Short-term decisions in lake restoration have long-term consequences for water quality

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Abstract

Ecological regime shifts from clear to turbid water states in shallow temperate lakes are quite well-investigated phenomena but critical time lags from human interaction with the lake and restoration activities are much less understood. This is a complex challenge for institutions who manage lakes but are usually less familiar with non-linear dynamics, slow and fast influences on water quality and how to manage those from a social-ecological perspective. We extend a well-known minimal model of shallow lake regime shifts to enable simulations over time with short- and long-term management measures (nutrient reduction, trawling, planting of aquatic vegetation). While we explore the mathematical conditions for ecological bistability, we also identify the necessary and sufficient extent of measures to restore the clear water state. Restoration scenarios evaluated by trajectories in the state space demonstrate the increased effectiveness from combined measures even when considering countereffective activities such as pike fishing. But, single measures alone may delay or even miss the overall restoration target. Our analysis demonstrates the importance of understanding transient dynamics where stable state analyses alone remain elusive about alternative ways to interact with bistability. We conclude that successful management of bistable systems, and particularly shallow temperate lakes, needs careful balancing between short-term improvements and long-term influence on the systems state.

Keywords Bistability · Shallow temperate lakes · Stylised model · Social-ecological system · Restoration

Introduction

Large-scale, persistent and often unexpected changes in a system are referred to as regime shifts (Scheffer et al. 2001). Ecological regime shifts are a prominent phenomenon occurring in different ecosystems with negative implications for human well-being and the sustainability of social-ecological systems (Biggs et al. 2018; Rocha et al. 2015; Gunderson et al. 2006). While the ecological feedbacks

that characterise different regimes and shifts between them are quite well understood in many systems, the social dynamics of interactions of people and institutions are much less known (Lade et al. 2013). For shallow lakes, for instance, several mathematical models exist to investigate regime shift dynamics between clear and turbid water states (Mooij et al. 2009; Beisner et al. 2003; Scheffer 1990). The purpose of these models is mainly to identify the values of the driver, usually nutrient concentration, at which a small change causes a large difference in the response (tipping point). They, however, often do not explore alternative measures how humans could manage such a bistable system over time, even after a tipping point to the undesirable state was transgressed. Shallow temperate lakes are the only system among freshwaters so far with empirical evidence for regime shifts happening between multiple stable states (Capon et al. 2015). Here, we explore alternative management responses to a shallow lake in the turbid water state and measures which support the restoration to improve water quality and therewith human well-being.

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Humans interact with and benefit in multiple ways from good water quality in freshwaters but at the same time affect it adversely through intensive agriculture and urbanisation. In most shallow temperate lakes, the accumulation of nutrients in the water column and sediments is the main driver for the shift towards the turbid water state (Scheffer et al. 1993), which has been the most serious environmental threat to lakes in the temperate zone over the last century (Jeppesen et al. 2007). Management measures thus often addressed the nutrient sources such as over-fertilization in agriculture or insufficient urban wastewater treatment (Jeppesen et al. 2007). Insufficient wastewater treatment by municipal and private systems is, for instance, contributing considerably to the eutrophication in the Baltic region (Wallin et al. 2013). Multiple measures have been tested for restoring lakes that have shifted into a turbid state (Mehner et al. 2004; Carpenter et al. 2001). Measures range from slow, long-term processes (relatively to lake restoration time) of nutrient load reduction or wetland construction, to short- and mid-term by directly interfering with lake-inhabiting species (biomanipulation by catching whitefish, stocking predatory fish or planting aquatic vegetation; Jeppesen et al. (2007)). Social dynamics in policy making and implementation can significantly delay and therewith change the effectiveness of restoration measures (Martin et al. 2020). That is why, often, a combination of measures is advisable to accelerate lake restoration but these combinations are so far rarely investigated.

Long-term measures which address slow variables are particularly relevant for the management of regime shifts because those variables slowly move the system towards the tipping point to the undesired regime (Biggs et al. 2018; Hughes et al. 2013). An example of a slow variable in lakes is the accumulation of nutrients in sediments. This slow process of accumulation is challenging to manage due to widely distributed and often diffuse sources (agriculture, wastewater treatment; Carpenter et al. (1998)), a mismatch between the scale at which the ecosystem operates and at which it is managed (Kininmonth et al. 2015), and conflicting interests among largely disconnected actors (Galaz 2005; Pahl-Wostl et al. 2012). Slow variables often remain unnoticed until it is too late which emphasises the need for timely management to monitor, understand and manage the dominant, long-term drivers in a system. Managing social-ecological systems characterised by processes at different temporal and spatial scales requires improved understanding of the dynamics of bistable systems (Martin et al. 2020), i.e. systems that can exhibit two different regimes for the same value of the slow variable. This is important because long-term measures may create a landscape of possible outcomes, such as two alternative regimes in bistable systems (Table 1), while

short-term measures can steer the system relatively fast towards the desired outcome.

Lake research has developed a range of empirically motivated and theoretical models to better understand and guide shallow lake management (Mooij et al. 2009). Simpler models were developed for the purpose of explaining multiple origins of bistability in lake ecosystems (Scheffer 1990) and analysing empirical bimodal data (Beisner et al. 2003). While the analysis of tipping points, early-warning signals (Dakos et al. 2014; Contamin and Ellison 2009) and underlying feedbacks causing equilibrium dynamics received plenty of attention (Scheffer et al. 2001), the analysis of transient dynamics with short- and long-term implications for managing a lake was much less explored. This is particularly relevant when accounting for time lags caused by delayed or slow human responses to an ongoing regime shift (Martin and Schlüter 2015; Martin et al. 2020), as well as the effects of simultaneous, counter-effective activities (fishing) or shifting baselines (climate change) (Selkoe et al. 2015; Duarte et al. 2009). Modelling regime shifts to understand their transient dynamics and how management may interact with them can be achieved from a theoretical perspective through the analysis of bistability. Bifurcation analysis is one method to identify zones of bistability and how they are defined by tipping points (Ashwin et al. 2012). Only few examples exist so far which analyse social dynamics as explicit as the ecological ones. For example, causal loop diagrams and dynamical systems theory can help explain the origin of tipping points and the corresponding processes driving regime shifts (Lade et al. 2015). Here, we aim to take a step in this direction by investigating the time needed for lake restoration as an outcome of one or multiple restoration measures. To this end, we extend a model of shallow lake bistability (Scheffer 1989) to examine the effect of measures for lake restoration which operate at different time scales. As a novel contribution, we investigate dynamics of a 3-dimensional model which allows us to study interlinked dynamics of bream, pike and vegetation impacted by different short- and long-term measures. Our study helps better understand the effectiveness of different (combined) restoration measures in shallow lakes by evaluating simulations in a social-ecological context while exploring the following questions:

- What can we learn from analyses of ecological bistability about the implications of different management interventions, i.e. short-term or long-term technical measures for lake restoration?
- How does a combination of measures accelerate restoration compared with single or short-term measures?

We present in the following the model design and explain how it is suitable to analyse the effects from short-

and long-term restoration measures. The results show an analysis of equilibrium points and long-term system dynamics, bifurcation analysis and robustness analysis of the extended model and explore scenarios of different combinations of restoration measures. We conclude by discussing insights and limitations from model design, analysis and implications for managing bistable systems.

Methods

A minimal model to describe bistability in shallow lakes was developed by Scheffer (1989), hereafter called M_0 . It consists of two differential equations for the predator-prey relationship between two fish species (pike, *Esox Lucius*; bream, *Abramis Brama*), while the density of submerged vegetation is represented as a function of bream. This model formulation allows studying the effects that bream and

pike may have on the lakes' system dynamics. Since the vegetation in M_0 is not described by an independent state variable but is directly related to the density of bream, the model does not incorporate properties of submerged vegetation and their contribution to the lake's system dynamics. In this way, model M_0 cannot assess effects of certain types of regulation (such as bream trawling or vegetation planting, Fig. 1) on lake restoration.

To better understand dynamical implications from social-ecological interactions in lake restoration, more specifically, how measures affect a shift towards the clear state, we extend the minimal system dynamics model M_0 (Fig. 1) by introducing vegetation as additional state variable. In Section “Model formulation”, we present assumptions and formulation of the extended model. In Section “Model analyses”, we briefly explain different approaches for the analysis of the model and highlight short- and long-term measures aiming to restore the clear water state, as well as human activities which reinforce or delay the restoration.

Table 1 Glossary of terms, adapted from Kuznetsov (2004)

Term	Description
State space	Space of all possible configurations or states of a dynamical system.
Equilibrium point	A state of a dynamical system at which the system will stay if it starts from that point.
Trajectory	A time-ordered set of states of a dynamical system that originate from an initial state following rule of evolution.
Attractor	A state (or set of states) of a dynamical system to which trajectories originating from initial conditions converge over time.
Basin of attraction	For each attractor, its basin of attraction is the set of initial states leading to long-time behaviour that approaches that attractor.
Stability	A property of a system to return to an attractor after perturbations.
Bistable system (bistability)	A dynamical system that has two attractors. Depending on the initial conditions, future states of the system tend to one of the two attractors.
Bifurcation	A qualitative change in system's dynamics as one (or more) parameter is varied.
Tipping points	Discontinuities between current and future states of the system when small perturbations in the driver variable around the tipping point cause large changes in the response variable.

Model formulation

M_0 has several underlying assumptions which are supported by empirical evidence:

- A_1 Bream reproduction is greater in nutrient-enriched waters.
- A_2 High bream densities limit the development of aquatic vegetation.
- A_3 Pike is a predator of bream.
- A_4 Pike reproduction requires aquatic vegetation.

In order to incorporate vegetation as a state variable, we introduced another assumption along with the basic ones:

- A_5 The mortality of aquatic vegetation is mainly driven by the density of bream but its recovery is driven by its intrinsic growth rate.

Using assumptions $A_1 - A_5$ and bream B , pike P and vegetation V as state variables, we extend model M_0 and formulate model M_1 as follows:

$$\begin{aligned}
 \frac{dB}{dt} &= r_B \frac{N}{N + H_1} B - c_B B^2 - p_r \frac{PB^2}{H_4^2 + B^2} + i_B, \\
 \frac{dP}{dt} &= p_r p_e \frac{B^2 P}{H_4^2 + B^2} \frac{V}{H_2 + V} - c_P P^2 - m_P P + i_P, \\
 \frac{dV}{dt} &= r_V V - c_V V^2 - m_V \frac{VB^2}{H_3^2 + B^2}.
 \end{aligned}
 \tag{M_1}$$

The first and the second equations in model M_1 define the rate of change in bream and pike through logistic

Fig. 1 Four regulation measures are explored in their single and combined effects on lake restoration time. Dashed lines indicate how fast or slow the measures change the stocks relatively to lake restoration time. The lake's main components are shown by a causal loop

diagram depicting the feedbacks from the original model including their parameters (Scheffer 1989) and our additions (highlighted) to enable independent manipulation of all state variables. “r” denotes the reinforcing loop, while “b” denotes the balancing loop

growth and predator-prey relations. Assumption A_1 implies that the growth rate of bream is a function of nutrients (hence the term $\frac{N}{N+H_1}$), while assumption A_3 leads to the pike-dependent mortality of bream (represented by $\frac{PB^2}{H_4+B^2}$). Assumptions A_3 and A_4 imply that the growth rate of pike depends on bream and vegetation, which is reflected in the term $\frac{B^2}{H_4+B^2} \frac{V}{H_2+V}$. The pike mortality rate due to fishing is given by the term $-m_P P$ and immigration rates for bream and pike are i_B and i_P , respectively. These two equations correspond to model M_0 .

The third equation defines the rate of change for vegetation through vegetation growth (modelled as a logistic growth represented by $r_V V - c_V V^2$) and vegetation mortality due to bream (given by $m_V \frac{VB^2}{H_3+B^2}$). According to assumption A_5 , the relation between vegetation and bream is one-sided: bream is detrimental to vegetation, but vegetation has no effect on bream. Because of this asymmetry, we assume that bream density determines the strength of bream–vegetation interaction. Bream has a weak negative effect on vegetation when its density is low, but this effect increases as bream density grows and finally levels off for high density of bream. We model this relation using the Holling type III response with bream as a variable.

Parameter definition and values are in Table 1 in the Online Resource (S1). To respect both the assumptions for M_0 and M_1 and maintain the basic, reversible bistability of the lake system, several alternative formulations were tested and parameters were calibrated.

From the mathematical perspective, model M_1 is a 3-dimensional nonlinear system. Nonlinearity makes such systems difficult, if not impossible, to solve analytically, but it is possible to investigate behaviour of solutions using stability and bifurcation analyses. We rely on numerical methods to conduct these analyses.

Model analyses

Dynamics between aquatic vegetation, bream and pike under change of nutrient concentration is defined by model M_1 . We make a distinction between two types of measures: (1) long-term measures, i.e. measures that are changing relations between interacting species by changing a parameter value or the functional form and consequently change the dynamics of the system; and (2) short-term measures, i.e. measures that are not influencing the dynamics of the system, but rather act quickly and change the initial conditions. As an example of a long-term measure, we point out pike fishing which increases pike mortality rate. Short-term examples are vegetation planting or bream trawling because these measures take a significantly shorter time to complete in comparison to time needed for their effect to take place. In other words, the short-term measure is a means to change the initial state of the system. Because of this dichotomy, the analysis of model M_1 is based on the analysis of the state space (for tracking long-term dynamics), bifurcation analysis and changes in trajectories resulting from different measures (for investigating transient behaviour from different initial states). By combining several types of analyses, we aim to disclose properties of the system dynamics and possibilities for designing restoration measures.

Meaning of the state space in shallow lake models In shallow lakes, an attractor corresponds to the clear state if its aquatic vegetation dominates and reinforces a relatively low level of bream (Carpenter et al. 2001). Conversely, an attractor corresponds to the turbid state if the bream population dominates and destroys large parts of the vegetation. Functional forms in differential equations in M_1 together with parameter values influence the number and

Table 2 Results of bifurcation analysis with N as a bifurcation parameter and $m_V = 0.007$ under variation of c_V (top) and $c_V = 0.00006$ under variation of m_V (below)

$r_V (\cdot 10^{-3})$ $c_V (\cdot 10^{-5})$	4	5	6	7	8
4	T	T	BI ($N > 0.28$)	C	C
5	T	T	BI ($N > 0.26$)	BI ($N > 0.89$)	C
6	T	T	B ($N \in [0.24, 1.4]$)	BI ($N > 0.7$)	C
7	T	T	B ($N \in [0.23, 0.83]$)	BI ($N > 0.57$)	C
8	T	T	T	B ($N \in [0.49, 2.65]$)	C
$m_V (\cdot 10^{-3})$					
4	T	C	C	C	C
5	T	B ($N \in [0.46, 2.06]$)	C	C	C
6	T	T	BI ($N > 0.57$)	C	C
7	T	T	B ($N \in [0.24, 1.4]$)	BI ($N > 0.7$)	C
8	T	T	B ($N \in [0.17, 0.6]$)	BI ($N > 0.28$)	BI ($N > 0.83$)

Abbreviations: T, single turbid attractor; C, single clear attractor; BI, imperfect bistability, i.e. one tipping point and hysteresis for low nutrient concentration but no hysteresis for high nutrient concentration; B, bistability with two tipping points with hysteresis. Interval of nutrient concentration for which bistability is possible is in brackets. The bold entry denotes our chosen baseline setting

position of attractors as well as the shape of their basins of attraction.

Bifurcation analysis and parameter variation Model M_1 tracks changes in three state variables, B , P and V , for a certain range of parameters. Since parameters can change (for example due to restoration efforts to reduce nutrient load) or they vary for different species, we study effects of parameter variation on the dynamic behaviour of the system. Bifurcation diagrams show changes in number, position and type of equilibrium points caused by changes in the

driving parameter. We use the nutrient concentration N as the driving parameter to explore how bistability responds to different values for vegetation reproduction, intraspecific competition and mortality rate (r_V , c_V and m_v , respectively, specified in Online Resources S1 Table 2).

Trajectories and short-term measures Starting from an initial state, the system evolves following the dynamics defined by model M_1 and given sufficient time it reaches an attractor. Plotting trajectories in the state space reveals the transient dynamics of the system. We use trajectories to measure time intervals from different initial states applying

Fig. 2 Bifurcation analysis for **a** pike, **b** bream and **c** vegetation density. The grey area denotes the bistable space explored in this analysis. The bifurcation diagrams illustrate a case of imperfect bifurcation for

nutrient concentrations greater than 1.6. The initial states for our experiments are shown by X1, X2 and X3, and linked to intensity ranges for short-term restoration measures depicted by the orange rectangles

long-term management measures to when they reach the stable clear state and compare their effectiveness.

Short-term measures, on the other hand, are changing initial conditions, but they are not changing the dynamics of the system. They can cause a shift from one basin of attraction to another and, by doing this, change the outcome. We study effects of combination of short- and long-term measures by combining the change in initial conditions with a change in dynamics (Fig. 2).

Assumptions for social-ecological activities Despite the widespread recognition of multiple benefits from clear water and increased costs with turbid water (Carpenter et al. 1998), policy making for and implementation of upgrading sewage treatment systems show considerable time lags in lake restoration processes. This was explored in an earlier social-ecological simulation model of lake restoration to identify the magnitude for time lags from regulation and policy implementation compared with ecological feedbacks in the lake (Martin et al. 2020). Assuming that restoration will only be triggered after detrimental effects from abundant nutrients are visible on all trophic levels (e.g. by decreasing pike populations), the adaptive responses for regulation and implementation of upgraded sewage systems by private households were estimated under different social reinforcement scenarios. Scenario simulations resulted in a restoration delay between 10 and 30 years under which the nutrient concentration was reduced between 50 and 80%. We use the simulation results as initial condition here to account for different long-term restoration measures (such as nutrient reduction and pike fishing) in response to lake eutrophication (Online Resources S1, Table 2).

We explore other more short-term responses which are prominent restoration measures and consider biomanipulation in the form of reducing bream through high-intensity trawling and the planting of submerged vegetation (Jeppesen et al. 2007). Since not all human activities at lakes target lake restoration, we also study the adverse effects from pike angling during the restoration period.

Experimental setup to explore options and risks for lake restoration

The baseline parameter set of M_1 was used to analyse the stable states in response to changed nutrient conditions in bifurcation analyses. While the original model (M_0) showed two tipping points delimiting the range for hysteresis behaviour, the number of tipping points for M_1 depends on several parameter choices and the system may have zero, one or two tipping points. Since we want to study the transition from the turbid to the clear state, we choose model parameter values which allow the existence of at least one tipping point and fulfil the main properties from M_0 .

Through bifurcation analysis, one can identify the trivial solution to long-term restoration which would be a nutrient reduction below the tipping point. We are interested, however, to explore non-trivial trajectories to restoration for bistable systems which are in transition between stable states (Fig. 2). For these restoration trajectories, single measures as trawling or planting vegetation or their combination are explored from different initial conditions. The initial conditions X_1 , X_2 and X_3 are extreme examples based on different time lags from regulation and intensities of wastewater treatment (Online Resources S1 Table 2, Martin et al. (2020)). X_1 represents a state from a minimal regulation time lag and an average wastewater treatment.

Fig. 3 Attractors and basins of attraction for model (M_1) are represented by blue and purple dots and corresponding coloured volumes. Used parameter values are $r_V = 7 \cdot 10^{-3} \text{ day}^{-1}$, $c_V = 6 \cdot 10^{-5} \text{ m}^2$,

$m_V = 7 \cdot 10^{-3} \text{ day}^{-1}$, $H_2 = 20$. **a** $N = 1.125$ and coordinates of turbid state (the blue disc) are (79.6, 0.038, 6.91) and of clear state (the purple disc) are (16.92, 2.86, 67.97). **b** $N = 0.8$. **c** $m_P = 2.475 \cdot 10^{-4} \text{ day}^{-1}$

X_2 assumes an improved acceleration of nutrient reduction. X_3 represents a state after experiencing the maximum regulation time lag.

Results

State spaces, equilibrium points and system dynamics

Figure 3 shows the position of attractors and shapes of basins of attraction for the baseline parameter set (Online Resource S1, Table 1). It allows investigation of consequences of various short-term measures for lake dynamics, as well as outcomes of combinations of long- and short-term measures.

The shape of the clear basin of attraction and the position of the clear attractor suggests that the system in a clear state and near the clear equilibrium is more resilient to changes in vegetation and bream than to decreases in pike density. A sufficiently large decrease of pike density can push the system from the clear basin of attraction into the turbid basin of attraction. With greater values for bream density, greater pike and vegetation values are needed for keeping the system in the clear state.

From the turbid state perspective, there exists a threshold of pike density which is necessary for reaching the clear basin of attraction. This threshold value decreases in less nutrient-rich water (Fig. 3b), but it increases with increased pike mortality, due to fishing for example (Fig. 3c). If the pike density is above the threshold value, reducing the bream density may be sufficient for pushing the system into the clear basin of attraction. Otherwise, increasing pike density becomes a necessary measure for restoration.

Decreasing the nutrient concentration and increasing pike mortality are countereffective to each other in terms of the resulting system dynamics. This can be seen by comparing the volumes of turbid basins of attraction in Fig. 3b and c. Combining these two measures can help balance system dynamics and keep the pike density threshold value low even under increased mortality due to fishing (Fig. 2b in Online Resources S2).

Properties of vegetation affect the shape of basins of attraction. The increased half-saturation constant H_2 , i.e. increased vegetation density needed for pike reproduction, leads to higher pike threshold values needed for reaching the clear state (compare Fig. 3a and Fig. 2a in Online Resources S2).

Bifurcation analyses show sensitivity of bistability to vegetation parameter variations

We explore a range of suitable values for the newly introduced parameters defining vegetation properties to better understand their effect on bistability in the system. Bistability is evaluated through bifurcation diagrams with nutrient concentration N as a bifurcation parameter. For our choice of baseline parameter values, we get a case of imperfect bifurcation, i.e. a case of a bistable system without hysteresis (Fig. 2a). Although this case is unsuitable to explore the process of eutrophication ($N \geq 1.5$), the attractor shapes for values $N \leq 1.5$ are sufficiently similar to the original model M_0 .

To study effects of change in nutrient concentration in lakes with different vegetation types, we expand the bifurcation analysis with N as a bifurcation parameter for several combinations of parameter values in r_V , c_V and m_V and present results in Table 2 and in Online Resources S3.

The upper part of Table 2 shows combinations of the vegetation growth rates and intraspecific competition for a constant mortality rate, while in the lower part, we vary mortality rates and keep the intraspecific competition constant. Given a low vegetation growth rate ($r_V \leq 0.005$), the system remains in a turbid state for all choices of intraspecific competition c_V and almost all choices of bream-induced mortality. For a high vegetation growth rate ($r_V = 0.008$), intraspecific competition has no effect on the stability of the system and it remains in a clear state, but high mortality ($m_V = 0.008$) can cause bistability. For medium vegetation growth rates ($r_V = 0.006$ or $r_V = 0.007$), increasing the intraspecific competition c_V or increasing the mortality rate m_V reduces the interval of bistability and may cause a shift from a unique clear stable state to bistability or from bistability to turbid state. At the same time, the unstable states between the clear and turbid attractor move closer to the clear attractor making it less resilient as in the example shown for pike density (Online Resource, S3, Fig. 4). The lake system (M_1) is more sensitive to changes in vegetation growth and mortality than to intraspecific competition.

Figure 5 in Online Resources shows comparison of bifurcation diagrams where vegetation mortality or intraspecific competition is varied but the growth rate is kept constant. It is evident that the nutrient concentration can lead to different outcomes for various types of aquatic vegetation. The interval of nutrient concentration for which the clear state is possible becomes shorter for higher values of vegetation mortality. In contrast to this, the interval of nutrient concentration is wider for higher vegetation

mortality rates. Whereas the clear state attractor is quite robust for pike against most variations in intraspecific competition, the unstable and turbid states are not. Namely, the turbid state is possible for lower nutrient concentrations when intraspecific competition rate increases.

Trajectories to reach the clear state with short-term measures

Trajectory simulations of the system in state space enable us to evaluate the outcome of a measure, particularly with what speed a system will evolve towards the clear state from a specific initial condition. Due to the nonlinear behaviour of the system, the visual proximity to the nearest stable state is insufficient to predict the time to reach it.

Table 3 shows the attainment of and duration for reaching the clear water state from combinations of short-term measures which placed the system on different initial states. We compare two measures: an increase in vegetation through planting indicated by increasing numbers of vegetation density, and a decrease in bream through trawling indicated by decreasing numbers of bream density. For example, if we start from the initial state of X1, introduced in Fig. 2, only a combination of very radical short-term measures such as a reduction of bream by at least 66% and an increase of vegetation by 750% through planting would result in a clear state. Assuming an initial state resulting from a slightly more efficient nutrient reduction, as depicted by X2, provides the most promising perspective for successful short-term measures. The more the bream population is reduced and at the same time vegetation increased, the shorter is the time to reach the clear state. However, the response of the system to these measures is initially very slow. Short-term measures of a vegetation increase and bream decrease towards $V = 15$ and $B = 20$, respectively, result in very long restoration times. However, a slight increase in both measures can here reduce the overall restoration time by more than two-thirds.

Table 3 also shows that for some initial conditions even a single measure, such as bream reduction or vegetation planting, can be sufficient to reach the clear state. However, comparing results for a single measure (blue entries) with the result for combined measures (the red entry), we come to the conclusion that combined application of measures reduces the restoration time in this case by more than half.

Within the same range of short-term measures but starting with X3 for pike density after a delayed nutrient reduction (Fig. 2), only the most intense applications of bream reduction (-75%) and planting ($+150\%$) result in a clear state after approximately 30 years (Online Resources S4, Table 2). This experiment shows that detrimental initial conditions for pike can be better compensated by vegetation planting than by bream reduction.

In a similar way is pike fishing (here represented as a continuous, i.e. long-term activity) a challenge for finding suitable restoration measures. Under these conditions, the system dynamics are changed fundamentally by increasing the threshold for the pike and vegetation density necessary for reaching the clear state (Online Resource, S4, Table 3). Here, planting measures need to be even stronger in order to plan for a successful restoration.

In summary, the more unfavourable the lake conditions are at the onset of short-term measures, for instance because the implementation of regulations for nutrient reductions is slow, the stronger or more radical restoration measures are necessary to reach the clear water state (Table 4). Vegetation planting was the most efficient single measure under initial conditions (except for X1) that are relatively close to the tipping point towards the clear state. For systems that are more distant from the tipping point, a combination of restoration measures is required. Long-term changes to the system dynamics, such as those resulting from increased pike mortality, are, however, likely to more strongly influence restoration time than short-term responses.

Table 3 Rounded time (in years) for reaching the clear state when applying short-term measures (targeted density values for bream reduction and/or vegetation planting) when starting from the initial system conditions with $N = 0.8$ (X2)

Vegetation\bream	60	55	50	45	40	35	30	25	20	15	10
10	T(X2)	T	T	T	T	T	T	T	T	T	26, s
15	T	T	T	T	T	T	T	T	78	23	16
20	T	T	T	T	T	T	48	28	21	16	14
25	T	58	44	36	30	26	22	19	16	14	12
30	26, s	25	23	22	20	18	16	15	14	12	11, c

T, the turbid state as result; s, (blue) single measures as restoration solutions; c, (red) particular examples for combined measure solutions. Bold numbers highlight very long restoration times

Table 4 Possible restoration solutions to reach the clear state with single or combined short-term measures from different initial states. Initial states X1, X2, X2' and X3 are shown in Fig. 2

Initial state	Single restoration measure	Combined restoration measures
X1	No restoration possible	66% bream reduction AND 750% planting
X2 (X1 + improved nutrient reduction)	80% bream reduction OR 200% planting	66% bream reduction AND 100% planting
X3 (X1 + improved nutrient reduction but 20 years delayed)	450% planting	(83% bream reduction AND 150% planting) OR (75% bream reduction AND 200% planting)
X2' (X2 + 10% increased pike mortality)	600% planting	83% bream reduction AND 250% planting

Discussion

For assessing the sustainability of bistable ecosystems, the challenge moved from identifying the properties of bistability to investigating the short- and long-term effects of ecosystem management measures aimed at restoring the desired state. We extended a well-known minimal model for shallow lake regime shifts to investigate how interlinked dynamics of bream, pike and vegetation are affected by the combination of measures to restore the clear water state. A better understanding of transient dynamics between alternative stable states is particularly relevant to improve water quality in shallow temperate lakes (Martin et al. 2020; Capon et al. 2015).

Model design with imperfect solutions

While designing the new model, bistability in response to changes in nutrient concentration was the core pattern to reproduce, since earlier empirical and modelling studies emphasised its relevance in managing lakes (Scheffer and Van Nes 2007; Mooij et al. 2019). This guided our choice of parameter values and variations for a robustness analysis. The properties of bistability were highly sensitive towards changes in parameter variation (by $\pm 16\%$). The investigated value range resulted in loss of bistability, bistability with hysteresis or bistability with imperfect bifurcation. This implies that vegetation properties, especially its growth rate and mortality induced by bream, can cause qualitatively different lake ecosystem dynamics. But, the validity of the model to better understand restoration dynamics is not necessarily improved by more precise ecological parameter values but by critically testing the implications from resulting stable state analyses. Thus, bifurcation analyses were used as a starting—rather than an endpoint—to design further model analyses and experiments. The choice of suitable parameter settings was finally a trade-off between expecting bistability with hysteresis and reproducing a sufficiently similar pattern of stable and unstable states compared with the original model, which left us to choose

the case of imperfect bistability for further investigation of lake restoration.

Lakes in transition can be restored to the clear state

While most lake restoration studies focus on a single driver (nutrients, Hilt et al. (2018); planktivorous fish reduction, Bernes et al. (2015)) and immediate effects from response measures (Biggs et al. 2009), we shifted the focus to a combination of measures and their transient dynamics affecting the whole lakes system state. Studying transient dynamics of restoration from the turbid to the clear water state in shallow lakes allows insights on the interactions between different restoration measures with long-term lake dynamics. A combination of short-term measures, in this case planting of aquatic vegetation and bream reduction, rather than solely relying on nutrient reduction may be needed for reaching the clear state. This is in agreement with studies on other ecosystems, for instance coastal systems suffering from eutrophication (Duarte et al. 2009), in which the reduction of the bifurcation driver alone was not sufficient for restoration (Smith 2003). While the manipulation of the driver for bistability provides trivial solutions for long-term restoration (i.e. sufficient reduction of nutrients), we explored to which degrees combinations of short-term vegetation and bream manipulation enable a restoration for lakes in transition. We found in our model that the restoration time could be more drastically reduced by planting more vegetation than by reducing planktivorous fish (Table 4). This observation is supported by empirical studies investigating long-term effects from restoration measures (Søndergaard et al. 2007). But since bistability is not the only discontinuity known for shallow lakes (Scheffer and Van Nes 2007), further investigations of lake transitions from the turbid to the clear water state are needed. Shallow lake management is a suitable example to learn about managing regime shifts in general since eutrophication is a generalist driver linking multiple ecosystems, actors and beneficiaries on local and regional scales (Rocha et al. 2015).

Social-ecological transients to manage bistability

Due to nonlinearity in many ecosystems, the proximity to the nearest stable state is insufficient to predict the time to reach it, let alone to assess the overall sustainability. Time to reach the stable state does not linearly correlate with the Euclidean distance between the initial condition and an attractor. That is why the investigation and differentiation between short- and long-term management measures and their effect on transient dynamics becomes crucial. At the same time, human responses to a deteriorating ecosystem state are highly unknown and seldom sufficiently pro-active to prevent a regime shift (Contamin and Ellison 2009; Biggs et al. 2009). One needs to account for diverse interests and directions to where humans influence the ecosystem, as for example also the turbid state of a lake can be reinforced by changing interests (Selkoe et al. 2015). This is where trajectory simulations enable a systematic evaluation of different initial states and exemplify transient dynamics under the assumption that the included interactions do not change over the simulated time span.

But further advancements in understanding human responses to regime shifts are necessary by making choices of adaptation and transformation during management more explicit in model simulations. While stable state analyses usually conclude with recommendations for preventing undesired tipping point transgressions, our analysis of transient dynamics exemplified how management measures can be effectively combined to reach an alternative state.

Conclusions

Our newly designed model increased the flexibility for testing and comparing suitable lake restoration measures in concert while keeping the parsimony and analytical strength of the original minimal model of lake bistability. The evaluation of transient dynamics resulting from short- or long-term measures provides new opportunities for understanding and identifying effective management of bistable systems. Our study enables an improved understanding of transient dynamics during regime shifts in shallow temperate lakes and serves as an example for how the transition towards a desired regime can be managed over time.

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