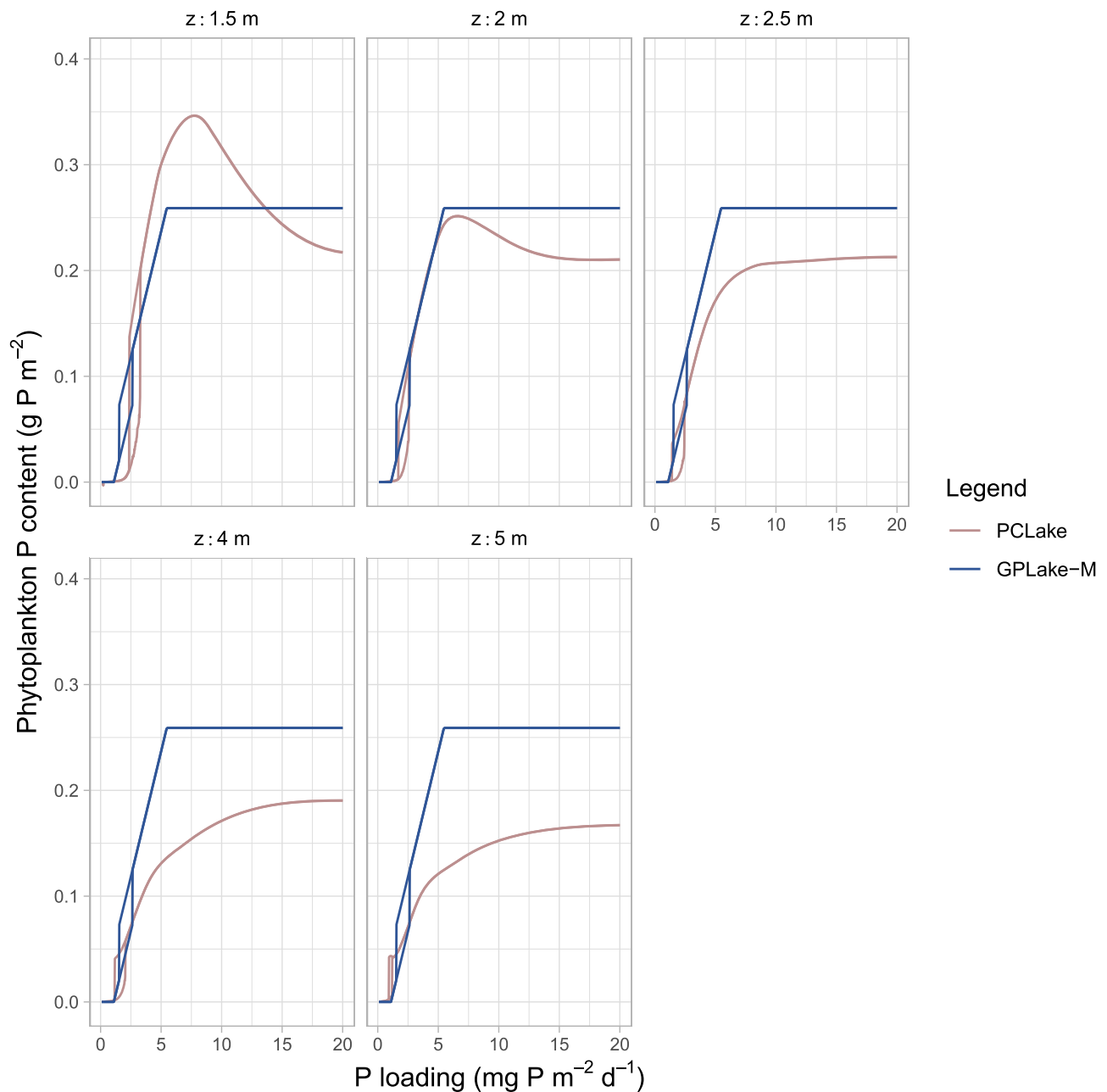


Fig. 4. Comparison of GPLake-M (blue) and PCLake (red) phytoplankton P content per depth (z : 1.5–5 m) with a constant hydraulic residence time of 100 d (set 1, 7, 8, 10 and 11, Table 1), assuming the scenario in GPLake-M of Vollenweider-type nutrient retention. For a range of z values, the models resemble 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.

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., 2019b) 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 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.

4.2.1. Slopes and Plateaus

For additional parameterization of Slopes and Plateaus one should

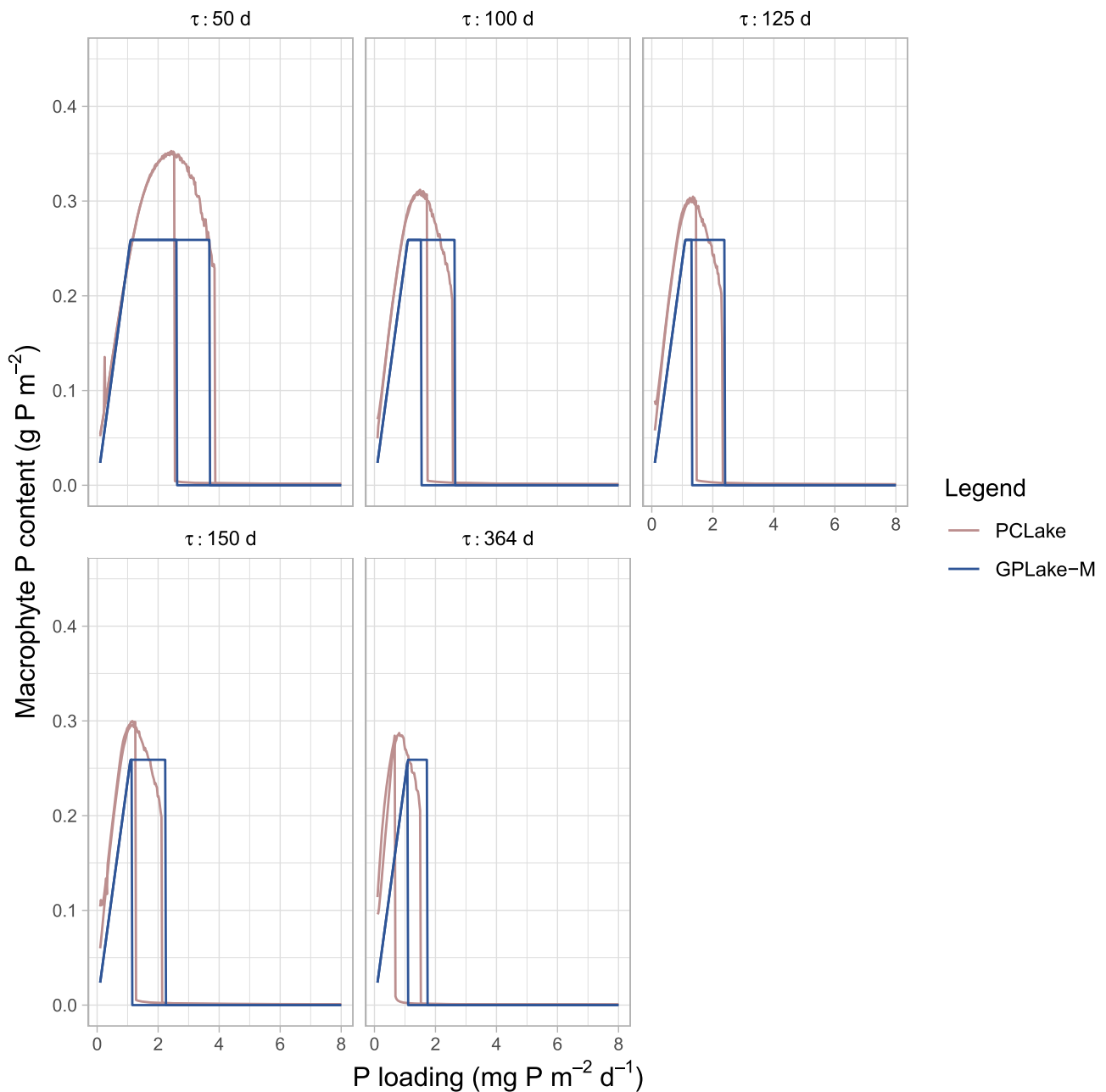


Fig. 5. Comparison of GPLake-M (blue) and PCLake (red) macrophyte P content per residence time (τ : 50–364 d) for depth 2 m (set 1–5, Table 1), assuming the scenario in GPLake-M of Vollenweider-type nutrient retention. For a range of τ values, the models resemble each other in terms of Slope, P content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

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 Q_{in} 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 $0.105\text{--}0.372 \text{ g P m}^{-2}$ 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 “Berge 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

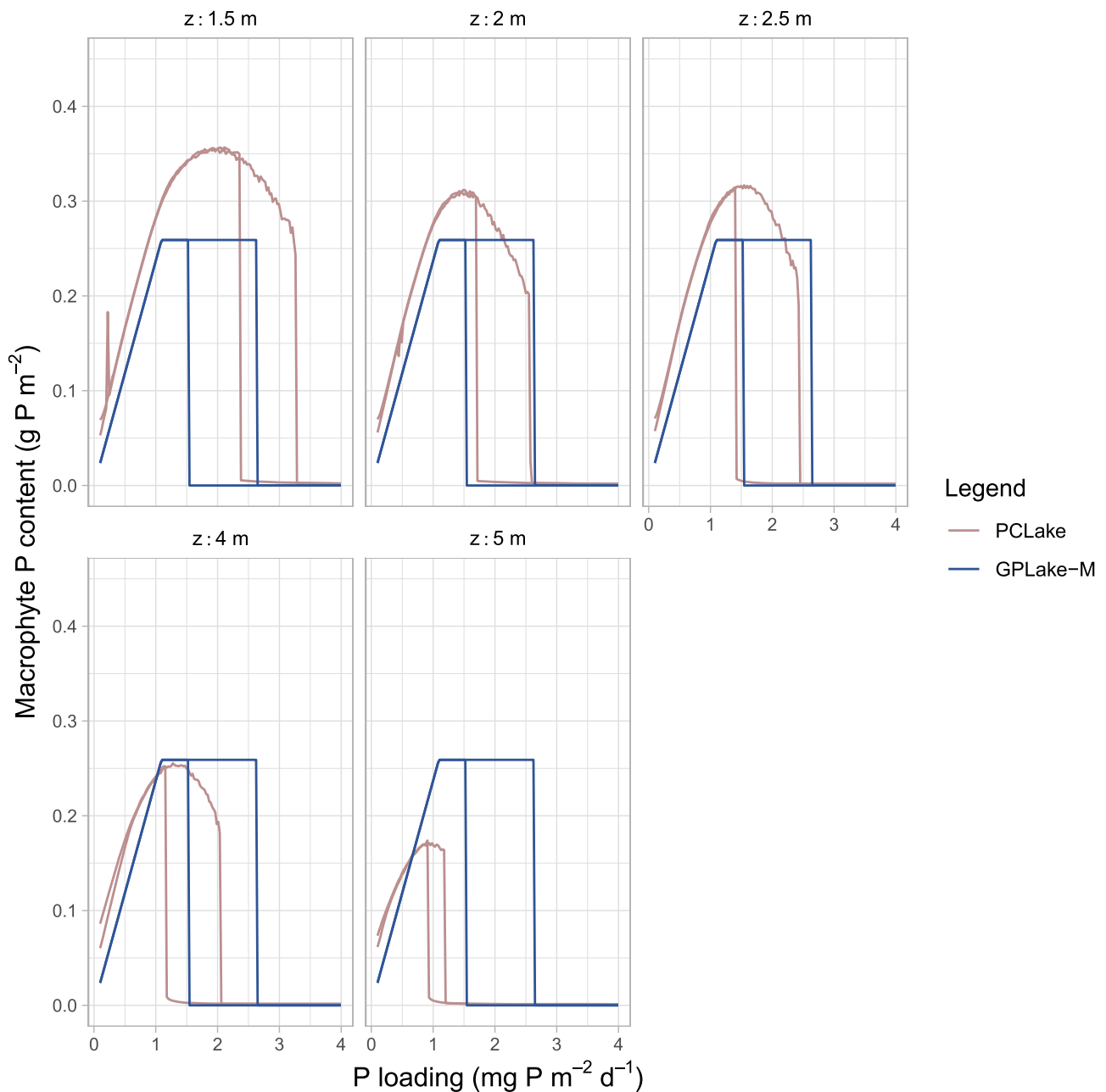


Fig. 6. Comparison of GPLake-M (blue) and PCLake (red) macrophyte P content per depth (z : 1.5–5 m) with a constant hydraulic residence time of 100 d (set 1, 7, 8, 10 and 11, Table 1), assuming the scenario in GPLake-M of Vollenweider-type nutrient retention. For a range of z values, the models resemble 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.

Hosper and Jagtman (1990) and Meijer et al. (1999)).

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 $1\text{--}2.5\text{ m}^{-1}$ 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 $2.5\text{--}6\text{ m}^{-1}$. 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 ($5.5\text{--}40\text{ mm d}^{-1}$)

(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).

4.3. Societal and scientific relevance of GPLake-M

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's (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.

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 enclosure 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.

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. 2) and mathematical (Section 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 3.4). 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 underlying 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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.watres.2023.119950](https://doi.org/10.1016/j.watres.2023.119950).

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