



Original Articles

Timing matters: Sampling frequency for early-warning indicators across food web components in a virtual lake

Alena S. Gsell^{a,*}, Sven Teurlinx^a, Rita Adrian^{b,c}, Annette B.G. Janssen^d

^a Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

^b Community and Ecosystem Ecology, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

^c Department of Biology, Chemistry and Pharmacy, Freie Universität Berlin, Berlin, Germany

^d Water Systems and Global Change Group, Wageningen University & Research, Wageningen, The Netherlands



ARTICLE INFO

Keywords:

Critical transition
Ecosystem model
PCLake+
Regime shift
Sampling frequency

ABSTRACT

Shallow lakes are known for sudden shifts between a desired clear and an undesired turbid state despite only incremental changes in the underlying drivers. Such sudden shifts are a major challenge for lake managers who can be confronted with abrupt losses of desired ecosystem services without easily observable warning signals. Predictive tools for the loss of ecosystem resilience are vital to respond with timely mitigation measures and avert a shift to the undesired state. Early-warning indicators (EWIs) have faithfully preceded critical transitions in minimal models but have proven more elusive in real-world data, suggesting a mismatch between measurement strategy and the detectability of EWIs. Here, we capitalize on data simulated using the aquatic ecosystem model PCLake+ which represents real systems more closely than reductionistic models and which allows the generation of critical transitions in response to gradual changes in phosphorus load. We tested the effect of different sampling intervals (daily to yearly) on the detection of three often-used EWIs across a range of food web and nutrient-related variables. Moreover, we included one integrated sampling interval (yearly average of daily measurements) to represent time-integrated measurements. EWIs generally performed better at shorter intervals (daily, weekly) but integrated measurements over the year also proved suitable to detect oncoming state shifts. We propose that lake managers should aim for high-frequency measurements of variables that can be easily and cheaply measured (e.g. oxygen, Secchi) or, alternatively, focus on integrated approaches using passive samplers or sedimented material.

1. Introduction

Our planet is experiencing far-reaching emergencies, such as environmental degradation, disease outbreaks or droughts (Ripple et al., 2017). Many of earth's environmental and societal systems are stabilized by internal positive feedback processes (Scheffer, 2009). The theoretical expectation is that once a pressure exceeds a critical threshold, such complex systems can suddenly shift to an alternative stable state stabilized by a new set of feedback processes (May, 1977; Scheffer et al., 2001). Against the backdrop of climate change and land-use intensification, this new state is generally unfavourable, resulting in catastrophic loss of biodiversity, health or economic value (Scheffer et al., 2009; Janssen et al., 2021). Such sudden shifts to an alternative stable state are notoriously difficult to predict as there is little overt change in ecosystem state variables despite climate and land use

change gradually undermining the resilience of these systems (Scheffer et al., 2009). Hence, reliable indicators for deteriorating ecosystem resilience are sought after to help preventative management taking timely countermeasures to avert an upcoming crisis. Early-warning indicators (EWIs) have been proposed as robust and relatively generic indicators of ecosystem resilience (Dakos et al., 2012; Van Nes and Scheffer, 2007).

Lake ecosystems have served as exemplary case studies to develop the theory of alternative stable states and associated EWIs that allow the prediction of an approaching regime shift. Shallow lakes are known for sudden shifts between a clear, macrophyte dominated regime and a turbid, phytoplankton dominated regime (Scheffer and Jeppesen, 2007; Scheffer and Carpenter, 2003). These sudden shifts can be caused by several mechanisms, e.g., by linear tracking of large changes in a key driver, by a non-linear but continuous response to a driver exceeding a

* Corresponding author at: Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708PB Wageningen, The Netherlands
E-mail address: a.gsell@nioo.knaw.nl (A.S. Gsell).

threshold, or, in the case of systems with more than one stable state, by a non-linear and discontinuous response to gradual changes in a driver generating a critical transition to an alternative stable state (Andersen et al., 2009). In the last case, the shift is not easily reversible as the new state is stabilised by its own set of positive feedbacks, and therefore a return to the original state requires a reduction of the driver beyond the initial threshold (i.e., hysteresis) (Beisner et al., 2003). In shallow lakes, various ecological mechanisms have been shown to generate critical transitions between alternative states (Scheffer, 2009), including (i) changes in the competitive ability of two or more species due to changes in e.g., nutrient load (May, 1977; Collie et al., 2004); (ii) trophic cascades triggered by in- or exclusion of top predators (Carpenter et al., 2001) and parasites (Gerla et al., 2013); and (iii) occurrence of intra-guild predation by resource competitors that also prey on each other (Verdy and Amarasekare, 2010; Scharfenberger et al., 2013). In shallow lakes, critical transitions driven by increasing nutrient load result in increased phytoplankton biomass, thereby decreasing the light availability for the submerged vegetation and hampering vegetation growth (Scheffer et al., 1993). The subsequent loss of vegetation increases turbidity as the sediment is no longer stabilised and sheltered from wind-induced resuspension (James et al., 2004; Vermaat et al., 2000). Moreover, loss of vegetation releases phytoplankton from grazing pressure as shelter for zooplankton becomes scarce (Timms and Moss, 1984) and from suppression by allochemicals excreted from submerged vegetation (Hilt and Gross, 2008). All these processes contribute to a feedback cycle stabilizing the turbid state (van Donk and Gulati, 1995; Ibelings et al., 2007). Conversely, with decreasing nutrient load, rooted submerged vegetation stabilises the sediment and provides shelter for zooplankton, thereby increasing the grazing pressure on phytoplankton and subsequently, light availability in the water column, which contribute to the feedback cycle stabilizing the clear state (see also examples in Scheffer and Jeppesen, 2007; Jeppesen et al., 2012). As each state (clear or turbid) is stabilized by its own feedback cycle, the tipping point under increasing nutrient loads (eutrophication) differs from that under decreasing nutrient loads (oligotrophication), leading to hysteresis (Scheffer et al., 1993). EWIs are based on trends in statistical output that assess the loss of temporal or spatial resilience of a system before a critical transition occurs (Dakos et al., 2012). Some EWIs are linked to critical slowing down, which is characterised by an increased recovery time after a minor perturbation as the system approaches its tipping point (Ives, 1995; Van Nes and Scheffer, 2007). If a system shows critical slowing down, it tends to become more similar to its own past, resulting in an increasing trend in autocorrelation at lag-1 (AR1) (Ives, 1995). This increase in short-term memory and lack of decay of the impact of past perturbations also leads to a build-up in variance, measured as an increasing trend in the standard deviation (SD) (Carpenter and Brock, 2006). A concurrent increase in SD and AR1 in a time series means higher variability in low-frequency processes compared to high-frequency processes in the power spectrum of a time series, which can be quantified as increasing density ratio (DR) of variance at low to high frequencies (Biggs et al., 2009).

While EWIs reliably precede critical transitions in reductionistic, minimal models, their detection in real-world systems has proven more elusive (Burthe et al., 2016; Gsell et al., 2016; Spears et al., 2016; Gilarranz et al., 2022). Real-world systems experience multiple ecological processes simultaneously, affecting typical indicator variables differently, adding noise and thereby potentially cloaking EWIs (Perretti and Munch, 2012). Moreover, EWIs are typically assessed on a limited set of ecosystem variables, partly for pragmatic reasons (choosing variables that can be measured cost-effectively, easily and reliably) and partly due to lack of insight about which variables are most relevant as input data for the calculation of EWIs. Furthermore, sampling frequency in water management is often dictated by the availability of financial resources or time, hence traditional sampling schemes may not be of optimal frequency and duration for robust detection of EWIs (Batt et al., 2019; Spears et al., 2017). In combination,

the choice of ecosystem variables to measure and the frequency of these measurements both influence the detection of EWIs. Insufficient insights into the effect of these choices leave lake managers without adequate tools to assess the ecological stability of their systems and respond in time to avert the occurrence of a potential regime shift (Pace et al., 2017). Mechanistic ecosystem-level models can help to bridge the gap between EWI theory developed with reductionistic minimal models and real-world complex natural systems.

Mechanistic lake ecosystem models, such as PCLake+, can generate large amounts of virtual data for lakes with a variety of settings (Janssen et al., 2019a). When such a model is well-grounded in reality and has proven applicability to real-world lake data, it can serve as a form of a virtual reality object (Kuiper et al., 2015). Such a virtual lake can be set up to represent idealized conditions for alternate stable states to occur and EWIs to be found. Moreover, the virtual lake can be sampled *ad libitum* at no cost across ecological components and time scales. Hence, such an approach can help to generate hypotheses regarding both sampling frequency and ideal variables to look for EWIs. In our study, we make use of the ecosystem model PCLake+ which has a long history of providing real-world management solutions (Janse and van Liere, 1995), has been shown to be able to produce critical transitions (Janse et al., 2008; Janssen et al., 2019a) and EWIs (Gsell et al., 2016) and has been previously employed successfully as a virtual lake to sample from for methodological comparison (Kuiper et al., 2015; Janssen et al., 2019b). We set up the model with a set of lake characteristics that are expected to produce a critical transition from a turbid to a clear state and vice-versa along a long gradient of nutrient loading. Using this virtual lake approach, we aim to improve understanding of the importance of sampling frequency and what ecosystem components (i.e., physical and chemical variables, food web components) are most suitable for EWI detection.

With gradual changes in nutrient load as an underlying driver, the regime shifts in our PCLake+ scenarios are caused by competition between phytoplankton and submerged vegetation; hence we expect to detect EWIs in phytoplankton related variables (e.g. chlorophyll-a, phytoplankton biomasses) with increasing (eutrophication) as well as decreasing nutrient loading (oligotrophication). These signals may resonate through other ecosystem components, allowing for the detection of EWIs in variables that have no direct mechanistic link to the driver of the regime shift but that absorb signals through the food web (e.g., zooplankton, fish, sediment nutrient content). We further hypothesize that with a high sampling frequency, the probability of EWI detection will be the highest in all components of the ecosystem. As sampling frequency decreases, the potential for EWI detection deteriorates, especially when important ecological process rates and sample frequency do not match (e.g., generation times of days with a sampling frequency of months).

2. Material and methods

To test our hypotheses, we ran PCLake+ for 50-year long eutrophication and oligotrophication scenarios and extracted the time series of all model state variables that pertain to inorganic nutrient stocks dissolved in the upper water column and in the sediment pore water as well as nutrient stocks locked in biomasses of food web components spanning primary producers, zooplankton and zoobenthos as well as omnivorous and predatory fish (see also Fig. 1 for an overview of variables and their connections). To evaluate the effect of sampling frequency and integration over time, we calculated three commonly used EWIs (AR1, SD and DR) on the residuals of the seasonally adjusted and detrended time series filtered at regular intervals to reflect relevant sampling frequencies that lake managers are likely to use (daily, weekly, monthly, quarterly, half-yearly and yearly) or integrated per year to reflect sampling strategies such as passive samplers or possibly paleolimnological approaches (yearly-integrated).

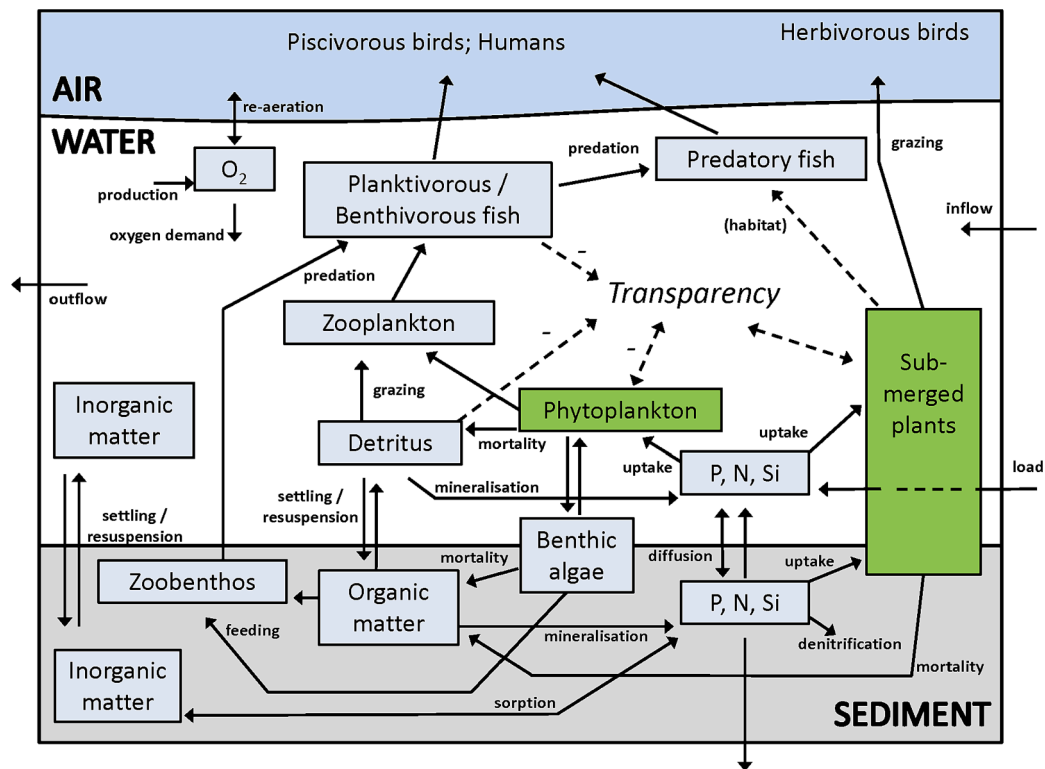


Fig. 1. Visualization of state variables and their interaction pathways in PCLake (Janse et al., 2008) modified from (Van Gerven et al., 2015). Boxes denote biomass compartments, arrows indicate flows. Green boxes indicate the two main competitors under nutrient changes: pelagic phytoplankton and submerged waterplants. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.1. PCLake+ runs

PCLake+ is an aquatic ecosystem model used to simulate food web dynamics in lakes (Janssen et al., 2019a) which is an extension of PCLake which was developed, parameterised and empirically validated for 43 European shallow lakes (Janse et al., 2010). The extended version PCLake+ can also model deep lakes (Janssen et al., 2019a) and includes floating and denitrifying cyanobacteria (Chang et al., 2020). For our simulations we made use of the default shallow lake settings of PCLake+. A default lake is configured with an average depth of 2 m, 1000 m fetch, and with varying water temperature (average 15 °C, ± 10 °C), evaporation and light curves based on sine wave functions reflecting Dutch weather conditions (for further details on lake definition and PCLake+ set up, see link to script in the data statement). The lake receives a constant inflow of water of 20 mm per day. Our virtual lake, with the given settings, constitutes a temperate, relatively small, shallow lake. We used PCLake+ to simulate a default lake going through a critical transition from either clear to turbid (eutrophication) or turbid to clear (oligotrophication). We simulated these critical transitions by respectively linearly increasing (from 0.00001 to 0.008 gP m⁻² d⁻¹) or decreasing (0.008 to 0.00001 gP m⁻² d⁻¹) the phosphorus load over a period of 50 years and a constant N:P ratio of 10. Prior to the simulation, we allowed the model to run to equilibrium (spin-off time of 50 years) as a start position for the initial states of the final runs. We aimed at assessing EWIs in the PCLake+ output as a result of daily weather variations as perturbations. To simulate weather variation, we added stochasticity in form of random fluctuations (Brownian motion) with a predetermined error distribution to the temperature function in PCLake+ using the “Dwiener” function available in Matlab (Siegert and Friedrich, 2001):

$$T_w(d) = [\overline{T_w} - T' \cos(2\pi(d-l))] + \alpha * \text{dwiener}(\beta)$$

where $T_w(d)$ is the water temperature (°C) as a function of the day in the year d , $\overline{T_w}$ the yearly average water temperature of 15 °C, T' the maximum water temperature variation of 10 °C, l the time lag compared with the atmospheric maximum temperature of 30 days and α and β the stochasticity parameters which are 0.5 (weight factor) for α and 1 (standard deviation of noise) for β . We obtained daily output for all state variables for further EWIs analysis.

2.2. Breakpoint detection and EWI analysis

For the breakpoint and EWI analysis of the daily time series each variable simulated with PCLake+ was z-scored (mean-centred and divided by the standard deviation) and decomposed in seasonal, trend and residual components using a LOESS filter (function “stl” in R (R Core Team, 2018) Fig. 2). The breakpoint date was calculated on the trend component using two methods, detection of structural change in the time series based on F-statistics (Zeileis et al., 2001); R package strucchange) and identification of absolute maximum in first-differenced time series. Visual inspection of the breakpoint results revealed four cases in which the breakpoints were in linear sections of the time series (eutrophication: Zooplankton dry weight (oDZooEpi) and P in dissolved PO₄ sediment pore water (sPO4S); oligotrophication: N in dissolved NO₃ (oNO3WEpi) and P in dissolved PO₄ (oPO4WEpi)). Hence, we calculated the median and standard deviation of all breakpoints per scenario (eutrophication or oligotrophication) and reanalysed the four outliers with the median as a breakpoint. Three commonly used EWIs (autocorrelation at lag-1 (AR1), standard deviation (SD) and density ratio of the power spectrum (DR)) were calculated on the time series of the residuals (i.e., the z-scored time series - seasonal component - trend component) using the last 10 years before the shift (Fig. 2). Early warning indicators are expressed as trends in AR1, SD and DR within rolling windows along the residuals time series using a non-parametric Kendall tau correlation (R package “earlywarnings”, (Dakos et al.,

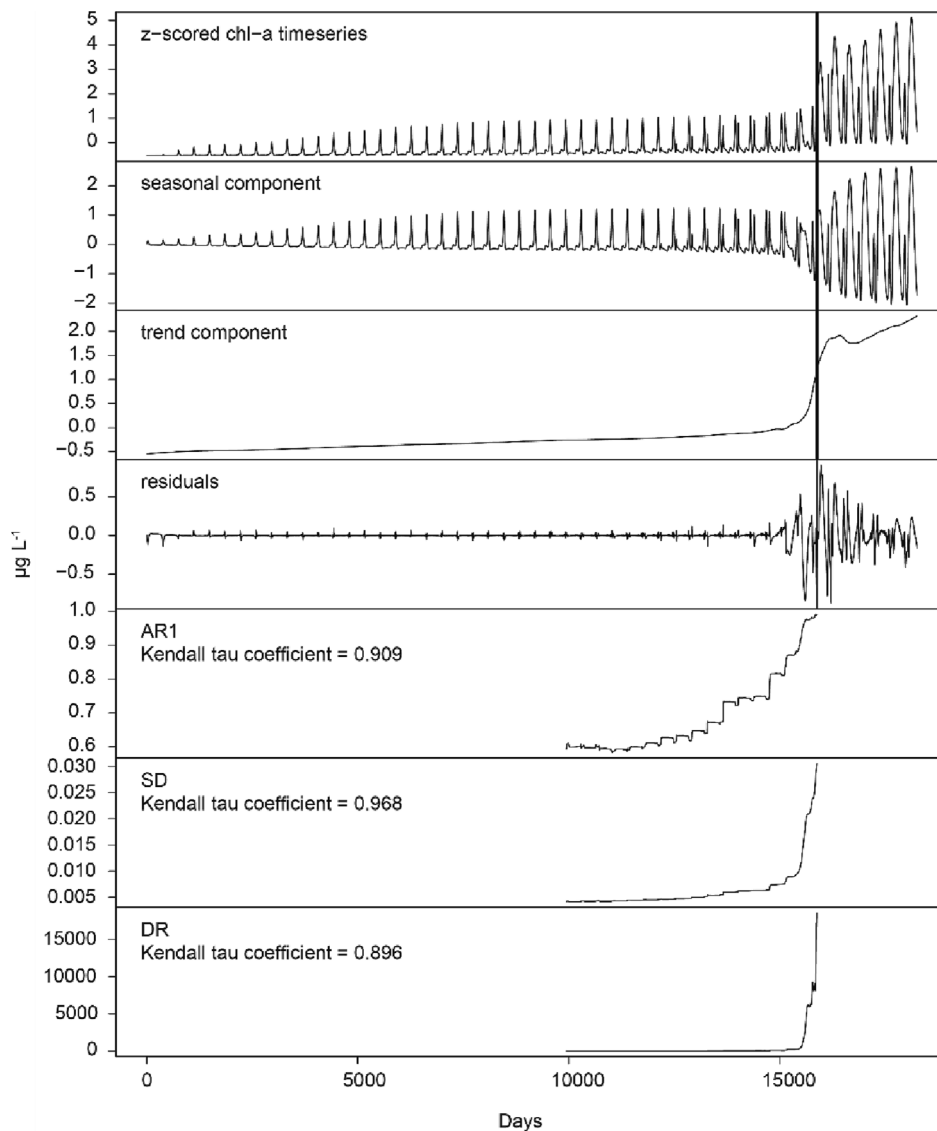


Fig. 2. Example of the decomposition of the original z-scored time series of daily epilimnion chlorophyll-a in the eutrophication scenario into its seasonal, trend and residual components and subsequent rolling-window-based detection of EWIs AR1, SD, and DR on the residual component. The vertical line in the uppermost three panels indicates the location of the tipping point.

2012)), see also Fig. 2). The residuals time series were log-transformed prior to analysis and the rolling window size was set to 50% in all cases.

To assess the effect of sampling intervals on the detection of EWIs, we chose six sampling intervals of which five represented typical lake sampling schemes ranging from daily; weekly (each 3rd day of the week); monthly (each 15th day of the month); quarterly (each 15th day of March, June, September and December), half-yearly (each 15th day of March and September) and yearly (each 15th of June). As a sixth sampling interval, the yearly average of all daily samples was chosen to reflect sampling strategies such as passive samplers or possibly paleolimnological approaches (yearly-integrated: i.e., averaging all daily measurements per calendar year). Each subsampled time series was then analysed for breakpoint timing and EWIs as described above.

3. Results

3.1. Overview PCLake+ runs

We ran PCLake+ to simulate critical transitions in both eutrophication and oligotrophication scenarios (see Fig. 3 for time series of

temperature, phytoplankton chlorophyll-a and macrophyte dry weight). The critical transition during eutrophication occurred when the phosphorus load rose roughly above $0.007 \text{ gP m}^{-2} \text{ d}^{-1}$. At a higher phosphorus load, the macrophytes disappeared and the phytoplankton chlorophyll-a suddenly increased. Year to year variation is visible in the chlorophyll-a after eutrophication has caused a shift, which can be attributed to temperature stochasticity. The critical transition during oligotrophication occurred when the phosphorus load was decreased to a lower level than with eutrophication and happened at $0.002 \text{ gP m}^{-2} \text{ d}^{-1}$. At that point, macrophytes re-established and phytoplankton chlorophyll-a was largely reduced. However, the macrophyte biomass did not establish to the same level as when it was thriving just before the shift with eutrophication, likely since they were still in a recovery period. The difference of $0.005 \text{ gP m}^{-2} \text{ d}^{-1}$ between the critical nutrient loads for eutrophication and oligotrophication can be attributed to positive feedbacks stabilizing either ecosystem state. Due to such stabilizing positive feedbacks, regime shifts are not easily reversible as e.g., phosphorus load needs to be reduced further than the eutrophication breakpoint before the system switches back to its clear state again (also called a hysteresis, e.g. Beisner et al., 2003).

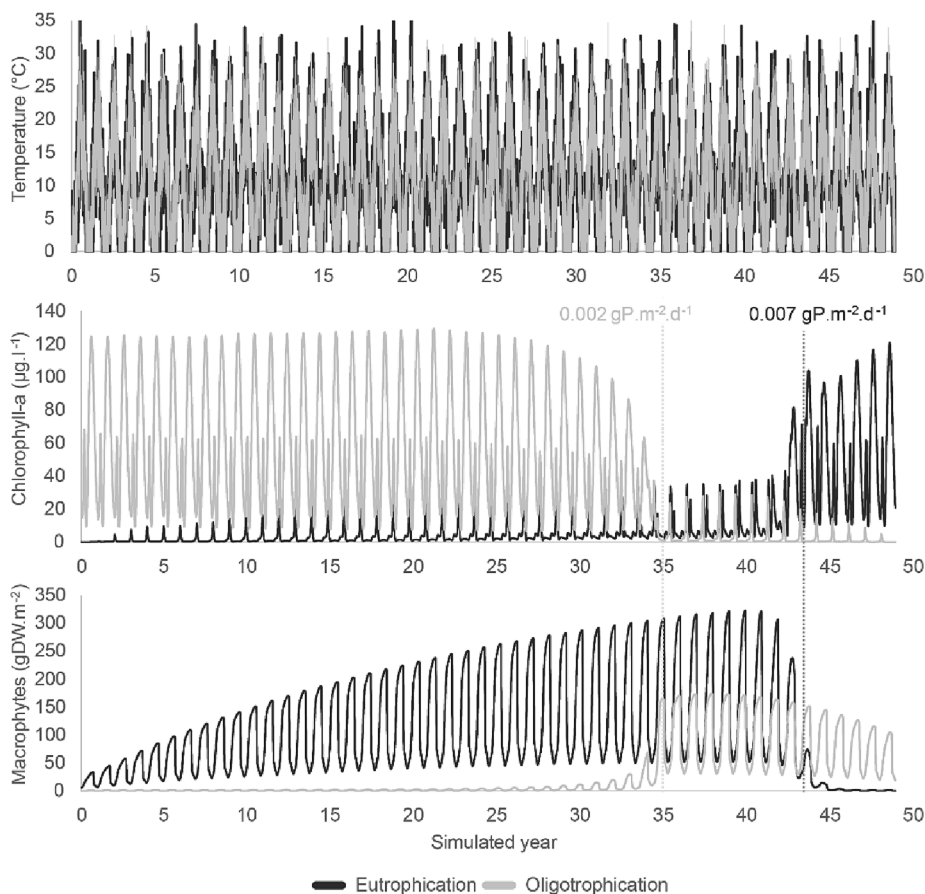


Fig. 3. Changing chlorophyll-a and macrophyte biomass over time for eutrophication and oligotrophication scenarios. While the regime shift was driven by gradual changes in phosphorus load, responses to perturbations in temperature patterns (top panel, black: temperature dynamics in the eutrophication scenario, grey: temperature dynamics in the oligotrophication scenario) allowed detection of EWI trends over time. In the eutrophication scenario (black lines) chlorophyll-a concentrations (middle panel) show a sudden increase concomitant to a sudden loss in macrophyte biomass (lower panel). In the oligotrophication scenario (grey lines) the opposite biomass patterns were observed.

3.2. Breakpoint and EWI detection

Both breakpoint analysis methods detected significant breakpoints in the time series of each variable around the shift from clear to turbid or vice versa (Table 1). The two methods for breakpoint detection yielded similar results in the eutrophication scenario (F-statistics *mean*: 42.49, *sd*: 3.12; first differencing *mean*: 43.73, *sd*: 2.24) which did not differ significantly ($t(39.886) = -1.5382, p = 0.1319$), and in the oligotrophication scenario (F-statistics *mean*: 35.18, *sd*: 2.31; first differencing *mean*: 33.89, *sd*: 5.43) which did not differ significantly either ($t(29.708) = 1.0459, p = 0.3041$).

The daily phytoplankton chlorophyll-a time series showed clear positive EWIs in both, eutrophication and oligotrophication scenarios (Fig. 4). All three EWIs were detected in weekly and monthly sampling frequencies, AR1 and DR were not detectable in longer sampling intervals of e.g., three months (quarterly) or six months (half-yearly) (Fig. 4). Sampling at yearly intervals during the growing season or integrating daily measurements per calendar year (yearly-integrated sampling) allowed again the detection of positive EWIs in AR1 and SD. The other variable directly involved in the competition underlying the regime shift, submerged vegetation dry weight, showed a similar pattern in the eutrophication scenario, but a rather different pattern in the oligotrophication scenario (Fig. 4). Overall, in the eutrophication scenario, SD indicated the change in variability across all sampling intervals quite robustly. Notably, DR could not be calculated on yearly intervals as yearly data have by default a frequency of one and therefore do not provide the data structure to compare low to high frequencies, precluding the use of this particular EWI in the yearly interval data.

Positive EWIs were detected also in almost all of the other variables, including those are directly involved in the competition underlying the regime shift (epilimnion chlorophyll-a (oChla), and submerged

vegetation biomass (sDVeg)), easily measurable variables that reflect changes in epilimnion chlorophyll-a (epilimnion transparency (aTransparencyEpi), Secchi depth (aSecchiEpi) or epilimnion oxygen saturation (oO2WEpi)), as well as higher trophic levels and dissolved nutrient stocks in the water column and the sediment pore water (Fig. 5). Again, detection of EWIs seemed to work more reliably with high-frequency data and deteriorated with increasing sampling intervals except for both, yearly intervals sampled during the growing season and integrated yearly samples representing an average of all daily measurements of a calendar year. This dependency in EWI detection on sampling frequency was more prominent in AR1 (Fig. 5 red dots) and DR (Fig. 5 blue dots), whereas it was much less pronounced in SD (Fig. 5 green dots).

4. Discussion

Using a virtual lake approach, we explored the best choice of variables and sampling frequencies to identify EWIs in shallow lakes undergoing a resource competition based regime shift driven by gradual changes in nutrient loading. We took advantage of time series of ecosystem and food-web variables generated in PCLake+ using long gradual eutrophication and oligotrophication scenarios. PCLake+ is a model known for its representation of both hysteresis as well as critical transitions in ecological states of lakes from clear, macrophyte dominated, to turbid phytoplankton dominated conditions. While the extend of water systems experiencing hysteresis is, and has been, debated in the past (van Nes and Scheffer, 2005; Capon et al., 2015; Andersen et al., 2020; Davidson et al., 2023), lakes are known to be able to show relatively sudden shifts in ecology (e.g., Carpenter et al., 2001; Ibelings et al., 2007). However, lake size and spatial heterogeneity play a critical role in determining whether or not critical transitions and hysteresis will occur, with large lakes unlikely to display hysteresis (Janssen et al.,

Table 1

Table of all tested PCLake+ variables with explanation and unit (N = nitrogen, P = phosphorus). Breakpoints (BP) dates are evaluated by F statistic and first differencing. Direction of change (d = decrease, i = increase) is indicated for both, eutrophication and oligotrophication scenarios. Median and standard deviation (sd) of breakpoints is noted at the end of the table.

Variable	Explanation	Eutrophication				Oligotrophication				Shift	
		BP date F test (year)	sup.F (Fstat)	BP p	BP date first diff (year)	BP date F test (year)	sup.F (Fstat)	BP p	BP date first diff (year)		
oChla	Total chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	43.200	502,410	< 2.2e-16	43.348	i	35.844	248,210	< 2.2e-16	35.140	d
aSecchiEpi	Secchi depth (m)	43.386	154,750	< 2.2e-16	43.337	d	36.197	729,610	< 2.2e-16	35.167	i
aTransparencyEpi	Transparency (m^{-1})	43.386	154,750	< 2.2e-16	43.192	d	36.197	729,610	< 2.2e-16	35.101	i
oNH4WEpi	N in dissolved NH_4 (gN m^{-3})	43.800	107,190	< 2.2e-16	43.825	d	35.200	30,012	< 2.2e-16	34.910	d
oNO3WEpi	N in dissolved NO_3 (gN m^{-3})	44.003	143,950	< 2.2e-16	44.011	d	28.049	823,180	< 2.2e-16	9.205	d
oPO4WEpi	P in dissolved PO_4 (gP m^{-3})	43.003	46,898	< 2.2e-16	44.145	d	28.786	560,540	< 2.2e-16	35.288	d
TP_Epi	Total phosphorus (gP m^{-3})	43.501	77,685	< 2.2e-16	43.921	i	35.803	155,490	< 2.2e-16	34.999	d
oSiO2WEpi	Dissolved SiO_2 (gSi m^{-3})	42.852	179,640	< 2.2e-16	43.008	d	36.246	287,900	< 2.2e-16	35.123	i
oO2WEpi	Dissolved O_2 ($\text{gO}_2 \text{m}^{-3}$)	43.033	120,270	< 2.2e-16	43.822	d	36.255	171,830	< 2.2e-16	34.981	i
oDDetWEpi	Detritus dry weight (gDW m^{-3})	44.003	143,590	< 2.2e-16	44.140	i	36.052	461,850	< 2.2e-16	35.244	d
oDIMWEpi	Inorganic matter dry weight (gDW m^{-3})	44.003	288,540	< 2.2e-16	44.904	i	35.099	28,820	< 2.2e-16	34.907	d
oDDiatWEpi	Diatom dry weight (gDW m^{-3})	43.896	215,010	< 2.2e-16	43.953	i	36.047	672,690	< 2.2e-16	34.973	d
oDGrenWEpi	Green algae dry weight (gDW m^{-3})	43.622	533,920	< 2.2e-16	43.945	i	34.438	66,370	< 2.2e-16	34.912	d
oDBlueWEpi	Cyanobacteria dry weight (gDW m^{-3})	43.115	109,430	< 2.2e-16	43.203	i	35.564	153,950	< 2.2e-16	35.096	d
oDZooEpi	Zooplankton dry weight (gDW m^{-3})	32.759	18,813	< 2.2e-16	43.945	i	36.241	2E + 06	< 2.2e-16	35.737	d
sDFiAd	Adult fish dry weight (gDW m^{-2})	44.003	22,564	< 2.2e-16	44.162	i	37.014	160,150	< 2.2e-16	35.866	i
sDFiJv	Juvenile fish dry weight (gDW m^{-2})	44.003	60,595	< 2.2e-16	44.523	i	36.309	971,580	< 2.2e-16	35.216	d
sDPisc	Predatory fish dry weight (gDW m^{-2})	44.000	431,580	< 2.2e-16	47.288	d	32.586	145,830	< 2.2e-16	31.838	i
sNH4S	N in dissolved NH_4 sediment pore water (gN m^{-2})	42.340	124,610	< 2.2e-16	45.096	d	35.841	104,660	< 2.2e-16	35.115	d
sNO3S	N in dissolved NO_3 sediment pore water (gN m^{-2})	40.756	1,714,200	< 2.2e-16	45.490	i	36.148	425,740	< 2.2e-16	35.123	d
sPO4S	P in dissolved PO_4 sediment pore water (gP m^{-2})	33.033	22,174	< 2.2e-16	34.356	i	36.351	131,590	< 2.2e-16	35.101	d
sDVeg	Submerged vegetation dry weight (gDW m^{-2})	43.756	236,560	< 2.2e-16	44.005	d	36.219	243,200	< 2.2e-16	35.197	i
sDBent	Zoobenthos dry weight sediment (gDW m^{-2})	44.003	96,244	< 2.2e-16	44.142	d	36.564	169,160	< 2.2e-16	35.214	i
median		43.501			43.953		36.052			35.115	

(continued on next page)

Table 1 (continued)

Variable	Explanation	Eutrophication			Oligotrophication							
		BP date F test (year)	sup.F (Fstat)	BP p	BP date first diff (year)	Shift	BP date F test (year)	sup.F (Fstat)	BP p	BP date first diff (year)	Shift	
standard deviation		3.119			2.235		2.310				5.430	

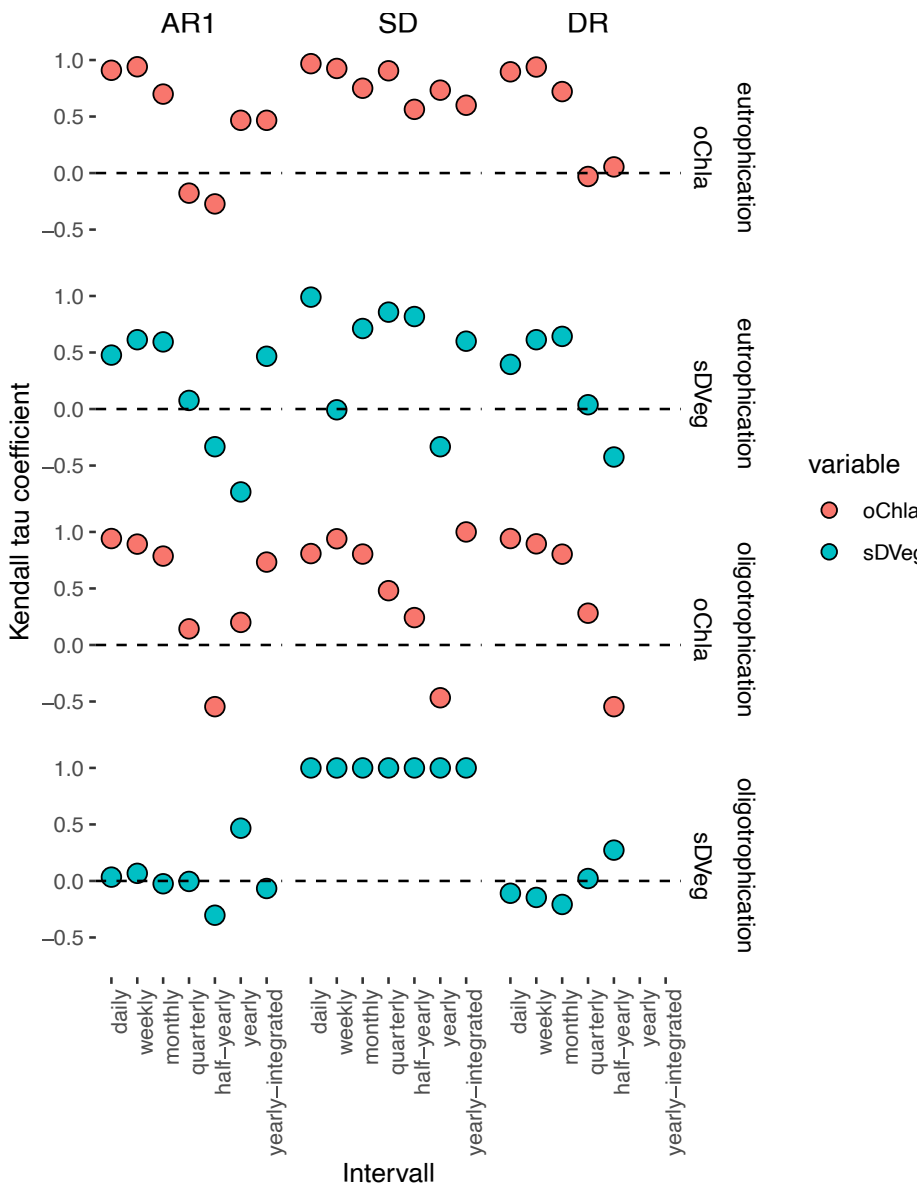


Fig. 4. Kendall tau coefficients for EWIs AR1, SD and DR (columns) for the PCLake+ variables epilimnion chlorophyll-a (oChla, orange) and submerged vegetation dry weight (sDVeg, green) in the eutrophication (upper two rows) and the oligotrophication (lower two rows) scenarios showing how all three EWIs were generally well detected in time series of daily to monthly and in the yearly-integrated frequency but not in time series of quarterly or half-yearly frequency. Note that the signals for submerged vegetation in the oligotrophication scenario deviate with high values overall for SD and a different pattern for AR1 and DR. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2014, 2017) (. Similarly, in smaller lakes, the spatial distribution of lake inflow of water and nutrients is key in determining both hysteresis as well as the linearity of the response of the lake (Janssen et al., 2019b). Here we simulated a lake without spatial differentiation in both nutrient load or water inflow, which translates to a lake with diffuse nutrient loading and water inflow originating from seepage and rainfall (i.e both being equally distributed over the lake). In drainage lakes, or point source loaded lakes, hysteresis would be less apparent. Nonetheless, sudden shifts can still occur, and hence early warning signals can also be expected in different lake types (Janssen et al., 2019b). Primarily though, when projecting our results on the real world they will fit best within the context of relatively small, temperate, diffuse, seepage shallow lakes. We virtually sampled 23 variables of PCLake+, tested

them for temporal breakpoints and evaluated the effect of sampling interval and temporal integration on the detectability of three commonly used EWIs. Breakpoints with high temporal consistency and positive EWIs were detected in variables directly involved in the critical transition (chlorophyll-a and phytoplankton biomasses). While chlorophyll-a showed the expected EWIs in both, the eutrophication scenario as well as the oligotrophication scenario, the submerged vegetation showed low values in AR1 and DR in the reoligotrophication scenario. This may be due to the very low amount of submerged vegetation at the start of the reoligotrophication period which may make it more difficult to pick up changes in temporal autocorrelation and density ratio. Moreover, breakpoints and EWIs were also detected in all the other variables tested, indicating that the changes in phytoplankton are

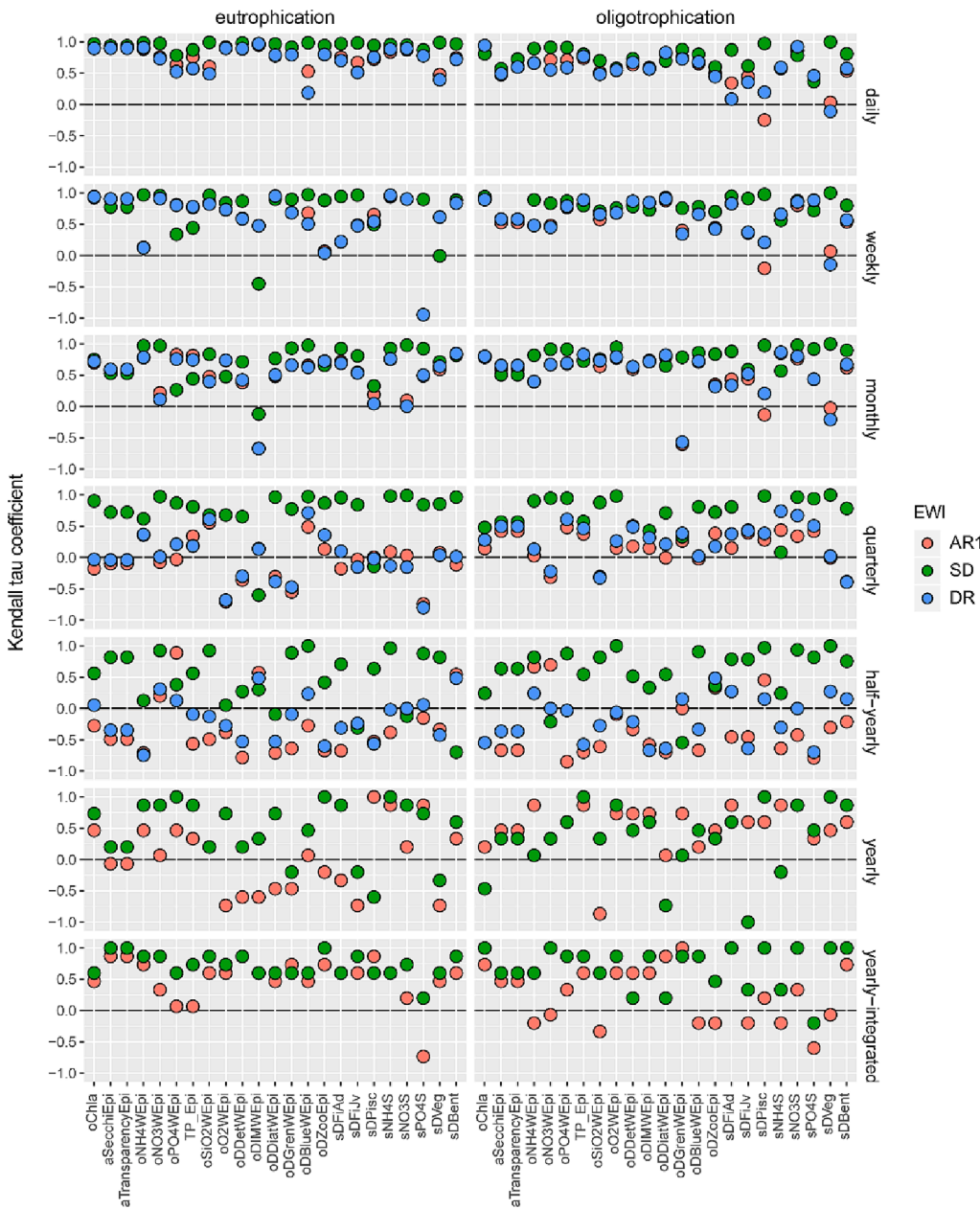


Fig. 5. Dot plot of Kendall tau coefficients for AR1 (red), SD (green) and DR (blue) per state variable in PCLake+ and per scenario visualising the distribution of the three EWIs. Note that intervals daily to half-yearly comprise three early warning indicators (autoregression at lag-1 (AR1), standard deviation (SD) and density ratio (DR)) while yearly and yearly-integrated comprise two early warning indicators (autoregression at lag-1 (AR1), standard deviation (SD)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

passed on through the entire food web. Based on daily time series, positive EWIs were found in all 23 variables except for predatory fish (negative AR1 in the oligotrophication scenario) and submerged vegetation (negative DR in the oligotrophication scenario). Overall, the probability of detecting positive EWIs decreased with longer sampling intervals except for yearly as well as yearly integrated sampling.

Realistically achievable sampling frequencies vary among water quality variables, contingent on costs, technical feasibility, or time constraints. We focused on testing relevant sampling frequencies that lake managers are likely to have available. First, sampling frequencies tested in our study included relatively high-frequency sampling (daily) that could be realised with automated sampling stations or probes (e.g. (Batt et al., 2019)), which give good temporal resolution but usually cover little spatial area and are only available for a limited set of biological variables such as photosynthetic pigments (chlorophyll-a, phycocyanin), or physical and chemical variables such as irradiance or dissolved oxygen. Second, we tested time intervals that are traditionally used for a wide variety of variables in long-term monitoring of water

bodies (weekly, monthly, quarterly, half-yearly and yearly) and typically vary per measured variable in their practically realisable temporal resolution and spatial coverage (e.g., zooplankton, fish, submerged vegetation). Third, we also tested a temporally integrated sampling interval (yearly-integrated) that corresponds to sampling methods such as passive samplers or paleolimnological approaches, which integrate over time (smoothing out extremes) but are also only available for a limited set of variables that preserve well, such as diatom frustules (Beck et al., 2018). We would also like to point out that our method did not account for observational errors, either systematic or random. In particular, random observational errors may end up in the residual timeline, resulting in lower confidence in detectability of the EWIs in real world observational data (Perretti and Munch, 2012).

Even if positive EWIs are found in empirical time series, their correct interpretation is often hampered by a lack of knowledge of the mechanisms causing the regime shift and, hence, the type of regime shift that the lake is approaching. Positive EWI patterns can also be found in a wider range of transitions and may indicate a potential increase in

system sensitivity to perturbations rather than the approach of an impending catastrophic transition (Boettiger et al., 2013; Kéfi et al., 2013). Therefore, a positive EWI on its own without mechanistic context is not a reliable indication for an approaching regime shift (Spears et al., 2017). False-positive EWIs provide a wrong prediction of the future trajectory of the ecosystem, and any management action based on these false positives would lead to waste of effort, resources and trust in scientific advice (Spears et al., 2016). In real-world systems, it is often difficult to ascertain whether an ecosystem state is in transit towards a critical transition. To assess the nature of a regime shift empirically would require that the ecosystem is observed for both deterioration and recovery trajectory to ascertain the presence of hysteresis. However, this would only be possible in hindsight, thereby refuting the idea of EWIs as preventative management indicators. Here, creating a virtual lake by calibrating PCLake+ for the lake in question and running a basic critical transition check can help assess whether the lake can show alternative stable states at all and thereby inform whether any observed positive EWIs are likely true or false positives. True positive EWIs are expected in variables directly affected by gradually changing pressures, in our case phytoplankton biomasses responding to changing nutrients. We found positive EWIs and clear breakpoints for all phytoplankton groups (diatoms, green algae, or cyanobacteria) as well as for derivative variables such as chlorophyll-a, transparency and Secchi depth. Temporal breakpoints and positive EWIs were also observed in other food web variables (e.g., zooplankton biomass, fish biomass), even though these have no direct mechanistic link to the changing nutrient pressure. These variables are linked to the changes in phytoplankton biomass and follow this change, hence EWIs observed in these variables represent a different type of regime shift not directly linked to critical transitions (Boettiger et al., 2013; Kéfi et al., 2013). Nonetheless, positive EWIs in these variables, suggest that the higher trophic level variables (e.g., zooplankton, fish) absorb signals of change in the lower levels of the food web and therefore can show a similar data structure as the phytoplankton variables.

In our virtual lake data, the detection of positive EWIs generally decreased with longer sampling intervals, particularly in the case of AR1 and DR. Interestingly, yearly sampling intervals yielded again a higher probability of detecting EWIs, likely helped by our choice of sampling during the summer and thus growth season and thereby close to the peak of productivity. Also, yearly averaging of daily measurements yielded a higher probability of detecting EWIs, explaining why time-integrated measures such as passive samplers or paleolimnological approaches can be quite successful at detecting EWIs (Frossard et al., 2015; Lenton et al., 2012; Spanbauer et al., 2014). Integration of high-frequency measurements over longer time scales has already been shown to capture trends in AR1 independently of time scale quite well (Batt et al., 2019; 2013) and therefore seems an advisable strategy if high-frequency data cannot be collected or is available but released or reliable only at lower frequencies. However, many existing monitoring schemes rely on measurements taken during field trips at regular intervals and therefore are better represented in our non-time-integrated sampling approach (i. e., daily to yearly point sampling). While our results show that the frequency of sampling intervals likely matters for the detection of EWIs, many variables are not easily or meaningfully measured at daily or even weekly intervals (e.g., fish, submerged vegetation). Our approach of using the ecosystem model PCLake+ to assess which variables and sampling intervals are promising for the detection of EWIs generates new avenues for lake managers to make informed choices on sampling schemes and alarm thresholds (Pace et al., 2017) for their lake in question.

Our study shows that variables for the detection of EWIs that are within the capacity of lake managers to measure appear to exist, both in terms of costs and in terms of time investment. Despite this promising news, a bigger question remains as to whether or not managers are capable of responding quickly enough to EWIs, particularly in the case of yearly measurements (Davidson et al., 2018; Spears et al., 2016). This

question is two-fold, on the one hand relying strongly on the efficacy of measures to turn the tide of an oncoming critical transition and on the other hand relying on the time frame in which measures may be implemented (Biggs et al., 2009; Pace et al., 2017). PCLake+ is already capable of implementing numerous measures (e.g., mowing (Kuiper et al., 2017), dredging (Janse and van Lieere, 1995), flushing and bio-manipulation (Janssen et al., 2019b)). In our example, the underlying mechanism for the regime shift is a change in competitive ability between phytoplankton and submerged plants driven by changes in nutrient loading. Few studies explore other mechanisms that can cause regime shifts in aquatic systems such as trophic cascades (Carpenter et al., 2001) or intraguild predation (Scharfenberger et al., 2013), and to our knowledge, none assessed the influence of sampling frequencies for variables in regime shifts caused by these mechanisms (Kéfi et al., 2019). Combined with expert knowledge on the time-to-act of such measures, PCLake+ could be used to design a monitoring scheme focussed on early-warning detection and measure deployment. Furthermore, the model may also serve to assess the continued utility of such a scheme in a changing world (Mooij et al., 2007; Nielsen et al., 2014).

5. Conclusions

Lake water quality management could benefit from early detection of ecological instability (Spears et al., 2016). Yet due to high uncertainties in the practical application of EWIs on empirical data from monitoring schemes in natural ecosystems (Burthe et al., 2016; Gsell et al., 2016), resilience-based management needs further development. Here we used a relatively complex model to mimic possible field measurement strategies. Creating virtual ecosystems for testing system resilience and response to management actions may provide a way forward to help make informed choices in ecosystem management. Our modelling approach elucidated three important suggestions that can push future resilient-based management forward. First, managers should aim for frequent measurements with a minimum of one measurement per month. Ideally, measurements are carried out weekly or daily, to improve EWI detection and strength. Strikingly though, yearly measurements in summer or even yearly time-integrated measurements from, for example, sediment cores may also serve as a good data basis for evaluating EWIs. The latter may be especially useful when sites are not easily accessible, or time or financial capacities are limited. In such cases, single summer measurements of chlorophyll-a or vegetation, or, alternatively, integrated samples of diatom abundances (Beck et al., 2018) or integrated phosphorus or nitrogen measurements using passive samplers (Rozemeijer et al., 2010) may prove useful. The drawback, however, is that the low sampling frequency may not leave enough time for reactive management. Second, easily measurable variables such as chlorophyll-a, transparency, Secchi depth and oxygen concentration showed good results indicating that EWI detection does not necessarily need very advanced and expensive equipment. This is especially useful when considered in the context of citizen science, allowing water managers to employ citizens as sensors armed with easily available measurement tools such as a simple Secchi disk or a cheap oxygen probe. Third, due to variation within the different PCLake+ variables, we suggest that a multi-variable approach in which a suite of variables is used to detect EWIs would improve the early detection of ecological instability. Based on our virtual lake exercise, we thus advise managers to ideally aim for high-frequency measurements of multiple easily and cheaply measurable variables that are known for their low observational errors (e.g., oxygen concentration) or focus on integrated approaches using passive samplers or sedimented material (e.g., yearly integrated phosphorus concentrations in water). Our work here shows that EWIs are likely detectable at time scales and in measurements widely available to water management, thereby making them an effective tool for lake managers in their struggle to prevent lake critical transitions in the face of global change.

6. Data statement

The script for the generation of the data through the ecosystem model PCLake+ and the resulting time series are available at 10.5281/zenodo.7042516.

CRedit authorship contribution statement

Alena S. Gsell: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Sven Teurlincx:** Conceptualization, Methodology, Software, Writing – original draft, Writing – review & editing. **Rita Adrian:** Conceptualization, Writing – review & editing. **Annette B.G. Janssen:** Conceptualization, Methodology, Software, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

The script for the generation of the data through the ecosystem model PCLake+ and the resulting time series are available at 10.5281/zenodo.7042516.

Acknowledgements

ASG and ABGJ were funded by the Talent Programme Veni of the Netherlands Organisation for Scientific Research (NWO) under Grant numbers 016.Veni.171.063 and VI.Veni.194.002 respectively. We also thank two anonymous reviewers for their thoughtful and constructive comments which helped improve the manuscript. The authors declare no financial interest or benefits arising from this work and no scientific or personal conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.110424>.

References

- Andersen, T., Carstensen, J., Hernandez-Garcia, E., Duarte, C.M., 2009. Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol. Evol.* 24 (1), 49–57.
- Andersen, T.K., Nielsen, A., Jeppesen, E., Hu, F., Bolding, K., Liu, Z., Søndergaard, M., Johansson, L.S., Trolle, D., 2020. Predicting ecosystem state changes in shallow lakes using an aquatic ecosystem model: Lake Hinge, Denmark, an example. *Ecol. Appl.* 30 (7), e02160.
- Batt RD, Carpenter SR, Cole JJ, Pace ML, Johnson RA. 2013. Changes in ecosystem resilience detected in automated measures of ecosystem metabolism during a whole-lake manipulation. *Proc. Natl. Acad. Sci.* 110(43):17398–17403.
- Batt, R.D., Eason, T., Garmestani, A., 2019. Time scale of resilience loss: implications for managing critical transitions in water quality. *PLoS One* 14 (10), e0223366.
- Beck, K.K., Fletcher, M.-S., Gadd, P.S., Hejnis, H., Saunders, K.M., Simpson, G.L., Zawadzki, A., 2018. Variance and rate-of-change as early warning signals for a critical transition in an aquatic ecosystem state: a test case from Tasmania, Australia. *J. Geophys. Res. Biogeosci.* 123 (2), 495–508.
- Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. *Front. Ecol. Environ.* 1 (7), 376–382.
- Biggs R, Carpenter SR, Brock WA. 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proc. Natl. Acad. Sci.* 106(3):826–831.
- Boettiger, C., Ross, N., Hastings, A., 2013. Early warning signals: the charted and uncharted territories. *Theor. Ecol.* 6 (3), 255–264.
- Burthe, S.J., Henrys, P.A., Mackay, E.B., Spears, B.M., Campbell, R., Carvalho, L., Dudley, B., Gunn, I.D.M., Johns, D.G., Maberly, S.C., May, L., Newell, M.A., Wanless, S., Winfield, I.J., Thackeray, S.J., Daunt, F., Allen, C., 2016. Do early warning indicators consistently predict nonlinear change in long-term ecological data? *J. Appl. Ecol.* 53 (3), 666–676.
- Capon, S.J., Lynch, A.J.J., Bond, N., Chessman, B.C., Davis, J., Davidson, N., Finlayson, M., Gell, P.A., Hohnberg, D., Humphrey, C., Kingsford, R.T., Nielsen, D., Thomson, J.R., Ward, K., Nally, R.M., 2015. Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. *Sci. Total Environ.* 534, 122–130.
- Carpenter, S.R., Brock, W.A., 2006. Rising variance: a leading indicator of ecological transition. *Ecol. Lett.* 9 (3), 311–318.
- Carpenter, S.R., Cole, J.J., Hodgson, J.R., Kitchell, J.F., Pace, M.L., Bade, D., Cottingham, K.L., Essington, T.E., Houder, J.N., Schindler, D.E., 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecol. Monogr.* 71 (2), 163–186.
- Chang, M., Teurlincx, S., Janse, J.H., Paerl, H.W., Mooij, W.M., Janssen, A.B., 2020. Exploring how cyanobacterial traits affect nutrient loading thresholds in shallow lakes: A modelling approach. *Water.* 12 (9), 2467.
- Collie, J.S., Richardson, K., Steele, J.H., 2004. Regime shifts: can ecological theory illuminate the mechanisms? *Prog. Oceanogr.* 60 (2–4), 281–302.
- Dakos, V., Carpenter, S.R., Brock, W.A., Ellison, A.M., Guttal, V., Ives, A.R., Kéfi, S., Livina, V., Seekell, D.A., van Nes, E.H., Scheffer, M., Yener, B., 2012. Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. *PLoS One* 7 (7), e41010.
- Davidson, T.A., Bennion, H., Reid, M., Sayer, C.D., Whitmore, T.J., 2018. Towards better integration of palaeoecology: from proxies to indicators, from inference to understanding. *J. Paleolimnol.* 60 (2), 109–116.
- Davidson, T.A., Sayer, C.D., Jeppesen, E., Søndergaard, M., Lauridsen, T.L., Johansson, L.S., Baker, A., Graeber, D., 2023. Bimodality and alternative equilibria do not help explain long-term patterns in shallow lake chlorophyll-a. *Nat. Commun.* 14 (1), 398.
- Frossard, V., Saussereau, B., Perasso, A., Gillet, F., 2015. What is the robustness of early warning signals to temporal aggregation? *Front. Ecol. Evol.* 3, 112.
- Gerla, D.J., Gsell, A.S., Kooi, B.W., Ibelings, B.W., Van Donk, E., Mooij, W.M., 2013. Alternative states and population crashes in a resource-susceptible-infected model for planktonic parasites and hosts. *Freshw. Biol.* 58 (3), 538–551.
- Gilarranz LJ, Narwani A, Odermatt D, Siber R, Dakos V. 2022. Regime shifts, trends, and variability of lake productivity at a global scale. *Proc. Natl. Acad. Sci.* 119(35): E2116413119.
- Gsell, A.S., Scharfenberger, U., Özkundakci, D., Walters, A., Hansson, L.-A., Janssen, A.B. G., Nöges, P., Reid, P.C., Schindler, D.E., Van Donk, E., Dakos, V., Adrian, R., 2016. Evaluating early-warning indicators of critical transitions in natural aquatic ecosystems. *Proc. Natl. Acad. Sci.* 113 (50).
- Hilt, S., Gross, E.M., 2008. Can allelopathically active submerged macrophytes stabilize clear-water states in shallow lakes? *Basic Appl. Ecol.* 9 (4), 422–432.
- Ibelings, B.W., Portielje, R., Lammens, E.H.R.R., Noordhuis, R., van den Berg, M.S., Jooze, W., Meijer, M.L., 2007. Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. *Ecosystems* 10 (1), 4–16.
- Ives, A.R., 1995. Measuring resilience in stochastic systems. *Ecol. Monogr.* 65 (2), 217–233.
- James, W.F., Best, E.P., Barko, J.W., 2004. Sediment resuspension and light attenuation in Peoria Lake: can macrophytes improve water quality in this shallow system? *Hydrobiologia* 515 (1–3), 193–201.
- Janse JH, van Liere L. 1995. PCLake: a modelling tool for the evaluation of lake restoration scenarios. *Water Sci. Technol.* 31(8):371.
- Janse, J.H., de Senerpont Domis, L.N., Scheffer, M., Lijklema, L., Van Liere, L., Klinge, M., Mooij, W.M., 2008. Critical phosphorus loading of different types of shallow lakes and the consequences for management estimated with the ecosystem model PCLake. *Limnologia* 38 (3–4), 203–219.
- Janse, J.H., Scheffer, M., Lijklema, L., Van Liere, L., Sloot, J.S., Mooij, W.M., 2010. Estimating the critical phosphorus loading of shallow lakes with the ecosystem model PCLake: sensitivity, calibration and uncertainty. *Ecol. Model.* 221 (4), 654–665.
- Janssen, A.B., Teurlincx, S., An, S., Janse, J.H., Paerl, H.W., Mooij, W.M., 2014. Alternative stable states in large shallow lakes? *J. Great Lakes Res.* 40 (4), 813–826.
- Janssen, A.B., de Jager, V.C., Janse, J.H., Kong, X., Liu, S., Ye, Q., Mooij, W.M., 2017. Spatial identification of critical nutrient loads of large shallow lakes: Implications for Lake Taihu (China). *Water Res.* 119, 276–287.
- Janssen, A.B., Teurlincx, S., Beusen, A.H., Huijbregts, M.A., Rost, J., Schipper, A.M., Seelen, L.M., Mooij, W.M., Janse, J.H., 2019a. PCLake+: A process-based ecological model to assess the trophic state of stratified and non-stratified freshwater lakes worldwide. *Ecol. Model.* 396, 23–32.
- Janssen, A.B., van Wijk, D., van Gerven, L.P., Bakker, E.S., Brederveld, R.J., DeAngelis, D.L., Janse, J.H., Mooij, W.M., 2019b. Success of lake restoration depends on spatial aspects of nutrient loading and hydrology. *Sci. Total Environ.* 679, 248–259.
- Janssen, A.B., Hilt, S., Kosten, S., de Klein, J.J., Paerl, H.W., Van de Waal, D.B., 2021. Shifting states, shifting services: Linking regime shifts to changes in ecosystem services of shallow lakes. *Freshw. Biol.* 66 (1), 1–2.
- Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), 2012. The structuring role of submerged macrophytes in lakes. Springer Science & Business Media.
- Kéfi, S., Dakos, V., Scheffer, M., Van Nes, E.H., Rietkerk, M., 2013. Early warning signals also precede non-catastrophic transitions. *Oikos* 122 (5), 641–648.
- Kéfi, S., Domínguez-García, V., Donohue, I., Fontaine, C., Thébaud, E., Dakos, V., Coulson, T., 2019. Advancing our understanding of ecological stability. *Ecol. Lett.* 22 (9), 1349–1356.
- Kuiper, J.J., Van Altena, C., De Ruiter, P.C., Van Gerven, L.P.A., Janse, J.H., Mooij, W.M., 2015. Food-web stability signals critical transitions in temperate shallow lakes. *Nat. Commun.* 6, 7727.

- Kuiper, J.J., Verhofstad, M.J., Louwers, E.L., Bakker, E.S., Brederveld, R.J., van Gerven, L.P., Janssen, A.B., de Klein, J.J., Mooij, W.M., 2017. Mowing submerged macrophytes in shallow lakes with alternative stable states: battling the good guys? *Environ. Manag.* 59 (4), 619–634.
- Lenton, T.M., Livina, V.N., Dakos, V., Van Nes, E.H., Scheffer, M., 2012. Early warning of climate tipping points from critical slowing down: comparing methods to improve robustness. *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.* 370 (1962), 1185–1204.
- May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269 (5628), 471–477.
- Mooij, W.M., Janse, J.H., De Senerpont Domis, L.N., Hülsmann, S., Ibelings, B.W., 2007. Predicting the effect of climate change on temperate shallow lakes with the ecosystem model PCLake. In: Gulati, R.D., Lammens, E., De Pauw, N., Van Donk, E. (Eds.), *Shallow Lakes in a Changing World*. Springer Netherlands, Dordrecht, pp. 443–454.
- Nielsen, A., Trolle, D., Bjerring, R., Søndergaard, M., Olesen, J.E., Janse, J.H., Mooij, W. M., Jeppesen, E., 2014. Effects of climate and nutrient load on the water quality of shallow lakes assessed through ensemble runs by PCLake. *Ecol. Appl.* 24 (8), 1926–1944.
- Pace, M.L., Batt, R.D., Buelo, C.D., Carpenter, S.R., Cole, J.J., Kurtzweil, J.T., Wilkinson, G.M., 2017. Reversal of a cyanobacterial bloom in response to early warnings. *Proc. Natl. Acad. Sci.* 114 (2), 352–357.
- Perretti, C.T., Munch, S.B., 2012. Regime shift indicators fail under noise levels commonly observed in ecological systems. *Ecol. Appl.* 22 (6), 1772–1779.
- R Core Team.** 2018. **R: A Language and Environment for Statistical Computing** [Internet]. **R Foundation for Statistical Computing**. <https://www.R-project.org>.
- Ripple, W.J., Wolf, C., Newsome, T.M., Galetti, M., Alamgir, M., Crist, E., Mahmoud, M. I., Laurance, W.F., 2017. 15,364 Scientist Signatories from 184 Countries., 2017. World scientists' warning to humanity: a second notice. *BioScience* 67 (12), 1026–1028.
- Rozemeijer, J., Van Der Velde, Y.P.E., de Jonge, H., van Geer, F., Broers, H.-P., Bierkens, M., 2010. Application and evaluation of a new passive sampler for measuring average solute concentrations in a catchment scale water quality monitoring study. *Environ. Sci. Tech.* 44 (4), 1353–1359.
- Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology Evolution.* 18(12)-648-56.
- Scharfenberger, U., Mahdy, A., Adrian, R., 2013. Threshold-driven shifts in two copepod species: Testing ecological theory with observational data. *Limnol. Oceanogr.* 58 (2), 741–752.
- Scheffer, M., 2009. *Critical Transitions in Nature and Society*. Princeton University Press, Princeton, Oxford.
- Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8 (8), 275–279.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413 (6856), 591–596.
- Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., Van Nes, E.H., Rietkerk, M., Sugihara, G., 2009. Early-warning signals for critical transitions. *Nature* 461 (7260), 53–59.
- Scheffer, M., Jeppesen, E., 2007. Regime shifts in shallow lakes. *Ecosystems* 10 (1), 1–3.
- Siegert, S., Friedrich, R., 2001. Modeling of nonlinear Lévy processes by data analysis. *Phys. Rev. E* 64 (4), 041107.
- Spanbauer, T.L., Allen, C.R., Angeler, D.G., Eason, T., Fritz, S.C., Garmestani, A.S., Nash, K.L., Stone, J.R., Aston, J.A.D., 2014. Prolonged instability prior to a regime shift. *PLoS One* 9 (10), e108936.
- Spears, B.M., Carvalho, L., Futter, M.N., May, L., Thackeray, S.J., Adrian, R., Angeler, D. G., Burthe, S.J., Davidson, T.A., Daunt, F., 2016. Ecological instability in lakes: A predictable condition? *Environ. Sci. Tech.* 50, 3285–3286.
- Spears, B.M., Futter, M.N., Jeppesen, E., Huser, B.J., Ives, S., Davidson, T.A., Adrian, R., Angeler, D.G., Burthe, S.J., Carvalho, L., Daunt, F., Gsell, A.S., Hessen, D.O., Janssen, A.B.G., Mackay, E.B., May, L., Moorhouse, H., Olsen, S., Søndergaard, M., Woods, H., Thackeray, S.J., 2017. Ecological resilience in lakes and the conjunction fallacy. *Nat. Ecol. Evol.* 1 (11), 1616–1624.
- Timms, R.M., Moss, B., 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol. Oceanogr.* 29 (3), 472–486.
- van Donk, E., Gulati, R.D., 1995. Van Donk E, Gulati RD. 1995. Transition of a lake to turbid state six years after biomanipulation. *Water Sci. Technol.* 32 (4), 197–206.
- van Gerven, L.P.A., Brederveld, R.J., de Klein, J.J.M., DeAngelis, D.L., Downing, A.S., Faber, M., Gerla, D.J., Hoen, J. 't, Janse, J.H., Janssen, A.B.G., Jeuken, M., Kooi, B. W., Kuiper, J.J., Lischke, B., Liu, S., Petzoldt, T., Schep, S.A., Teurlincx, S., Thiange, C., Trolle, D., van Nes, E.H., Mooij, W.M., 2015. Advantages of concurrent use of multiple software frameworks in water quality modelling using a database approach. *Fundam. Appl. Limnol./Archiv für Hydrobiologie.* 186 (1-2), 5–20.
- van Nes, E.H., Scheffer, M., 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* 86 (7), 1797–1807.
- Van Nes, E.H., Scheffer, M., 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *Am. Nat.* 169 (6), 738–747.
- Verdy, A., Amarasekare, P., 2010. Alternative stable states in communities with intraguild predation. *J. Theor. Biol.* 262 (1), 116–128.
- Vermaat, J.E., Santamaria, L., Roos, P.J., 2000. Water flow across and sediment trapping in submerged macrophyte beds of contrasting growth form. *Arch. Hydrobiol.* 148 (4), 549–562.
- Zeileis A, Leisch F, Hornik K, Kleiber C. 2001. *strucchange*. An R package for testing for structural change in linear regression models.