

## Critical phosphorus loading of different types of shallow lakes and the consequences for management estimated with the ecosystem model PCLake

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### Abstract

Shallow lakes typically can be in one of two contrasting states: a clear state with submerged macrophytes or a turbid state dominated by phytoplankton. Eutrophication may cause a switch from the clear to the turbid state, if the phosphorus loading exceeds a critical value. Recovery of the clear state is difficult as the critical loading for the switch back during oligotrophication is often lower. A system of interacting ecological processes makes both states stabilize themselves causing the observed hysteresis. The ecosystem of shallow lakes is analysed with PCLake, a dynamic model of nutrient cycling and biota – including phytoplankton, macrophytes and a simplified food web. The model was used to calculate the switchpoints in terms of critical phosphorus loading levels for a number of lake types. It turned out that the predicted critical phosphorus loadings differ per lake type, e.g. they decrease with lake area, mean depth and retention time, increase with relative marsh area and fishing intensity, and differ per sediment type. The findings were grossly comparable with empirical evidence. These outcomes were also used to build a metamodel. The results may be useful for lake management, by comparing the critical loadings for a given lake with the actual loading. If the actual loading clearly exceeds the upper switchpoint, nutrient reduction measures are recommended. If the loading approaches the upper switchpoint, or is in the intermediate range, a manager could try to increase the critical loading values of the lake, e.g. by hydromorphological measures. If the loading is well between the two switchpoints, an alternative is to force a switch by direct food web management.

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### Introduction

Evidence for the existence of alternative stable states in ecosystems is increasing (Beisner et al. 2003). These

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state shifts are referred to as regime shifts (Scheffer and Carpenter 2003) and have been observed in a range of ecosystems, e.g. the shift from a hard coral dominance to macroalgae dominance on coral reefs (Hughes 1994), the shifts from tropical forests to Savanna grasslands (Sternberg 2001) and the shifts from clear water to turbid water in temperate shallow lakes (Scheffer et al. 1993; Carpenter 2003). Transitions between alternative states are driven by gradual changes in a stressor, such as nutrient availability or predation pressure. The response to an increase of this driver is often different from the response to a decrease of that driver, a phenomenon known as hysteresis. This is related to the resilience of an ecosystem: its capacity to withstand disturbances without shifting to a qualitatively different state (Holling 1973).

### Alternative stable states in shallow lakes

Shallow lakes are known to be in one of two contrasting equilibrium states: a clear state with submerged macrophytes or a turbid state dominated by phytoplankton (Timms and Moss 1984; Jeppesen et al. 1990a; Scheffer et al. 1993; Carpenter 2003). Several factors determine which state prevails in a certain case. A general constraint is set by the external nutrient loading. At a very high loading, only the turbid state is stable, whereas the opposite is true for very low loadings. In the intermediate range, both states may exist and switches between the two states are possible. Because both states possess a number of self-stabilizing buffering mechanisms, the system shows hysteresis: the critical loading level at which a shift occurs is dependent on the initial state of the system. The shift from turbid to clear occurs at a much lower loading level than the opposite one. The phytoplankton-dominated turbid state is generally considered as undesirable, because natural communities characterized by macrophytes and a rich fish fauna disappear and biodiversity decreases.

### Regime shifts in shallow lakes

Although shifts in alternative stable states in shallow lakes have been observed to be predominantly triggered by changes in nutrient loading (Meijer et al. 1999a), more often more than one mechanism is involved in the occurrence of alternative stable states in nature (Bachmann et al. 1999; Gulati and Van Donk 2002; Carpenter 2003; Ibelings et al. 2007). Several authors have derived critical nutrient loadings or (mostly) in-lake concentrations from empirical information (Lijklema et al. 1989; Hosper 1997; Portielje and Van der Molen 1999). Direct empirical data on individual lakes shifting between the clear and turbid states are scarce, but some information can be derived from multi-lake data sets

(Jeppesen et al. 1990a). As biomanipulation generally can be effective in the ‘intermediate’ phosphorus range only, biomanipulation experiments can also supply information about critical phosphorus levels (Jeppesen et al. 1997; Meijer et al. 1999a; Gulati and Van Donk 2002). In order to meet one of the core targets of the European Water Framework Directive, fresh water bodies throughout Europe need to improve their ecological status. For shallow lakes, a ‘good’ ecological status is considered as associated with a clear, macrophyte-dominated state. As nutrient load with phosphorus and nitrogen constitutes the biggest obstacle to the restoration and preservation of a ‘good’ ecological status, universal guidelines for critical nutrient loadings are called for. Most of the above-mentioned empirical findings, however, are highly time- and space-specific, making it difficult to derive general guidelines for water managers.

### The ecosystem model PCLake compared to other models

The role of nutrient loading in the establishment of alternative stable states and the effect of hysteresis can be modelled by the ecosystem model PCLake (Janse 1997, 2005). This dynamical model combines a description of the dominant biological components of shallow lake ecosystems with a description of a closed nutrient cycle. Empirical regression models based on multi-lake data sets formed an early generation of lake eutrophication models, relating the external nutrient loading to, among others, TP and TN concentrations, chlorophyll-*a* levels and transparency (Reckhow and Chapra 1983; Hosper 1997). These models remain very useful to give an estimate of the trophic state and possible algal biomass of a lake, but they are essentially not apt for predictions for situations where aquatic macrophytes play a role. Later, many dynamic, process-oriented, eutrophication models were developed, differing in complexity and in the factors and variables included (for overviews see for instance Jorgensen 1995, 1999). Other models focus on subsystems, or elaborate on general mechanisms, like minimodels (Scheffer 1998). PCLake differs from most of the other dynamic eutrophication models in that it incorporates a broad range of functional groups, i.e. macrophytes, zooplankton, phytoplankton, planktivorous and piscivorous fish, and that it puts equal emphasis on the biotic and abiotic components. Recently, PCLake has been applied in the context of the impact of climate change on shallow lakes (Mooij et al. 2005, 2007, 2008).

### Objectives of this paper

In the present study we will analyse the dynamics and the long-term behaviour of the model PCLake at

different nutrient loadings. In addition, we determined how the critical nutrient loading depended on specific lake characteristics, allowing for a practical application by water managers. Hence, the objectives of this paper are to:

1. estimate the critical phosphorus loadings that trigger a regime shift, both ‘forward’ and ‘backward’;
2. determine how these critical loadings depend on lake features and (combinations of) management factors;
3. identify the key features determining the regime shift;
4. test the predictions of the model against empirical lake data.

## Methods

### Model description

PCLake has been designed to simulate the main nutrient and food web dynamics of a non-stratifying lake in response to eutrophication and related restoration measures (Janse et al. 1992; Janse and Van Liere 1995a,b; Janse 1997, 2005). It was calibrated against nutrient, transparency, chlorophyll-*a* and vegetation data on >40 lakes and a systematic sensitivity and uncertainty analysis was performed (Aldenberg et al. 1995; Janse 2005). The model describes a completely mixed water body and comprises both the water column and the sediment top-layer (10 cm), with the most important biotic and abiotic components. Optionally, a wetland zone with helophytes can be added. No further horizontal (like depth variations) or vertical distinction within the lake is taken into account. Mathematically, the model is composed of a number of coupled differential equations, one for each state variable.

### State variables and underlying relationships

All biota are modelled as functional groups (Fig. 1). The main groups in the water phase are three groups of phytoplankton (‘diatoms’, ‘greens’ and ‘cyanobacteria’), zooplankton, planktivorous/benthivorous fish and piscivorous fish. Submerged macrophytes are included, consisting of a shoot and a root fraction. Further groups in the top-layer of the sediment are the settled fractions of the three types of phytoplankton as well as zoobenthos. For a detailed description of the way each of the functional groups is entered in the model, see Janse (2005).

### Default lake settings

Long-term simulations have been carried out for a hypothetical lake which may be considered as representative for

many Dutch shallow lakes. Its main characteristics are: mean depth = 2 m, fetch = 1000 m, areal hydraulic loading =  $20 \text{ mm d}^{-1}$  ( $7.2 \text{ m y}^{-1}$ ), no infiltration or seepage, no surrounding wetland zone, a lightly clayish sediment (30% dry matter, of which 10% organic matter, and 10% lutum of inorganic matter), and a fishing intensity of  $0.00137 \text{ d}^{-1}$  ( $0.5 \text{ y}^{-1}$ ). The simulated summer-averaged results after 20 years were used for the analyses. Dynamic simulations and previous experience showed that in most instances, a period of 20 years is, for practical purposes, in general sufficient for the model to come quite close to the (new) equilibrium situation, although a complete equilibration of the phosphorus levels may take a longer period (up to 50 years), dependent on the starting conditions and input variables. For each parameter combination the model was evaluated for P loading rates ranging from 0.1 to  $20 \text{ g P m}^{-2} \text{ d}^{-1}$  in 35 steps, for both the turbid and the clear initial condition. The critical loading values were calculated by linear interpolation. A summer-averaged vegetation coverage of 20% has been chosen as a criterion for critical loading; but as the relations are mostly quite steep, the exact value does not matter very much.

### Assessing the impact of different lake characteristics on critical nutrient loading

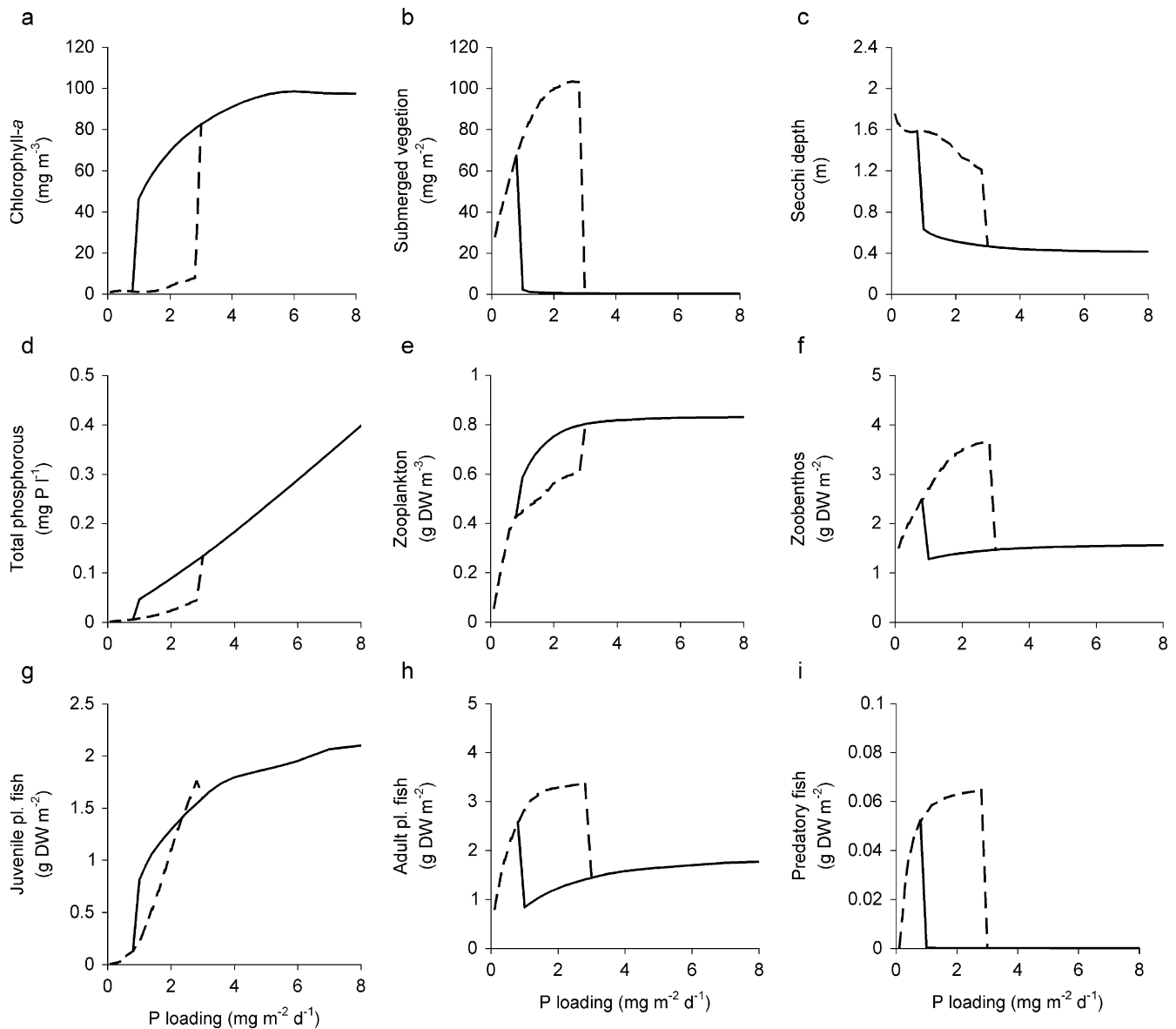
The same kind of simulations was carried out for different combinations of other lake features. The following factors were varied, both one-at-a-time and combined (*Note*: an asterisk (\*) denotes the value for the ‘default lake’):

- Hydraulic loading rate: 10, 20\*, 40 or  $80 \text{ mm d}^{-1}$ .
- Water depth: 1, 1.5, 2\*, 3 or 4 m.
- Fetch: 100, 300, 1000\* or 3000 m.
- N/P ratio in loading: 10\* or  $3 \text{ g N g P}^{-1}$ .
- Marsh area: 0.001\*, 0.15, 0.3 or  $1.0 \text{ m}^2 \text{ marsh m}^{-2}$  lake.
- Sediment type: 1 = clay\*, 5 = peat, 6 = sand.
- Fishery rate: 0,  $0.00137^*$  or  $0.01 \text{ d}^{-1}$ , equivalent to  $0.5^*$  or  $3.65 \text{ y}^{-1}$ .

### Evaluation of the model by comparing current or historic loadings with simulated critical nutrient loading in actual lakes

By the same method, the switchpoints were calculated for each of the 43 lakes (mainly Dutch, and some in Belgium, Ireland and Poland) that were used in the calibration of the model, as well as 7 Danish and 2 Spanish lakes that were used for comparison (Janse 2005). Lake data were taken from the studies by Lijklema et al. (1989), Portielje and Van der Molen





**Fig. 2.** Simulations for an average shallow lake for a range of phosphorus loadings. All simulations have been done for two initial states, a clear-water state dominated by macrophytes (dashed lines) and a turbid state with a phytoplankton dominance (solid lines). Results are summer-averages after 50 years with the same loading conditions: (a) chlorophyll-*a*; (b) submerged vegetation; (c) Secchi depth; (d) total P; (e) zooplankton; (f) zoobenthos; (g) juvenile planktivorous fish; (h) adult benthivorous fish; and (i) predatory fish.

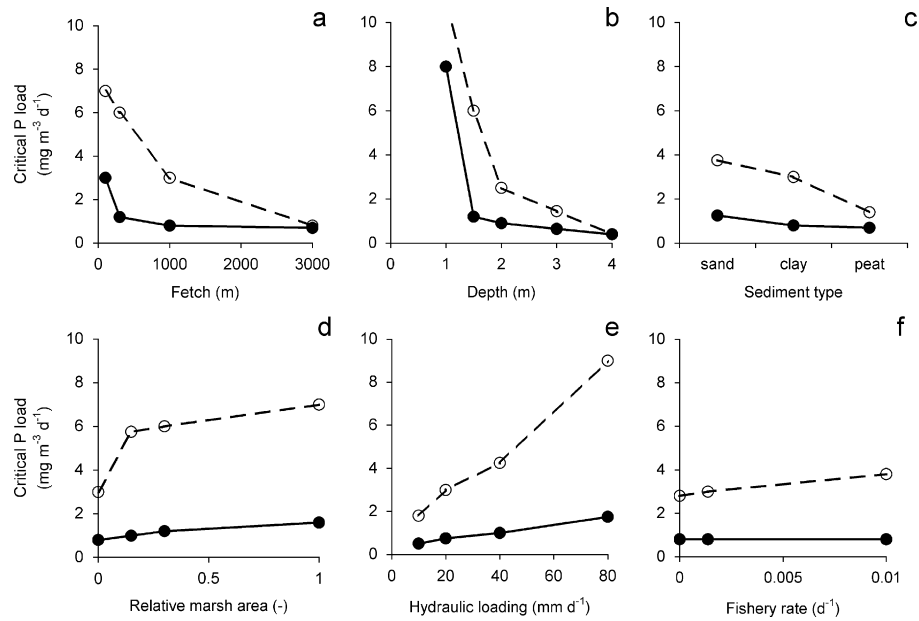
markedly (Fig. 3d). The critical load increases with (but less than proportional to) the hydraulic loading rate (Fig. 3e). Please note that, although in this context the factors are shown as independent of each other; in practice, nutrient loading and hydraulic loading rate are often positively correlated. A higher fishing rate tends to increase the critical loading, but the effect is modest (within the investigated range) and mainly confined to the ‘turbidification’ switchpoint (Fig. 3f). The relation with the N loading, when this nutrient is made limiting with P in excess ( $N/P$  ratio in loading =  $3 \text{ g g}^{-1}$ ), resembles the one for P limitation (graph not shown). For the ‘default lake’ the simulations indicate a critical N loading of ca.  $22 \text{ mg N m}^{-2} \text{ d}^{-1}$  for turbidification and ca.

$7 \text{ mg N m}^{-2} \text{ d}^{-1}$  for restoration if N is the limiting nutrient (and assumed that no N fixation takes place).

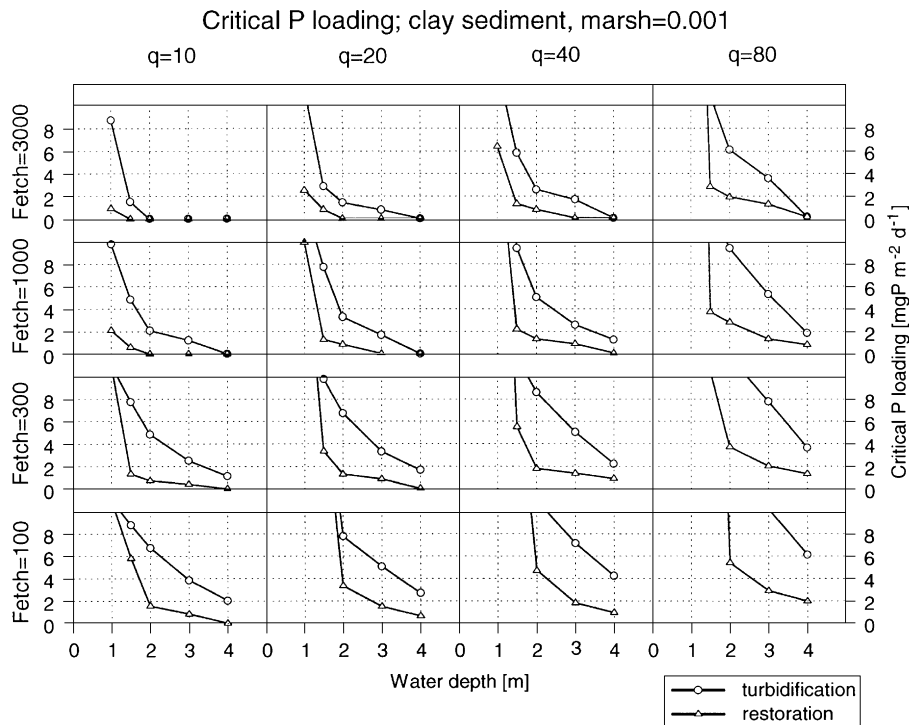
While in Fig. 3 the effect of the factors are shown independently, interacting effects are important, as shown in Fig. 4 where the effects of depth, fetch and hydraulic loading rate are combined for a lake with a clay sediment and no marsh zone.

### Regression analyses on the response of two critical loading values and lake characteristics

A linear regression analysis was performed of critical loading values for turbidification and clarification



**Fig. 3.** Critical P-loadings (mg P m<sup>-2</sup> d<sup>-1</sup>) for different types of lakes: (a) varying fetch (m); (b) varying water depth (m); (c) varying sediment type: (clay, peat, sand); (d) varying relative marsh area; (e) varying hydraulic loading rate (mm d<sup>-1</sup>); (f) varying fishery rate (d<sup>-1</sup>). The different lake characteristics were varied one by one, keeping the others at the value for the 'default lake'. All simulations have been done for two initial states, a clear-water state dominated by macrophytes (dashed lines) and a turbid state with a phytoplankton dominance (solid lines).



**Fig. 4.** Critical phosphorus loading levels dependent on lake characteristics. Each composite graph shows the influence of the factors water depth (m), fetch (m) and water inflow rate (q, mm d<sup>-1</sup>) on the critical loading levels (mg P m<sup>-2</sup> d<sup>-1</sup>). Other characteristics as for the default lake for all panels: clay sediment, no marsh zone. All simulations have been done for two initial states, a clear-water state dominated by macrophytes ('turbidification', circles) and a turbid state with a phytoplankton dominance ('restoration', triangles).



(as natural logarithm) on the variables reciprocal water depth, fetch, hydraulic loading, marsh area and sediment type, both with and without two-factor interaction terms (Table 1). Sediment type was included as two dummy variables (0/1), viz. 'Clay' and 'Peat'; if both are 0 the sediment type is 'Sand'. Excluding interactions (Table 1A), all coefficients were significant for both critical loadings, except for the intercept for the lower switchpoint. The regression explained 61 (turbidification) resp. 72% (clarification) of the variation. Lake depth, water inflow rate and fetch are the most influential, followed by the marsh area and the sediment type. Including interactions, the fraction explained variation (adjusted *R*-squared) increased to 0.71 (turbidification) resp. 0.78% (clarification). Nearly all factors and interactions were significant (Table 1B), which indicates that the impact of each factor is influenced by the other ones. Analysis of residuals, as well as visual inspection of conditional plots (Fig. 4), revealed that the linear model described the relations far from perfectly, despite the high regression coefficients. Other transformations of the variables that we tried did not improve this. It thus remains difficult to capture the relation between critical loadings and lake features in a simple formula. The critical loading of a particular lake type might better be estimated from conditional graphs or by an additional model run.

Because the regression model could not handle the strong nonlinearities in the output, a so-called metaverison was developed for a quick assessment of the critical P loadings per (type of) lake. The results of a large number of simulations were stored in a database and the critical loadings (the limit for >5% cover of submerged macrophytes) were determined. Values for 'new' cases can now be estimated from the database by a Matlab<sup>TM</sup> interpolation procedure. The model is available at the website <[www.mnp.nl/modellen/pclake](http://www.mnp.nl/modellen/pclake)> (in Dutch). Users can enter the most important characteristics (as listed under 'Methods') of their lake of interest. The model estimates the critical loading values (in  $\text{mg P m}^{-2} \text{d}^{-1}$ ) and/or the corresponding summer-averaged P concentrations ( $\text{mg P L}^{-1}$ ).

### Simulated critical nutrient loading for the lakes in the data set, compared with the current or historic loading

In 11 out of the 43 calibration lakes, the observed phosphorus loading was lower than the modelled switchpoint for clarification, in 6 lakes the observed loading was between the two thresholds, and in the remaining 26 lakes the loading was higher than the turbidification switchpoint, in 12 of the latter lakes with a factor 5 or more (Table 2). For the majority of lakes, the observed loadings correspond to their actual state,

clear or turbid, except for two Danish and one Spanish lake, that are turbid despite of a P loading lower than the calculated critical level. Part of the data for the two Spanish lakes (#51, 52) were rough estimates. One of the Danish lakes (#49) had recently been restored but submerged vegetation failed to develop for uncertain reasons. Some lakes (denoted by a C in brackets) cannot unambiguously be classified, as they have distinct vegetated and unvegetated parts.

## Discussion

### Why does PCLake show hysteresis?

The hysteresis effect as shown by the simulations can be explained by several positive feedback mechanisms present in the model. The crux is that both the phytoplankton and the submerged macrophytes, directly or indirectly, promote their own favourite environmental conditions and deteriorate the conditions for the other, giving rise to two stable states in an intermediate range of the nutrient loading.

Light limitation is the main factor for aquatic macrophytes: they need clear water with light reaching the bottom. At the same time they keep the water clear, by several mechanisms: their specific light absorption is low (much lower than that of phytoplankton), they reduce resuspension by stabilizing the sediment, and they hamper phytoplankton growth by uptake of nutrients (Ozimek et al. 1990; Van Donk et al. 1993; Jeppesen et al. 1998). Furthermore, they promote the top-down control of phytoplankton by favouring predatory fish. Phytoplankton, on the other hand, wins the competition in darker or deeper waters, as it needs less light for growth (Sand-Jensen and Borum 1991). Once dominant, it keeps the water turbid because of its high light absorption and because it keeps the nutrients recycling in the water column. The unvegetated sediment is more subject to resuspension due to wind action (waves) and to stirring by benthivorous fish. So there are three main factors or pathways working together: light, nutrients and food web effects.

Other mechanisms have been demonstrated or suggested that may add to this picture, like the release of allelopathic substances by macrophytes that hamper algal growth (Van Donk and van de Bund 2002; Gross 2003; Mulderij et al. 2005a,b), and a shift towards bigger zooplankton species in clear water once relieved from predation (e.g. Perrow et al. 1999). Other mechanisms, on the other hand, may weaken the picture, such as the development of defence mechanisms by phytoplankton to reduce grazing loss (Van der Stap et al. 2007), and possible shifts in fish species composition. Although the model results are in agreement with Diehl and Kornijów (1998) with a higher benthivorous

**Table 1.** Regression analysis for the effect of lake characteristics on the log-transformed critical P loading values ( $\text{mg P m}^{-2} \text{d}^{-1}$ )

Factor	Turbidification switchpoint			Clarification switchpoint		
	Value	S.E.	Pr(> t )	Value	S.E.	Pr(> t )
(A) Regression without interactions						
Intercept	−0.0524	0.0668	0.4322	−2.3293	0.0767	<0.0001
Clay	−0.1028	0.0265	0.0001	−0.3241	0.0304	<0.0001
Peat	−0.2962	0.0265	<0.0001	−0.5295	0.0304	<0.0001
CQIN	0.0235	0.0008	<0.0001	0.0265	0.0009	<0.0001
invDEPTH	2.9668	0.0811	<0.0001	4.9804	0.0931	<0.0001
FETCHkm	−0.4560	0.0189	<0.0001	−0.6109	0.0217	<0.0001
FMARSH	0.6319	0.0565	<0.0001	0.9570	0.0649	<0.0001
Residual S.E.	0.9475			1.088		
d.f.	1913			1913		
R <sup>2</sup>	0.6125			0.7232		
(B) Regression including two-factor interactions						
Intercept	0.4952	0.1101	<0.0001	−2.1930	0.1132	<0.0001
Clay	−0.2547	0.0695	0.0003	−0.7475	0.0822	<0.0001
Peat	−0.6186	0.0695	<0.0001	−1.0349	0.0822	<0.0001
CQIN	0.0194	0.0019	<0.0001	0.0292	0.0015	<0.0001
invDEPTH	2.3666	0.1626	<0.0001	4.8943	0.1526	<0.0001
FETCHkm	−1.3417	0.0483	<0.0001	−1.4504	0.0572	<0.0001
FMARSH	1.1929	0.1449	<0.0001	1.7396	0.1715	<0.0001
Clay:CQIN	0.0018	0.0009	0.0386	0.0049	0.0010	<0.0001
Clay:invDEPTH	0.2675	0.0867	0.0021	0.6540	0.1026	<0.0001
Clay:FETCHkm	−0.1010	0.0202	<0.0001	−0.1687	0.0239	<0.0001
Clay:FMARSH	0.1348	0.0604	0.0258	0.1818	0.0715	0.0110
Peat:CQIN	0.0040	0.0009	<0.0001	0.0061	0.0010	<0.0001
Peat:invDEPTH	0.6245	0.0867	<0.0001	0.8266	0.1026	<0.0001
Peat:FETCHkm	−0.2449	0.0202	<0.0001	−0.2407	0.0239	<0.0001
Peat:FMARSH	0.2748	0.0604	<0.0001	0.2357	0.0715	0.0010
CQIN:invDEPTH	0.0068	0.0026	0.0097	–	–	n.s.
CQIN:FETCHkm	0.0039	0.0006	<0.0001	0.0052	0.0007	<0.0001
CQIN:FMARSH	−0.0058	0.0018	0.0018	−0.0133	0.0022	<0.0001
invDEPTH:FETCHkm	0.9209	0.0618	<0.0001	0.7701	0.0731	<0.0001
invDEPTH:FMARSH	−1.0252	0.1850	<0.0001	−0.7373	0.2189	0.0008
FETCHkm:FMARSH	0.3228	0.0430	<0.0001	0.2357	0.0509	<0.0001
Residual S.E.	0.8274			0.9789		
d.f.	1899			1899		
R <sup>2</sup>	0.7067			0.7775		

‘Clay’ and ‘Peat’ are dummy variables for the sediment type with the value 0 or 1 (if both 0, the sediment type is ‘Sand’); CQIN = hydraulic loading rate ( $\text{mm d}^{-1}$ ); invDEPTH = inverse water depth ( $\text{m}^{-1}$ ); FETCHkm = fetch (103 m); FMARSH = relative marsh area (–); n.s. = not significant.

fish biomass in the vegetated state related to a higher food supply of zoobenthos, in clear lakes a shift may occur towards fish species that are better in feeding between the vegetation (Jeppesen et al. 1998). But the main point holds that the bioturbation effect of benthivorous fish is minimized in the vegetated state. Likewise, the piscivorous fish might be underestimated by the model in the turbid state, as a shift may occur to species that are not or less dependent on vegetation, be it with a lower biomass (Klinge et al. 1995). The representation of the fish groups is probably too much

a generalization. Another simplification is the lumping of the organic detritus in one pool, since algae-derived and macrophyte-derived detritus may differ in their metabolic properties. All these mechanisms have not been included in the model, as they are considered of secondary importance and in order to keep the complexity within limits. Furthermore, uncertainties or natural variations in parameter values propagate in uncertainties (confidence limits) around the critical loading levels calculated by the model, estimated at about  $\pm 50\%$  (Janse 2005).



**Table 2.** Comparison for the lake dataset

#	Name	Area (ha)	Depth (m)	Fetch <sup>a</sup> (m)	Marsh part <sup>b</sup> (m <sup>2</sup> m <sup>-2</sup> )	Connected <sup>c</sup>	Sediment type <sup>d</sup>	Inflow (mm d <sup>-1</sup> )	Retention time (d)	Threshold P-load for restoration (mg m <sup>-2</sup> d <sup>-1</sup> )	Threshold P-load for turbidification (mg m <sup>-2</sup> d <sup>-1</sup> )	Observed P-load (mg m <sup>-2</sup> d <sup>-1</sup> )	Loading category (L/M/H/HH) <sup>e</sup>	Current state (Clear/ Turbid)
1	Hollands-Ankeveen	85	1.3	922	0.1	n	5	3.5	357	0.82	3.09	0.14	L	C
2	Bergse Achterplas	41	2	640	0.001	n	1	19.3	103	1.12	2.67	8.1	H	T
3	Bergse Voorplas	60	2	775	0.001	n	1	21.1	95	1	2.48	8.16	H	T
4	Beulakerwijde	1300	1.8	3606	0.001	y	5	10	175	0.22	0.32	5.12	HH	T
5	Botshol, Grote Wije	53	2	731	0.1	n	5	12.9	157	1.27	2.3	0.88	L	C
6	Kaag, Norremeer	320	2.4	1789	0.001	y	1	109.6	22	3.07	5.29	96.71	HH	T
7	Langeraar, Geerplas	28	1.9	529	0.001	y	5	4.4	431	0.29	1.03	1.46	H	T
8	Loosdrecht	940	2.2	3065	0.001	n	5	8.4	256	0.18	0.27	0.89	H	T
9	Naarden, Grote Meer	170	1.3	1304	0.1	n	6	10	125	2.98	5.91	0.68	L	C
10	Naarden, Wijde Blik	38	1	612	0.1	n	6	5.2	193	4.31	5.69	0.68	L	C
11	Reeuwijk, Nieuwenbroek	104	1.8	1020	0.001	n	5	5.5	327	0.25	0.75	1.1	H	T
12	Nieuwkoop, Noordeinder	150	3	1225	0.001	n	5	6.3	475	0.15	0.54	0.85	H	T
13	Nieuwkoop, Zuideinder	100	3	1000	0.001	n	5	27.4	110	0.72	1.28	1.75	H	T
14	Reeuwijk, Elfhoeven	109	2	1044	0.001	n	5	16.4	122	0.6	1.09	5.48	HH	T
15	Westeinderplassen	852	2.8	2919	0.001	y	6	20.7	135	0.78	0.98	12.88	HH	T
16	Zuidlaardermeer	600	1	2449	0.001	y	6	43.5	23	6.06	9.48	11.95	H	T
17	Nannewijld	100	1	1000	0.001	n	5	6.8	148	0.87	3.95	0.96	M	T
18	Blankaart (B)	30	1	548	0.001	n	1	71.4	14	12.33	16.95	18.7	H	T
19	Maten 13 (B)	3	0.8	171	0.001	n	6	92	8	68.71	73.05	9.32	L	C
20	Visvijver (B)	1	0.8	86	0.001	n	1	3	267	3.3	3.3	0.16	L	C
21	Gara, South (IR)	203	1	1425	0.001	n	5	137	7	26.51	29.01	10.18	L	C
22	Maumwee (IR)	27	2	520	0.001	n	5	54.8	37	2.07	3.72	1.84	L	C
23	Mullagh (IR)	35	2.3	592	0.001	n	5	4.7	489	0.22	0.91	0.83	M	(C)
24	Pollaphuca (IR)	1974	6.8	4443	0.001	n	5	33.3	204	0.08	0.08	1.83	HH	(C)
25	Ramor (IR)	741	3	2722	0.001	n	5	48.3	62	0.6	1.26	6.36	HH	T
26	Luknajno (PL)	630	1.8	2510	0.1	n	6	3.2	567	0.54	0.57	0.11	L	C
27	Waalboezem	78	3.8	883	0.001	n	1	20	190	0.36	1.14	11.23	HH	T
28	Binnenbedijkte Maas	158	4	1257	0.001	n	1	14.6	274	0.17	0.67	5.48	HH	T
29	Brielse Meer	491	5.5	2216	0.001	y	1	40.7	135	0.1	0.1	17.26	HH	T
30	Volkerak	4570	5	6760	0.001	y	6	45.9	109	0.58	0.57	12.99	HH	(C)
31	Zoommeer	1580	6	3975	0.001	y	6	105.6	57	0.76	0.75	14.13	HH	(C)
32	Oude Venen 2	10	1.3	316	0.001	y	5	17.1	73	2.37	5.1	6.84	H	T
33	Veluwemeer	3240	1.6	5692	0.05	y	2	26.7	58	1.56	3.42	3.73	H	(C)
34	Wolderwijd	1800	1.9	4243	0.001	y	6	16.5	117	0.95	1.62	1.37	M	(C)
35	Nulder nauw	870	2.1	2950	0.001	y	6	47	44	1.78	2.71	7.53	H	T
36	Drontermeer	540	1.3	2324	0.05	y	6	69	18	6.48	10.28	9.84	M	T
37	Braassemermeer	452	3.9	2126	0.001	y	1	62.9	62	0.81	1.64	37.26	HH	T
38	Langeraar, Noordeinde	75	1.9	866	0.001	y	5	3.4	558	0.19	0.66	2.6	H	T
39	Mooie Nel	116	4.5	1077	0.001	y	6	88.1	51	1.19	1.64	179.45	HH	T
40	Het Hol	30	1	548	0.1	n	5	6.4	157	2.83	7.01	0.87	L	C
41	Kortenhoef	193	1.2	1389	0.001	n	5	5.9	204	0.45	1.38	4.58	H	T

Table 2. (continued)

#	Name	Area (ha)	Depth (m)	Fetch <sup>a</sup> (m)	Marsh part <sup>b</sup> (m <sup>2</sup> m <sup>-2</sup> )	Connected <sup>c</sup>	Sediment type <sup>d</sup>	Inflow (mm d <sup>-1</sup> )	Retention time (d)	Threshold P-load for restoration (mg m <sup>-2</sup> d <sup>-1</sup> )	Threshold P-load for turbidification (mg m <sup>-2</sup> d <sup>-1</sup> )	Observed P-load (mg m <sup>-2</sup> d <sup>-1</sup> )	Loading category (L/M/H/HH) <sup>e</sup>	Current state (Clear/ Turbid)
42	Stichts-Ankeveen	100	1	1000	0.1	n	5	3.3	303	1.29	3.63	0.09	L	C
43	Frisian Lakes (average)	518	1.4	2276	0.001	y	5	9.3	147	0.42	0.79	3.9	H	T
44	Enso (DK)	11	1.9	326	0.001	n	3	27.1	70	2.4	5.91	0.05	L	C
45	Nederso (DK)	14	1.6	374	0.001	n	3	320	5	70	73.27	2.47	L	(C)
46	Soby (DK)	72	3	849	0.001	n	6	10.1	300	0.67	1.6	0.19	L	C
47	Hinge (DK)	91	1.2	954	0.001	n	3	60	20	8.13	13.03	8.49	M	T
48	Kvind (DK)	15	1.9	387	0.001	n	6	126.7	15	8.73	13.83	10.96	M	T
49	Lading (DK)	45	1	671	0.001	n	3	14.7	68	6.22	10.16	1.37	L	T
50	Silkeborg-Langso (DK)	46	2	678	0.001	n	6	250	8	21.28	24.68	18.63	L	T
51	Honda (SP)	9	1	307	0.001	n	3?	7.8	128	1.08	4.62	4.16	M	T
52	Nueva (SP)	27	1.5	521	0.001	n	3?	1.8	820	0.31	1.25	0.12	L	T

Data on lakes 1–43 were used for the calibration of the model, lakes 44–52 were only used for comparison (Janse 2005).

<sup>a</sup>Fetch is estimated as the square root of the water surface area.

<sup>b</sup>If the existence of a marsh zone connected to the lake is known from the data, it is taken as 0.1 or 0.05, otherwise set to a low value of 0.001.

<sup>c</sup>‘Yes’ means that the lake is known to receive a substantial water inflow from other lakes, otherwise ‘no’.

<sup>d</sup>Sediment types: 1 = clay, 3 = clay/sand, 5 = peat, 6 = sand.

<sup>e</sup>Actual loading with respect to the critical loading values. L = low, M-intermediate, H = high, HH = very high.

## How do the results for the lake features fit into this picture?

Increasing the fetch causes lower critical loading values in our model exercises. In the model, the factor fetch mainly figures in the resuspension and settling equation: a larger fetch makes the resuspension rate increase and the settling rate of algae and suspended solids decrease to mimic the greater influence of wind-induced waves in larger lakes.

The effect of depth on the model results can partly be explained by the dependence of submerged macrophytes on the under-water light climate: the exponential decrease of light intensity with depth sets a limit to the depth where plants can survive (Wetzel 2001; Spence 1982). Also the lower sedimentation losses in deeper shallow (non-stratified) lakes favour phytoplankton, as well as the longer retention time at a given hydraulic loading. On the other hand, the resuspension rate is lower in deeper shallow lakes, as well as the impact of benthivorous fish, and the greater mixing depth for nutrients and suspended solids reduces the maximum algal concentrations. The net effect, as it appears from the model results, is a marked decrease of the critical loading with depth.

An increase of the hydraulic loading (or water inflow rate), keeping the nutrient load constant (which is a theoretical exercise), increases the phytoplankton loss rate, thus reducing algal biomass (e.g. George et al. 2007) and favouring the competitive power of macrophytes that are fixed to the bottom, causing increased critical loading values in the model predictions. On the other hand, the loss factor zooplankton grazing is also reduced. Another effect is a shift within the phytoplankton from the slow-growing cyanobacteria to the faster growing diatoms and 'other' ('green') algae that can better compensate for the high dilution rate (Reynolds 1989). In practice, the hydraulic loading and nutrient loading are most often partly correlated, but for this analysis, the factors have been dealt with independently.

The factor sediment type is a composite factor, made up of the porosity, organic and lutum fractions in the upper sediment; lutum is again linked to Fe and Al fractions. Resuspension increases with porosity in the model, which may explain why life becomes more difficult for macrophytes going from sand to clay to peat lakes. The factor lutum acts in the same direction, as the higher lutum fraction in clay and peat sediments increases the amount of phosphorus that is retained in the system and recycled to the water column, promoting algal growth. The extra amount of organically bound nutrients in peat sediment also adds to the increased phosphorus availability.

The positive effect of a marsh zone in the predictions can be attributed to several mechanisms in the model: the addition of an extra sedimentation area, uptake of

nutrients by the marsh vegetation, extra opportunity for denitrification (Johnston 1991; Mitsch 1995) and the presence of a good habitat for predatory fish (modelled as a higher carrying capacity for this group) (Klinge et al. 1995). It is assumed in the model that the exchange of nutrients to the marsh zone goes via the lake, and that the initial composition of the lake and marsh sediment are equal. In practice, a marsh zone might temporarily also release nutrients, but the long-term effect in the model is a net retention.

## Empirical evidence for critical nutrient loadings in shallow lakes

The model results are consistent with the existing evidence that shallow lakes may have two alternative states, a clear-water state dominated by macrophytes and a turbid state dominated by phytoplankton (Timms and Moss 1984; Jeppesen et al. 1990a, 1997; Moss 1990; Scheffer 1990, 1998; Hosper 1997). The general constraint nutrient loading puts on the functioning of the lake ecosystem can be translated into critical nutrient loadings. For the majority of the 52 lakes for which we calculated critical nutrient loadings, the actual observed P loadings were indicative of their state, be it clear or turbid.

Based on empirical relations between chlorophyll-*a* and Secchi depth in Dutch lakes, Hosper (1997) derived critical TP concentrations of  $0.055 \text{ g P m}^{-3}$  for lakes with a depth of 1 m and  $0.023 \text{ g P m}^{-3}$  for depth = 2 m. These values relate to the 'backward' or clarification switch-point. The maximum ratios were comparable to those derived in a similar way by Lijklema et al. (1989) and Portielje and Van der Molen (1999). If non-algal turbidity is high, even lower TP values are required (Hosper 1997). In a study of shallow floodplain lakes in the Netherlands, Van Geest et al. (2003) find that a high macrophyte coverage may sometimes coincide with TP concentrations much higher than  $0.1 \text{ g m}^{-3}$ , even up to  $0.4 \text{ g m}^{-3}$ . They found, however, no significant relation with TP or TN concentrations or land use. As their data set was dominated by rather small lakes (range 0.01–45 ha), the impact of morphometry probably overshadowed the potential impact of nutrient status in this range. Moreover, many of these lakes were characterized by periodical drought and fish kills, and probably in a transient state in which the food web is not yet in equilibrium with the nutrient loading. This might explain a macrophyte dominance at higher TP.

Jeppesen et al. (1990a) concluded from a multi-lake study on Danish lakes that shallow lakes >3 ha were generally macrophyte-dominated at TP levels <ca.  $0.05 \text{ g P m}^{-3}$  and turbid at levels >ca.  $0.125 \text{ g P m}^{-3}$ , with alternative states possible at intermediate levels. In small lakes (<3 ha) the upper limit could be substantially higher (the highest data point with macrophytes

was  $0.65 \text{ mg P m}^{-3}$ ). In contrast to the Dutch lakes, the low-TP lakes were generally dominated by green algae instead of cyanobacteria. The authors suggest a relation with the generally higher winter and spring temperatures in the Netherlands; it could possibly also be related to a generally longer retention time. From these findings, together with the results of several whole-lake biomanipulation experiments, the authors conclude that the threshold level for long-term effects of biomanipulation in lakes  $> 10 \text{ ha}$  (not severely limited by nitrogen) is ca.  $0.10$  ( $0.08$ – $0.15$ )  $\text{g P m}^{-3}$ . For the Danish situation, this corresponds to loadings of  $0.5$ – $2.0 \text{ g P m}^{-2} \text{ y}^{-1}$ , depending on lake morphometry and flushing rate. The authors state that values between  $1$  and  $2 \text{ g P m}^{-2} \text{ y}^{-1}$  refer to lakes with a high flushing rate, but this is not further quantified. They add that in small lakes ( $< 3 \text{ ha}$ ) the threshold level may be higher because of more favourable conditions for submerged macrophytes and piscivorous fish. Based on some more biomanipulation experiments in later years, Jeppesen et al. (1997) reduce the threshold TP concentration somewhat to  $0.050$ – $0.10 \text{ g P m}^{-3}$ . In case of nitrogen limitation, the threshold P level is higher.

In general terms, these findings agree with conclusions drawn on basis of biomanipulation experiments in other European lakes: a critical P loading (roughly estimated in the range of  $0.6$ – $0.8 \text{ g m}^{-2} \text{ y}^{-1}$ ) should not be exceeded for biomanipulation to be effective (Benndorf 1987; Benndorf and Miersch 1991). Only if the P loading is below this threshold will top-down induced reduction of P concentrations via sedimentation, translocation (vertical migration of grazers) and P incorporation into grazer biomass result in a sustainable reduction of phytoplankton in deep stratified lakes (Benndorf et al. 2002). If P loading is higher, a combined strategy, load reduction down to the threshold, further improvement of water quality by biomanipulation, seems most promising and cost effective (Benndorf 1990, 2005).

Biomanipulation experiments in the Netherlands were less conclusive on the definition of critical nutrient loadings (Meijer et al. 1994, 1999a; Meijer 2000), although there was a tendency that the chance for long-term success of a biomanipulation measure decreased with higher P levels. The authors conclude that in the initial phase of the restoration, zooplankton grazing, once relieved from fish predation, plays a key role in getting clear water in spring. If vegetation then develops, its stability depends on other factors, like its resistance to herbivory and nitrogen limitation of the phytoplankton, and the presence of piscivorous fish.

Following a different approach, based on an empirical relation between TP concentration and total fish biomass, and an estimate of maximum piscivorous fish biomass, Klinge et al. (1995) derived a maximum P concentration for a clear, mesotrophic, vegetation-dominated lake in which pike is the main predator, of

$0.1$ – $0.2 \text{ mg L}^{-1}$ . Above this limit, the balance between bottom-up and top-down forces is disturbed and the lake shifts to the turbid state void of vegetation.

For a limited number of cases, i.e. lakes that have switched in the past between the clear and the turbid state, estimates have been made of their critical loading, based on available information. The Swedish lakes Takern and Krankesjön (average depth  $1.0$  and  $1.5 \text{ m}$ , respectively) both shifted several times between both states in the course of the last century, probably due to the direct or indirect effects of water level fluctuations ( $> 0.5 \text{ m}$ ). Both lakes had low TP concentrations: L. Takern  $0.031 \text{ mg P L}^{-1}$ , L. Krankesjön  $0.02$ – $0.06 \text{ mg P L}^{-1}$  (Blinndow 1992; Blindow et al. 1993). In another lake switching between clear and turbid state, Lake Botshol in the Netherlands, the critical loading of the lake was estimated as  $0.3 \text{ g P m}^{-2} \text{ y}^{-1}$  ( $= 0.8 \text{ mg P m}^{-2} \text{ d}^{-1}$ ); the data do not allow a conclusion about a possible difference between forward and backward switchpoints. The PCLake model calculates somewhat higher values of  $2.3 \text{ mg P m}^{-2} \text{ d}^{-1}$  (forward) and  $1.3 \text{ mg P m}^{-2} \text{ d}^{-1}$  (backward) (Table 2). The cause of the switches in this small peat lake has been reported as differences in nutrient leaching from the surrounding peatland between wet winters (high leaching) and dry winters (lower leaching) (Rip et al. 2005).

Lake Veluwe, also in the Netherlands and belonging to the ‘Randmeren’, represents the littoral zone of an originally larger lake (the ‘Randmeren’ were created when large parts of lake IJssel were reclaimed in the 1950s and 1960s; lake IJssel itself originates from embankment of a former estuary in 1932). Lake Veluwe started in the clear state, switched to the turbid state in the 1960s as a result of eutrophication, and was restored to the clear state in the 1990s due to a combined management strategy (phosphorus diversion, flushing, fishery). Based on observed TP levels during switchpoints, combined with water and nutrient budgets, a model study and other ecological information, Meijer et al. (1999b) estimate the critical TP concentration for a stable clear-water state at  $0.10$ – $0.15 \text{ mg P L}^{-1}$  and the critical loading at about  $1.0 \text{ g P m}^{-2} \text{ y}^{-1}$  ( $= 2.7 \text{ mg P m}^{-2} \text{ d}^{-1}$ ). The tentative values of  $3.4 \text{ mg P m}^{-2} \text{ d}^{-1}$  (forward) and  $1.6 \text{ mg P m}^{-2} \text{ d}^{-1}$  (backward) calculated by PCLake (see Table 2) are in the same range. In a later analysis on this same lake, Ibelings et al. (2007) derived TP concentrations of  $> 0.1 \text{ mg P L}^{-1}$  for the turbid state and  $0.04$ – $0.06 \text{ mg L}^{-1}$  for the stable clear-water state.

Based on historical reconstructions of the former ‘clear state’ and other ecological studies in the Dutch Zuidlaardermeer (Klinge et al. 2000), Klinge (unpublished results) estimates the maximum permissible loading for restoration of this lake at  $0.7 \text{ g P m}^{-2} \text{ y}^{-1}$  ( $= 1.9 \text{ mg P m}^{-2} \text{ d}^{-1}$ ) in summer, and  $1.0$ – $1.5 \text{ g P m}^{-2} \text{ y}^{-1}$  ( $= 2.7$ – $4.1 \text{ mg P m}^{-2} \text{ d}^{-1}$ ) in winter (when retention is lower). This is lower than the restoration threshold derived by PCLake of  $6.1 \text{ mg P m}^{-2} \text{ d}^{-1}$ . The non-algal turbidity of the inflowing

stream water has possibly been underestimated in this calculation.

In some cases, one can only speculate about the causes of a (periodical) switch of a particular lake (Scheffer 1998). For some lakes, it might even be an intrinsic feature caused by internal mechanisms: a gradual accumulation of nutrients in the vegetated state until the system can no longer absorb them, followed by a switch to the turbid state, a gradual wash-out of the nutrients due to the lower retention, until nutrient limitation makes the phytoplankton collapse again, followed by a switch back to the clear state. Another mechanism could be the gradual build-up of sediment organic matter in the clear state, causing anaerobic conditions and increased P release promoting a shift to the turbid state, in which the sediment organic matter decreases again. Van Nes et al. (2007) speculated on this using two minimodels, and concluded that such cycles will only occur in particular cases. The plausibility of these switches and the ranges of their possible occurrence could also be explored by means of PCLake simulations, for other combinations of mechanisms as well. In general, the above-mentioned observations indicate that the critical P values are dependent on water depth and other lake features.

### Impact of different lake characteristics on critical nutrient loading, comparison with empirical information

The model predicts that smaller lakes are more favourable to macrophytes than larger ones, in agreement with observations in the field (e.g. Van Geest et al. 2003). Higher settling and lower resuspension rates in small lakes (less wave action) is the explanatory mechanism in PCLake. Although the prediction is in agreement with observations, other mechanisms than this one may contribute to the impact of lake size. Wind or wave stress may hamper vegetation growth or survival directly as well. Other mechanisms are related to the generally greater relative shore length in small lakes, shore length and lake size often being strongly correlated. Small lakes tend to have more shallow parts along the shores which are more favourable places for colonization by macrophytes that can spread over the rest of the lake (Van den Berg et al. 1999). A larger shoreline, often partly overgrown with helophytes, may also favour top-down effects, by enhancing piscivorous fish (mainly pike) and by providing a refuge to zooplankton (Jeppesen et al. 1990b; Grimm 1989). Finally, Jeppesen et al. (1990b) suggested that natural winter fish kills due to oxygen depletion occur more frequently in small lakes. However, fish kills might also be related to factors like shallowness or low water transport that are correlated with size. In addition, Van

Geest et al. (2003) report more frequent fish kills in small lakes, but again, the relation with size is probably indirect, as the fish kills were related to periods of low water level in summer. Anyway, the occurrence of fish kills acts as a natural biomanipulation experiment, that could certainly promote vegetation dominance in certain lakes. Van Geest et al. (2003) conclude, from a cross-analysis study of shallow floodplain lakes in the Netherlands, that the colonization argument and the top-down mechanisms are the most likely explanations for the negative impact of lake area on submerged macrophytes dominance. In their data set, submerged macrophyte cover decreased significantly with the surface area, depth and age of the lakes.

The dominating effect of the water depth, viz. a lower chance for the survival of submerged macrophytes with increasing depth, is consistent with well-documented empirical studies on the maximum colonization depth of macrophytes as a function of water transparency (Spence 1982; Chambers and Kalff 1985) reviewed in Moss (1988) and Scheffer (1998a). These studies do not include very shallow and/or very turbid waters. The PCLake model predicts a sharp increase of the critical loadings at a water depth of 1 m or less, implying that these very shallow lakes have a high chance of maintaining their 'clear' state despite a rather high turbidity or nutrient level. The model seems a bit too optimistic in this respect, as compared to for instance studies in the Dutch Randmeren (Meijer et al. 1999b). A possible cause is that the model includes one prototypic macrophyte group, with the above-ground biomass equally distributed over depth and emerging in spring from overwintering parts. Species with other growth forms, like charophytes, that grow closer to the bottom, will be more vulnerable. Blindow (1992) showed that, although charophytes can grow to greater depths in clear water (due to their higher light affinity), angiosperms are in favour in more turbid water, as they have a greater part of their biomass near the surface. It is also recalled that the model uses the mean depth only, neglecting spatial differences.

In support of our results on the positive effect of a marsh zone on critical P loadings are the clear indications of a purifying effect of wetlands on adjacent lakes, see e.g. Johnston (1991), Mitsch (1995), Verhoeven and Meuleman (1999), among others. Richardson et al. (1997) conclude that natural wetlands may retain phosphorus loading of up to  $1\text{--}2\text{ g P m}^{-2}\text{ y}^{-1}$ . Artificial wetlands may perform even better, depending on their construction and management. The example of the Kis-Balaton wetland system (Somlyódy 1998), which was used to protect Lake Balaton (Hungary) by purifying the water of a river before it entered the lake, showed a considerable purifying effect, but at the same time demonstrated deteriorating effects of eutrophication on the natural wetlands themselves.

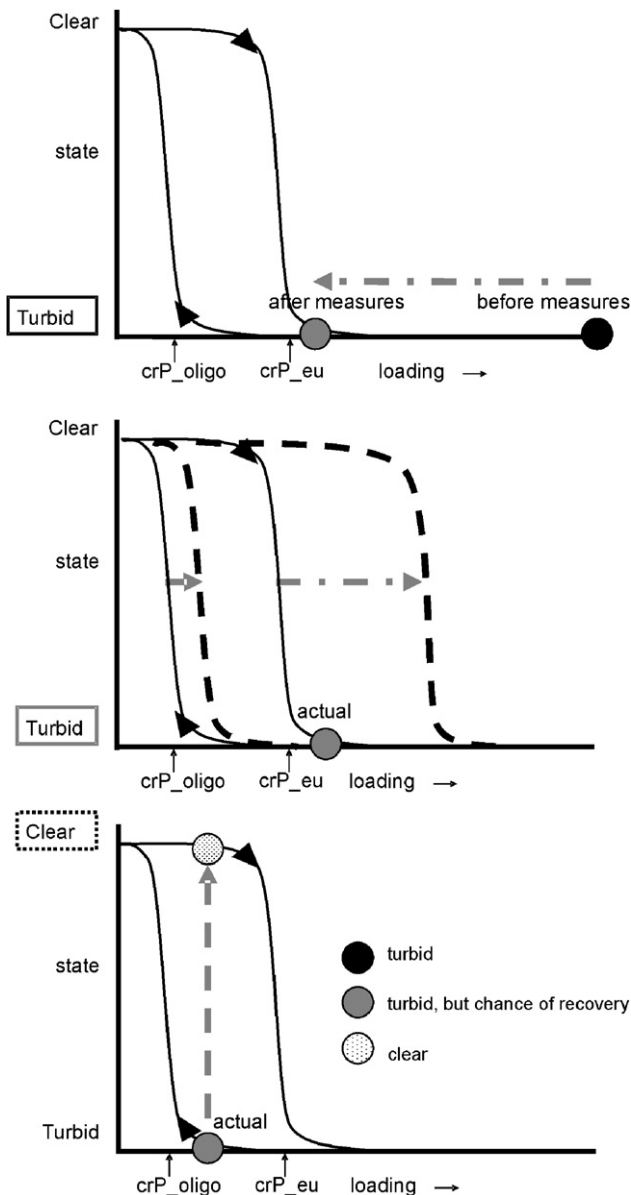


The model results comply with the general evidence that wetland zones should cover an extensive area to have a significant impact on water quality. Quantitative data about natural systems are rare, but the loss of former wetland areas and flood plains around for instance the Friesian lakes (in the north of the Netherlands) is suspected to have enhanced the shift of these lakes to the turbid state. These wetlands were the result of a naturally fluctuating water level, that has later been

fixed by means of water engineering works (Klinge et al. 1995).

### Management implications, including biomanipulation

Based on our analysis with PCLake on the relation between critical phosphorus loading and lake properties, we come to the following recommendations for improving lake transparency. The first step is to estimate the critical loading values and compare them with the actual P loading of your lake. This can be done with the available metamodel, which takes into account the effect of lake features on the critical phosphorus loadings. The metamodel is composed of a database of precalculated values of the critical loadings, performed for a lot of combinations of the main lake features, coupled to a Matlab<sup>TM</sup> interpolation routine. When using the metamodel, the uncertainties in both the original model and the interpolation procedure have to be kept in mind. The metamodel is available (in Dutch) on internet <[www.mnp.nl/modellen/pclake](http://www.mnp.nl/modellen/pclake)>. From here, there are four possibilities: (1) the actual loading is considerably larger than the critical loading at eutrophication: the only option is to decrease the external phosphorus loading (Fig. 5, upper panel); (2) the actual loading is close to the critical loading at eutrophication: try to increase the critical loading and hence the ‘carrying capacity’ of the lake (e.g. by hydromorphological measures like marshlands and water level fluctuations) (Fig. 5, middle panel); (3) the actual loading is well between the critical loading at eutrophication and oligotrophication: consider direct food web management (biomanipulation) (Fig. 5, lower panel); or (4) the actual loading is below the critical loading at oligotrophication; no extra measures are needed and due to the resilience of the system, the lake will likely remain in the desired transparent state. However, continuous monitoring of the nutrient loading and the lake’s state is recommended.



**Fig. 5.** Schematic overview how the results of this study can be applied in lake management by comparing the critical loadings for a given lake with the actual loading. If the actual loading exceeds the upper switchpoint (upper panel), nutrient reduction measures are recommended. In the intermediate range, a manager could try to increase the switchpoints (middle panel), e.g. by hydromorphological measures, or alternatively, force a switch by direct food web management (lower panel).

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