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ORIGINAL PAPER

Chemical contamination-mediated regime shifts in planktonic systems

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Abstract
Abrupt transitions leading to algal blooms are quite well known in aquatic ecosystems and have important implications for the environment. These ecosystem shifts have been largely attributed to nutrient dynamics and food web interactions. Contamination with heavy metals such as copper can modulate such ecological interactions which in turn may impact ecosystem functioning. Motivated by this, we explored the effect of copper enrichment on such regime shifts in planktonic systems. We integrated copper contamination to a minimal phytoplankton–zooplankton model which is known to demonstrate abrupt transitions between ecosystem states. Our results suggest that both the toxic and deficient concentration of copper in water bodies can lead to regime shift to an algal-dominated alternative stable state. Further, interaction with fish density can also lead to collapse of population cycles thus leading to algal domination in the intermediate copper ranges. Environmental stochasticity may result in state transition much prior to the tipping point and there is a significant loss in the bimodality on increasing intensity and redness of noise. Finally, the impending state shifts due to contamination cannot be predicted by the generic early warning indicators unless the transition is close enough. Overall the study provides fresh impetus to explore regime shifts in ecosystems under the influence of anthropogenic changes like chemical contamination.

Keywords Copper pollution · Phytoplankton–zooplankton system · Alternative stable states · Stochasticity · Early warning signals

Introduction

Ecosystems may undergo abrupt transitions to states with fundamentally different characteristics (Scheffer et al. 2001; Scheffer and Carpenter 2003; Rietkerk et al. 2004; Carpenter et al. 2011). Such transitions, also known as regime shifts, are often undesirable and may lead to catastrophic consequences in terms of environmental health (Petrovskii et al. 2017; Sekerci and Petrovskii 2015a, b). The existence of alternative stable states in ecosytems is thought to be the key reason behind such phenomenon (Beisner et al. 2003). In the case of lake ecosystems, shifts between turbid or algal-dominated state and clear water state are known to occur and have been of interest to environmental scientists since long (Scheffer et al. 1993; Folke et al. 2004). Consequences of algal domination in water bodies include anoxic conditions leading to losses of fish and wildlife and also economic costs in the form of loss of recreational activities (Wilson and Carpenter 1999; Carpenter 2008). These shifts are induced by interplay of several factors which includes food web interactions as well as nutrient dynamics (Scheffer 1997). Overenrichment of water bodies with nutrients like phosphorus can enhance algal growth resulting in such blooms which are not easily reversible (Carpenter 2005). However, chemical pollutants like lipophilic substances and many metals can also negatively impact aquatic communities leading to species loss. Further, these pollutants may accumulate within the organisms through food and water and are passed through

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trophic interactions to higher levels in the food chains (Kooi et al. 2008). The combined effect of how the pollutants' internal concentration within these organisms might affect various life history traits and modulate ecological interactions determines the actual nature of ecosystem functioning (Huang et al. 2013; Kooi et al. 2008; Garay-Narváez et al. 2013; Huang et al. 2015). Hence, a deeper insight into how contamination-mediated alterations affect aquatic ecology is required to build a better understanding of regime shifts in contemporary world.

Industrial wastes and run-offs from agricultural fields often end up in water bodies thus making them prone to copper pollution (Jorgensen 2010). Elevated copper concentrations in water bodies may have a toxic effect on several organisms (Flemming and Trevors 1989; Clements et al. 1992; WHO 1998) including both phytoplankton and zooplankton. Copper stress on phytoplankton cells negatively affect photosynthesis (Havens 1994) and the concentration of chlorophyll (Fargašová et al. 1999). Moreover, direct inhibition of growth has also been reported in many species due to bioaccumulation of the metal (Yan and Pan 2002). In model zooplankton species like *Daphnia*, there are evidences that toxicity due to copper can lead to reduced body length (Knops et al. 2001), growth (Koivisto et al. 1992) and survival (Ingersoll and Winner 1982). Nevertheless, copper is also biologically essential for most species (Mertz 1981) and may lead to deficiency effects when present in very low concentrations (Bossuyt and Janssen 2003). This hormetic dose-response relationship makes the study of copper even more interesting. Additionally, changing copper concentration can also modulate the trophic interaction of plankton in the food chain because of modification in behavioral traits like swimming velocity and mobility (Sullivan et al. 1983; Gutierrez et al. 2012).

Recent models of copper contamination have reinforced our understanding of plankton dynamics in polluted environments (Prosnier et al. 2015; Camara et al. 2017; Kim et al. 2018). Surprisingly, the impact on zooplankton predation by fish has been neglected in these studies, albeit fish density is a crucial factor in the context of water quality. Empirical studies (Mills et al. 1987; McQueen and Post 1988) indicate that zooplankton populations collapse when fish density crosses a critical threshold (top-down effect) (Luecke et al. 1990). Trophic cascade via zooplankton allows the fish population to indirectly regulate the phytoplankton density. This has been captured by the classic minimal model by Scheffer et al. (2000) which accounts for the complex nonlinearities involved in such interactions and the interplay between nutrient and fish density. The model demonstrates that a critical fish density can switch the ecosystem to the phytoplankton-dominated state. Further, predator-prey oscillations have been shown to favour the abrupt shift to phytoplankton domination. Although an earlier work by Banerjee et al. (2019) took into consideration the effect of copper on fish predation, unfortunately it failed to study its impact on discontinuous transitions in planktonic systems.

Here, in this paper, we will address this gap and also ask whether in the presence of predation pressure by fish, copper contamination can independently lead to such transitions in planktonic systems. Since the importance of top-down effects on planktonic regime shifts are known and both chemical influx and fish can be manipulated externally, with the help of a mathematical model we attempt to understand the interplay between contamination and fish density. Environmental stochasticity often alters the system dynamics from that predicted by its deterministic counterpart (Dennis 1998; Hastings 2004; Baudena et al. 2007). In particular, in the case of bistable models, stochasticity can induce or inhibit attractor switching the manner of which is not intuitive (Guttal and Jayaprakash 2007; Møller et al. 2009; Sharma et al. 2015). Therefore, we analyze the stochastic version of our model and lastly investigate whether generic early warnings signals can predict the regime shifts in contaminated environment.

Methods

First, the original model by Scheffer et al. (2000) is discussed briefly before incorporating the effect of copper enrichment in the system. A detailed description of the deterministic copper enriched model is provided followed by addition of stochasticity. Thereafter, the models are analyzed in order to understand how changing copper concentration influences ecological dynamics, especially regime shifts, in plankton ecosystem.

Model description

The model by Scheffer et al. (2000) is a two-dimensional phytoplankton–zooplankton model as described below:

$$\begin{aligned}\frac{dP}{dt} &= rP(1-P/K) - \frac{aPZ}{k_P+P} + i(K-P),\\ \frac{dZ}{dt} &= \chi\frac{aPZ}{k_P+P} - dZ - \frac{fZ^2}{k_Z^2+Z^2}\end{aligned} \tag{1}$$

Here, P and Z denote phytoplankton and zooplankton densities respectively. The phytoplankton population is assumed to follow a logistic growth with carrying capacity K and intrinsic growth rate r. They are predated upon by the zooplankton such that the predation follows a saturating functional response with the maximum predation rate denoted by a and the half saturation constant denoted by k_P. The parameter i in the last term of the first equation represents a diffusive inflow of phytoplankton. This is proportional to the difference between phytoplankton density in the part where the study is assumed to be carried out and the part where zooplankton is absent so that the phytoplankton are at carrying capacity. Although justification for this term has been discussed in detail in Scheffer and De Boer (1995), it is worth mentioning here that incorporation of such a stabilizing term brings the patterns generated by the minimal model close to biological reality (Scheffer et al. 2000). Further, χ denotes the conversion efficiency of the predator and d denotes its natural mortality rate. Since zooplankton forms only a part of the diet of many fish, the overall fish dynamics may not strongly depend on the zooplankton. Hence, it is reasonable to describe the fish predation as an additional mortality term in the zooplankton dynamics rather than considering explicitly the whole dynamics of fish population. This way the model complexity is also significantly reduced. The Holling type-III term used to model predation by fish signifies a type of learning behavior exhibited by fish whereby it switches to increased level of foraging on zooplankton once the prey density crosses a certain threshold (Real 1977; Hassell et al. 1977). The rate of predation continues to increase until some saturation density of the zooplankton is reached. Moreover, in this model, the term is actually representative of the average effect of such behavior demonstrated by many different fish. Here, f denotes maximum predation by fish and k_Z denotes the half saturation constant.

In order to study how copper enrichment affects plankton dynamics, we adopt the approach by Prosnier et al. (2015). The effect of copper is introduced in the above system (1) by multiplying each term in the model with the response of the associated trait to different copper concentrations. Such a response is denoted by Ψ_x, where x denotes the model parameter to which it is multiplied and the final model can be described as follows:

$$\begin{aligned}\frac{dP}{dt} &= \Psi_r \times rP(1-P/K) - \Psi_a \times \frac{aPZ}{k_P+P} + i(K-P),\\ \frac{dZ}{dt} &= \Psi_a \times \chi\frac{aPZ}{k_P+P} - \Psi_d \times dZ - \Psi_f \times \frac{f\,Z^2}{k_Z^2+Z^2}\end{aligned} \tag{2}$$

We make two important assumptions while including copper's effect in the model. First, the diffusion of phytoplankton in the system is not altered by the changing concentration of copper. There are no studies that we are aware of which have investigated the effect of copper on phytoplankton diffusion. Furthermore, it is important to note that the incorporation of the diffusive inflow term does not affect any qualitative behavior of the phytoplankton–zooplankton model (Scheffer et al. 2000) and so this model assumption helps us avoid unwarranted complexity during simulations. Second, it is assumed that copper enrichment has neither any effect on phytoplankton carrying capacity nor on the half saturation constants of functional responses. It must be noted that Ψ_x are not parameters but they are dependent on copper concentrations. A particular trait of an organism would respond to the change in internal copper concentration, C. In the following paragraphs, we explain how Ψ_x can be expressed as a function of C for each parameter x. Further, if the copper concentration in the external environment is E, then the copper present within the organism will depend on the external environment and thus can be expressed as a function of E, i.e., $C(E)$.

Modeling responses due to copper

From above, if the external copper concentration corresponding to higher E_{C50} or toxicity is denoted by h_x and lower E_{C50} or deficiency is denoted by l_x, then the corresponding internal concentration is given by $C(h_x)$ and $C(l_x)$, respectively. Suffix P and Z have been used henceforth to identify the concerned organism as phytoplankton and zooplankton, respectively. m_x and n_x are the positive and negative slope of the effect curve Ψ_x. The effect of copper, which is vital for organisms but at the same time detrimental when present in large amount, can be captured using an asymmetric double sigmoid function (see Fig. 1A, B). In case of algae, the growth rate becomes negative in the deficient and toxic ranges of copper concentrations and becomes optimum at some intermediate ranges of copper. In order to capture this, the function, Ψ_r has been chosen with a range between -1 to 1, where the maximum value is achieved at some in-between concentrations (Prosnier et al. 2015) (Fig. 1A):

$$\begin{aligned}\Psi_r =& -1 + tanh(m_r(C_P(E) - C_P(l_r)))\\ &- tanh(n_r(C_P(E) - C_P(h_r)))\end{aligned} \tag{3}$$

There are hardly any empirical studies which connects copper concentration with grazing effort. However, it has been established that the movement of zooplankton like *Daphnia* can be largely affected by copper concentration (Untersteiner et al. 2003; Gutierrez et al. 2012). In particular, there is an increased movement at an intermediate copper concentration which is an advantage for predators like *Daphnia*. As such, the effect curve of copper on grazing by zooplankton, Ψ_a can also be expressed as a double sigmoid function with maximum value 1 at the intermediate levels and minimum value 0 at toxic and deficient levels (Prosnier et al. 2015)(Fig. 1B):

$$\begin{aligned}\Psi_a =& \frac{1}{2}tanh(m_a(C_Z(E) - C_Z(l_a)))\\ &- \frac{1}{2}tanh(n_a(C_Z(E) - C_Z(h_a)))\end{aligned} \tag{4}$$

Although the increased mobility of the zooplankton helps them in their predation, it also increases their visibility to predators like fishes which mostly depend on visual cues

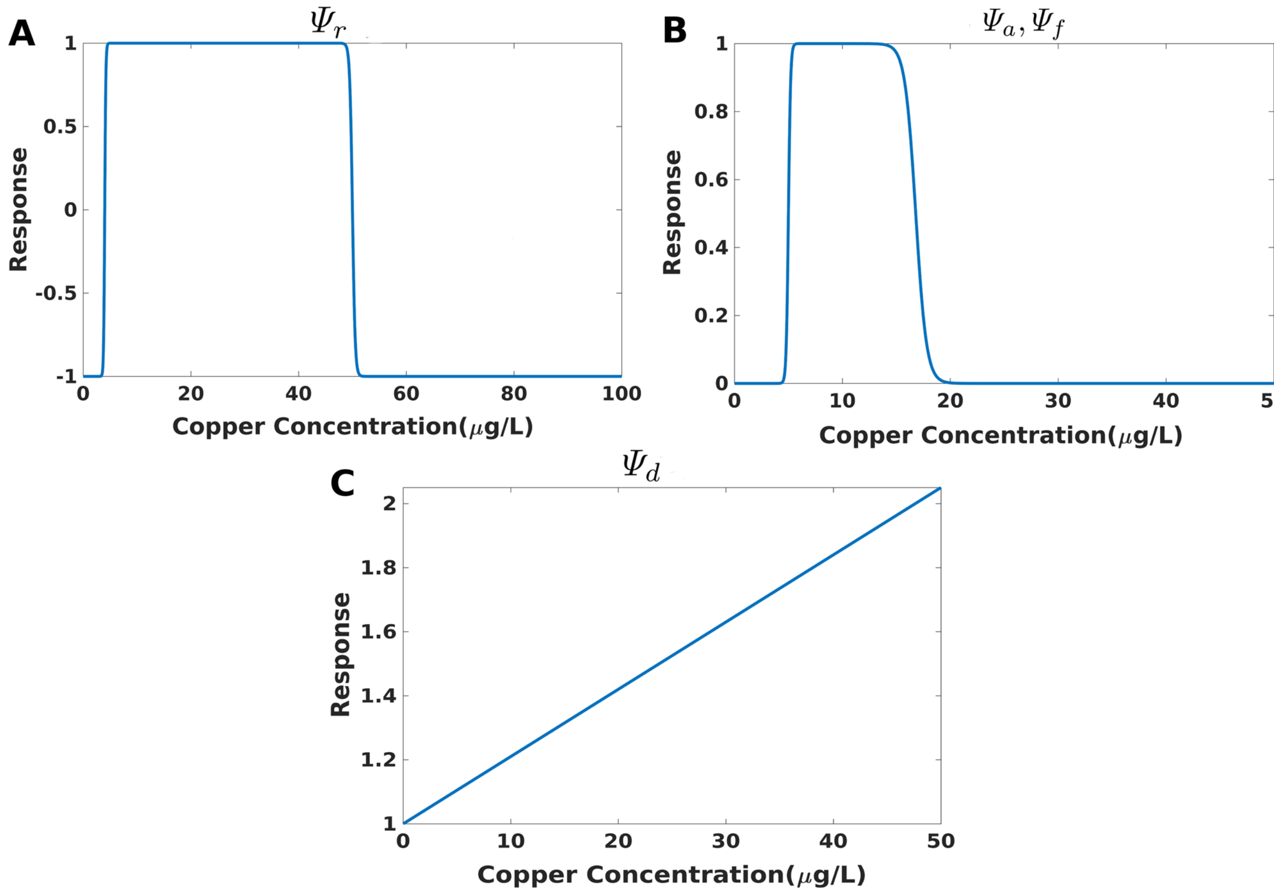

Fig. 1 The effect of internal copper concentration (C) on different parameters: **(A)** intrinsic growth rate (Ψ_r), **(B)** maximum rate of predation (Ψ_a) and mortality due to fish predation (Ψ_f), **(C)** natural mortality (Ψ_d)

to detect their prey (Wright and O'Brien 1982; O'Keefe et al. 1998). As such, the predation by fish is also maximum at intermediate copper and minimum when copper is toxic or deficient. Thus the effect curve, Ψ_f also ranges from 0 to 1 and it is assumed to have the same functional form as Ψ_a (Fig. 1B), i.e., Ψ_f=Ψ_a. Finally, since there is no evidence of decrease of mortality at high copper concentration, the effect on the death rate, Ψ_d can be modeled as a linear function which is as follows (Prosnier et al. 2015) (see Fig. 1C):

$$\Psi_d = 1 + m_d \times C_Z(E) \tag{5}$$

In order to analyze our model, a specific functional form of $C(E)$ is required and so we describe in the next paragraphs how this function can be derived from a dynamic model of internal copper concentration.

Modeling internal copper concentration

The rate of change of internal copper concentration for plankton can be expressed with a model adapted from Luoma and Rainbow (2005):

$$\frac{dC(t)}{dt} = \frac{u_m E}{u_c + E} + (C_{food} \times A_Z \times I_Z) - u_e \times C(t) \tag{6}$$

The first term on the right-hand side represents bioaccumulation or direct uptake from environment. Such uptake is considered to be a saturating function of the copper present in the environment (E) where u_m and u_c are the maximal intake rate and half saturation constant respectively. This is plausible because of the competition that is present among the copper ions (Lebrun et al. 2012). The second term takes into account the intake from food which is responsible for biomagnification. Here, C_{food} denotes the copper present in the food, I_Z denotes the ingestion rate of the zooplankton given by $\frac{aP}{k_P + P}$ and the assimilation efficiency is denoted by A_Z which is equal to χ in our model. This term must not be present in the case of photosynthetic organisms like phytoplankton which does not prey upon another organism. The last term denotes the loss rate of the internal copper. Equating the right-hand side of Eq. (6) to zero and in view of the above, one can easily calculate the steady state internal copper concentration for phytoplankton (C_P) and zooplankton

(C_Z) in terms of E (Prosnier et al. 2015). An extra subscript P or Z is added to each of the parameter to indicate its association with the particular organism.

$$\begin{aligned} C_P(E) &= \left(\frac{E \times u_{mP}}{E + u_{cP}}\right) \times \frac{1}{u_{eP}}, \\ C_Z(E) &= \left(\frac{E \times u_{mZ}}{E + u_{cZ}} + \chi \times \frac{a \times P}{k_P + P} \times C_P\right) \times \frac{1}{u_{eZ}} \end{aligned} \tag{7}$$

Stochastic model

Random environmental fluctuations are crucial to the understanding of ecological system and may have consequences in its community stability and persistence. Moreover, the complexity induced by the combined effect of stochasticity and nonlinearity in a system is fascinating and its investigation is especially warranted when there is bistability (Guttal and Jayaprakash 2007). As such, we explore the above system in the presence of stochasticity. Let the deterministic model (Eq. 2) be denoted as:

$$\frac{dY}{dt} = G(Y) \tag{8}$$

Here, $Y = [P, Z]^T$ where T denotes transpose of the vector and $G(Y)$ are the functions on the right hand side of the Eq. 2. Here, we add an extrinsic multiplicative noise to the system after which it can be expressed as follows:

$$\frac{dY}{dt} = G(Y) + \sigma Y \xi(t) \tag{9}$$

where, σ denotes intensity of noise and $\xi(t)$ denotes Gaussian white noise with zero mean and unit variance. While other alternatives like additive noise (Kéfi et al. 2013) can be used to model stochasticity, multiplying the noise term with the state variable is a more commonly used characterization of environmental fluctuations in ecological models (Evans et al. 2013; Sharma et al. 2015). In this case, there is significantly reduced fluctuations around low density states and when the state is zero, the noise will vanish.

Analyses

Model parameterization and bifurcations

While the parameters related to the population dynamics in plankton were largely adapted from Scheffer et al. (2000), few parameters were also taken from an empirical study by Murdoch et al. (1998). All parameters are chosen with respect to algae and the often studied zooplankton, *Daphnia*. The values for model parameters related to modeling the internal copper concentration and effect of copper were obtained from an earlier study Prosnier et al. (2015). All model parameters with their values and descriptions are enlisted in Table 1. Analyses throughout this paper have been carried out using the same set of parameters as given therein unless stated otherwise.

We rely on bifurcation theory to study the asymptotic behavior of the model with respect to changes in parameters which imitate different environmental conditions. Abrupt changes in the dynamics of the system as a consequence of gradual shift of a parameter lead to a bifurcation. We examine the system for such bifurcations with respect to environmental copper concentration in the system (E). Also, since the predation pressure by fish can be externally manipulated by altering harvesting strategies, it is important to understand the simultaneous impact of contamination and fishing on the planktonic system. For this, we carry out a two parameter bifurcation analysis with respect to E and fish predation, f. The bifurcation diagrams were produced using numerical continuation software MATCONT (Dhooge et al. 2008) in MATLAB environment.

Stochastic simulations

The stochastic model was also simulated in MATLAB using Euler Maruyama method (Higham 2001). The time step of integration is $\triangle t$=1 where each unit time represents one day in our model. To analyze the stochastic model, we ran the simulation up to 20000 days and calculated the mean of last 5 years (1825 days). We used 10000 such realizations in order to plot the probability density of phytoplankton and zooplankton. Since we are interested to understand the conditions at which the system shifts to phytoplankton-dominated state, the initial conditions for all stochastic simulations are zooplankton-dominated ($P = 0.5\, mgCL^{-1}$, $Z = 3$ $mgCL^{-1}$). In mathematical terms, this also ensures that in the deterministic counterpart, the initial phytoplankton and zooplankton density always lie within the basin of attraction of the zooplankton-dominated equilibrium. Additionally, we increase redness of the noise in the system to understand how the dynamics of the system changes with increase in lag-1 autocorrelation. For this, we consider the Gaussian stochastic process ξ to have a temporal autocorrelation following $1/f^{\beta}$ frequency spectrum. This has been suggested as a good model for many autocorrelated noise in biology including environmental fluctuations (Halley 1996). To generate a stochastic signal with spectral exponent β, we use algorithm prescribed in (Stoyanov et al. 2011) where the extreme situation $\beta \to 0$ is a white noise and $\beta > 0$ means red shifted or positively autocorrelated.

Early warning signals

Lastly, we also check the robustness of established early warning indicators in predicting critical transition in such a

Table 1 Parameter values used in our simulation

Parameters	Value	Unit	Description	Reference
Population dynamics				
K	3	$mgCL^{-1}$	algal carrying capacity	(Murdoch et al. 1998)
r	0.5	d^{-1}	algal intrinsic rate of natural increase	
a	0.4	d^{-1}	maximum intake rate of *Daphnia*	The value of these
k_P	0.6	$mgCL^{-1}$	half saturation constant of *Daphnia*	parameters are same
χ	0.6	-	*Daphnia* conversion efficiency	as used in
k_Z	0.5	$mgCL^{-1}$	half saturation constant for fish predation	Scheffer et al. (2000)
f	0.1	$mgCL^{-1}d^{-1}$	fish predation rate	
i	0.03	d^{-1}	diffusive inflow of algae	
d	0.05	d^{-1}	*Daphnia* natural mortality rate	(Murdoch et al. 1998)
σ	0.035-0.045	d^{-1}	noise intensity	
Copper concentration				
E	0–100	μgL^{-1}	external copper concentration	
u_{mP}	20	$\mu gg^{-1}d^{-1}$	algal maximal intake rate	All parameters
u_{mZ}	15	$\mu gg^{-1}d^{-1}$	*Daphnia* maximal intake rate	related to copper internal
u_{cP}	6	μgL^{-1}	algal half saturation constant	concentration were
u_{cZ}	7	μgL^{-1}	*Daphnia* half saturation constant	taken from
u_{eP}	1	μgd^{-1}	constant loss rate for algae	Prosnier et al. (2015)
u_{eZ}	1	μgd^{-1}	constant loss rate for *Daphnia*	
Effect of copper				
l_r	4	μgL^{-1}	algal growth's deficiency EC_{50}	
h_r	50	μgL^{-1}	algal growth's toxicity EC_{50}	All parameters related
m_r	5	-	copper effect on algal growth	to copper effects on
n_r	2	-	copper effect on algal growth	algae and *Daphnia*
l_a	5	μgL^{-1}	*Daphnia* predation's deficiency EC_{50}	predation/mortality
h_a	16.8	μgL^{-1}	*Daphnia* predation's toxicity EC_{50}	were taken from
m_a	5	-	copper effect on *Daphnia* predation	Prosnier et al. (2015)
n_a	1	-	copper effect on *Daphnia* predation	
m_d	0.021	$g\mu g^{-1}$	copper response coefficient for *Daphnia* mortality	

system. Early warning signals are statistical measures which precede some catastrophic transition (Scheffer et al. 2009; Petrovskii et al. 2017). As the system approaches a bifurcation point, it is predicted that certain features of the time series like variance and autocorrelation increases. Although these signals were not originally developed to predict stochastic state shift, it has been recently debated upon whether the early warning indicators are relevant for stochasticity-induced attractor switching (Drake 2013; Boettiger and Hastings 2013). So it is useful to investigate briefly the robustness of metric-based early warning indicators in this context. We used Early Warning Signal toolbox to analyze the simulated time series preceding a state shift (Dakos et al. 2012). The time series were subjected to Gaussian detrending with bandwidth 25 before they were analyzed to calculate the autocorrelation at lag-1 and the standard deviation. The moving window chosen for calculating each of the metrics is half the size of the simulated time series.

Results

We begin by demonstrating the dynamics of plankton under changing copper enrichment. Since critical transition to the phytoplankton-dominated state is known to be possible as a consequence of high fish density, we also investigate the dynamics due to interplay between changing copper concentration and fish density. Thereafter, the effect of stochasticity in the bistable region is discussed and the simulated time series is tested for early warning signals of regime shifts.

Plankton dynamics under changing copper concentration

The bifurcation diagram in Fig. 2 demonstrates the change in densities of phytoplankton and zooplankton with respect to environmental copper concentration. Similar to the earlier studies (Prosnier et al. 2015; Banerjee et al. 2019),

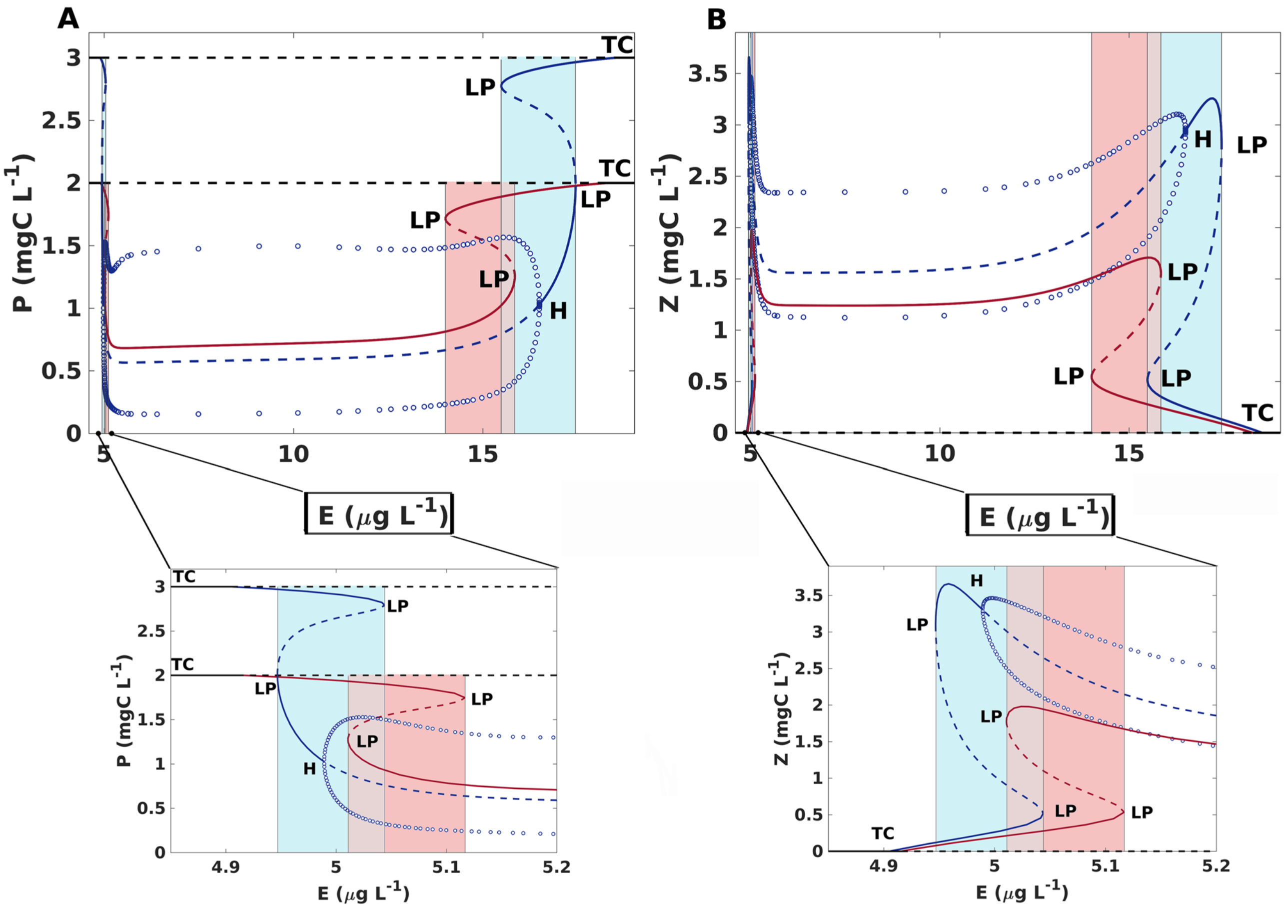

Fig. 2 One parameter bifurcation diagram for (**A**) phytoplankton and (**B**) zooplankton densities with respect to environmental copper concentration (E) for two different carrying capacities when $f = 0.1$ $mgCL^{-1}d^{-1}$. The interior equilibrium is denoted by the red lines for $K = 2$ $mgCL^{-1}$ and blue lines for $K = 3$ $mgCL^{-1}$. The red (blue) shaded region denotes the parameter ranges for which bistability is observed when $K = 2$ $mgCL^{-1}$ ($K = 3$ $mgCL^{-1}$). In both cases, the phytoplankton only equilibrium is denoted by black lines at $P = 2$ $mgCL^{-1}$ and 3 $mgCL^{-1}$ respectively. The circles denotes the maximum and minimum amplitudes of oscillation while the solid and dashed lines denote stable and unstable equilibria respectively. LP: Limit Point; TC: Transcritical; H: Hopf

zooplankton ceases to exist via a transcritical bifurcation (TC) when copper concentration is larger or smaller than a certain threshold. Additionally, we find that both toxic or deficient copper concentrations lead to a pair of limit points or fold bifurcations (LP) resulting in bistability. Mathematically, such fold bifurcations are seen when the stable interior equilibrium collides with the unstable equilibrium as parameter passes through these points. These bifurcations lead to regime shifts whereby a small change in environmental copper concentration can result in an abrupt transition of ecosystem state from phytoplankton-to zooplankton-dominated state or vice versa. Also, such changes are not easily reversible because the parameter must return much beyond the initial point of bifurcation for the system to return to its original state.

We further investigate how different nutrient enrichment (K) might influence the manner in which copper affects the behavior of the system (see Fig. 2). For this, we track the bifurcations in the system with respect to environmental copper concentration for $K = 2\,mgCL^{-1}$ and $K = 3\,mgCL^{-1}$. In both cases, the phytoplankton density is lowest at intermediate copper concentration level and when moving towards toxic or deficient concentrations, there is bistability between phytoplankton-dominated state and zooplankton-dominated state. Additionally, when $K = 3\,mgCL^{-1}$, at some intermediate concentration, the stable interior equilibrium loses its stability via Hopf bifurcation (H) giving rise to population cycles. As a result of this, in certain parameter ranges the model also exhibits bistability between population cycles and phytoplankton dominance.

Interplay between copper contamination and fish predation

Since abrupt transition to phytoplankton-dominated water has been attributed to zooplankton predation by fish beyond a critical threshold (Scheffer et al. 2000), it is natural to ask whether the rate of fish predation can also have an impact on how the plankton dynamics might respond to changing environmental copper concentration. For this, we carry out the bifurcation analysis after increasing the fish predation rate to $f = 0.15\, mgCL^{-1}d^{-1}$ (see Fig. 3). From the extreme ends of the copper concentration axis, as we move towards the intermediate ranges, first there is bistability between population cycles and a phytoplankton-dominated equilibrium and then cycles grow in amplitude until it vanish abruptly via homoclinic bifurcations. Also, unlike the previous case in Fig. 2, a phytoplankton-dominated state is always present and stable wherever a coexistence is possible thus leading to high phytoplankton density through out all ranges of copper concentration.

In view of the above unintuitive results, it appears necessary to understand the complete dynamics exhibited by the system at different external copper concentration and fish predation pressure. The interplay between the two is demonstrated in Fig. 4. The system is in stable coexistence equilibrium in region 1 when the predation rate, f, is very high. On reducing the predation by fish, which is equivalent to reducing fish density, the system becomes unstable leading to oscillatory dynamics. The population cycles can be observed in region 2 and 3 bounded on both sides by Hopf bifurcation lines (H). In region 3, along with the oscillatory dynamics, depending on initial conditions, the system may also converge to phytoplankton-dominated state. Embedded within 3, is region 5 where the system has only one stable state which is phytoplankton-dominated in nature. This bistable system dynamics extends to region 4, where the system can switch between two stable coexistence equilibria: high phytoplankton–low zooplankton density and low phytoplankton–high zooplankton density state. Mathematically, such a behavior arise due to the two cusp points (CP) which are observed in both toxic and deficient copper regimes. When copper concentration is too low or high, the system undergoes transcritical bifurcation so that the zooplankton population becomes extinct and only the phytoplankton is able to survive in region 6.

Effect of stochasticity in the bistable regime

Although deterministic models are easy to analyze, in reality however, ecological systems are subject to environmental fluctuations and uncertainty that may be captured by a

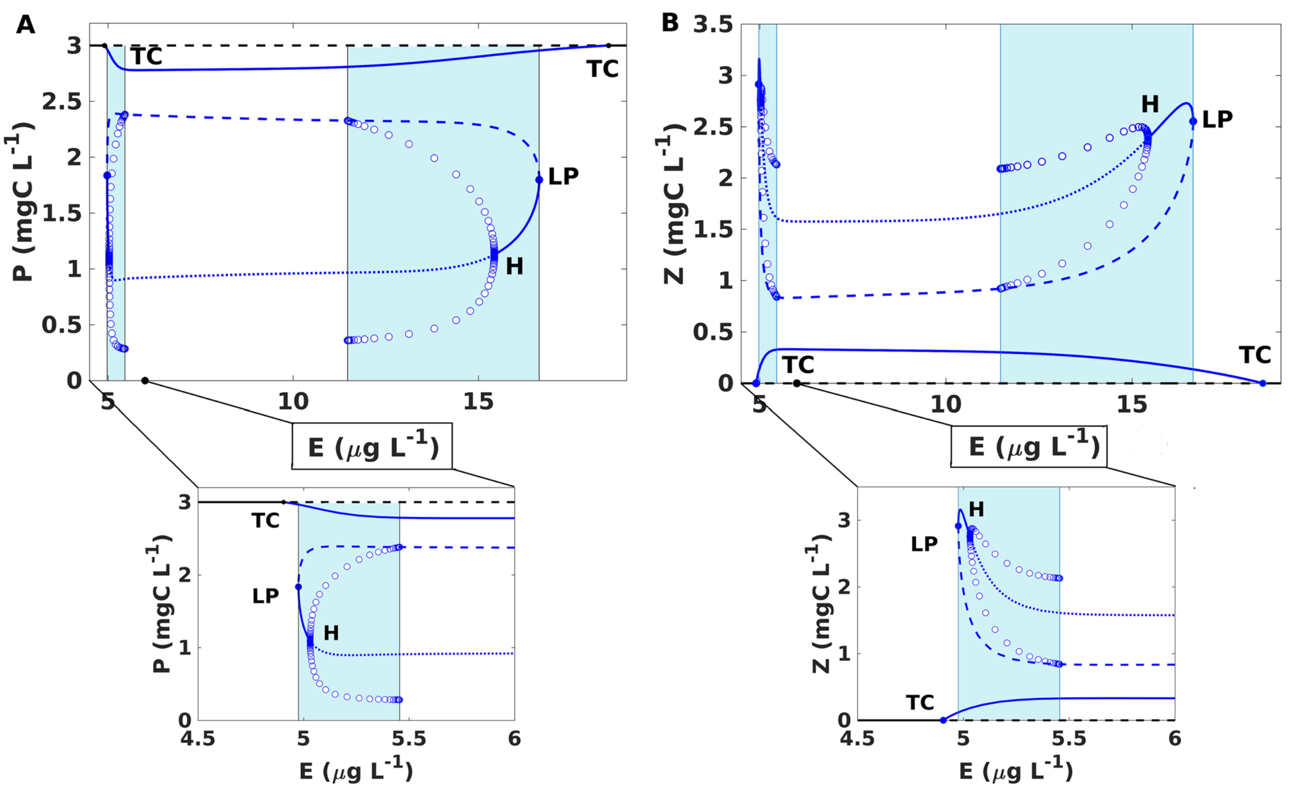

Fig. 3 One parameter bifurcation diagram for (**A**) phytoplankton and (**B**) zooplankton densities with respect to environmental copper concentration (E) when $f = 0.15\ mgCL^{-1}d^{-1}$. The interior equilibrium is denoted by blue lines whereas the phytoplankton-only equilibrium is denoted by black lines. The shaded region denotes the parameter ranges for which bistability is observed. The maximum and minimum amplitudes of oscillation is denoted by circles while the solid and dashed lines denote stable and unstable equilibria respectively. LP: Limit Point; TC: Transcritical; H: Hopf

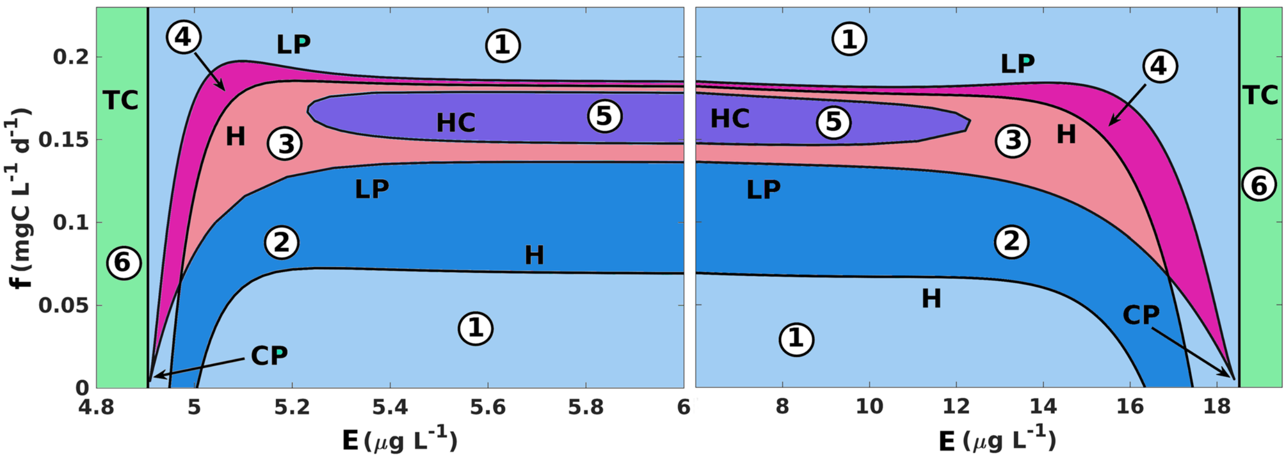

Fig. 4 Two parameter bifurcation diagram with respect to copper concentration (*E*) and fish (*f*). Regions (1),(5): Stable coexistence, (2): Population cycle, (3): Bistability between stable coexistence and population cycle, (4): Bistability between two stable coexistence states, (6): Phytoplankton only state. All parameters are as given in Table 1

stochastic noise term. It is particularly interesting to study how environmental fluctuations influence a system with alternative stable states. When carrying capacity, K, is set to 2 $mgCL^{-1}$ we investigate the probability with which different values of phytoplankton and zooplankton densities are observed in the long run under three different external copper concentrations (see Fig. 5). The concentrations which led to bistability between phytoplankton and zooplankton-dominated state in the deterministic set up were chosen and noise with intensity $\sigma = 0.04\ d^{-1}$ was used. When the environmental copper concentration, E, was 14.1 μgL^{-1} and $E = 14.5\ \mu gL^{-1}$, the probability density was unimodal with the mode around the zooplankton-dominated and phytoplankton-dominated state respectively. Here, the shift to phytoplankton domination occurs much prior compared to the deterministic model where the system tips only at $E = 15.84\ \mu gL^{-1}$. An increased noise intensity ($\sigma = 0.045$ d^{-1}) under such conditions lead to a decreased skewness of the probability density and vice versa. In between these two scenarios, when copper concentration is 14.3 μgL^{-1}, the density becomes bimodal where the system has almost equal chance to end up in phytoplankton-dominated state or zooplankton-dominated state. This bimodality is however lost also at this intermediate E value when the noise intensity is increased. In the remaining sections, we only focus on the effect of stochasticity in the toxic copper concentration ranges but the same analyses can also be carried out for the bistability range of low copper as well. In fact, a similar behavior as described above was demonstrated on addition of stochasticity in the deficient copper concentrations (see Appendix).

Since the phytoplankton-dominated state in the previous analyses is close to the environmental carrying capacity of the algae, it is only natural to ask what impact does stochasticity have when the environmental carrying capacity is increased due to nutrient enrichment. In order to answer this, we investigated the effect of noise with intensity $\sigma = 0.04\ d^{-1}$ in the bistable regime when $K = 3\ mgCL^{-1}$ (Fig. 6). We observe a similar transition from unimodal peak around the zooplankton-dominated equilibrium at copper concentration 15.7 μgL^{-1} to phytoplankton-dominated state at copper concentration 16.2 μgL^{-1}. At the intermediate concentration, E=16 μgL^{-1}, we observe bimodal peak where the system has equal probability to converge to either low or high phytoplankton density. Thereafter, we increase the redness of the noise to $\beta = 0.15$ and then $\beta = 0.3$ and subsequently compare the probability densities to the $\beta = 0$ case for all the three copper concentrations (Fig. 6). Our results show that, similar to that of increasing noise intensity, red shifted noise also decrease the skewness of the probability densities. Moreover, in case where there was a bimodal density in presence of white noise, increasing redness leads to significant reduction in the peak height.

For the bimodal cases corresponding to both the carrying capacities (Figs. 5B, E and 6B, E), looking at a specific simulated time series of the stochastic model, we observe stochastic switching between the equilibria (Fig. 7). In the case when $K = 2\ mgCL^{-1}$, multiple switch is observed unlike that of the other case where once the system switches to a phytoplankton-dominated equilibrium, it is unable to return back.

Robustness of early warning signals

Since the switch to the phytoplankton-dominated state is most likely irreversible when $K = 3$, we analyzed the portion of the time series prior to such a shift denoted by the yellow shaded region in Fig. 7B. Zooplankton biomass is known to

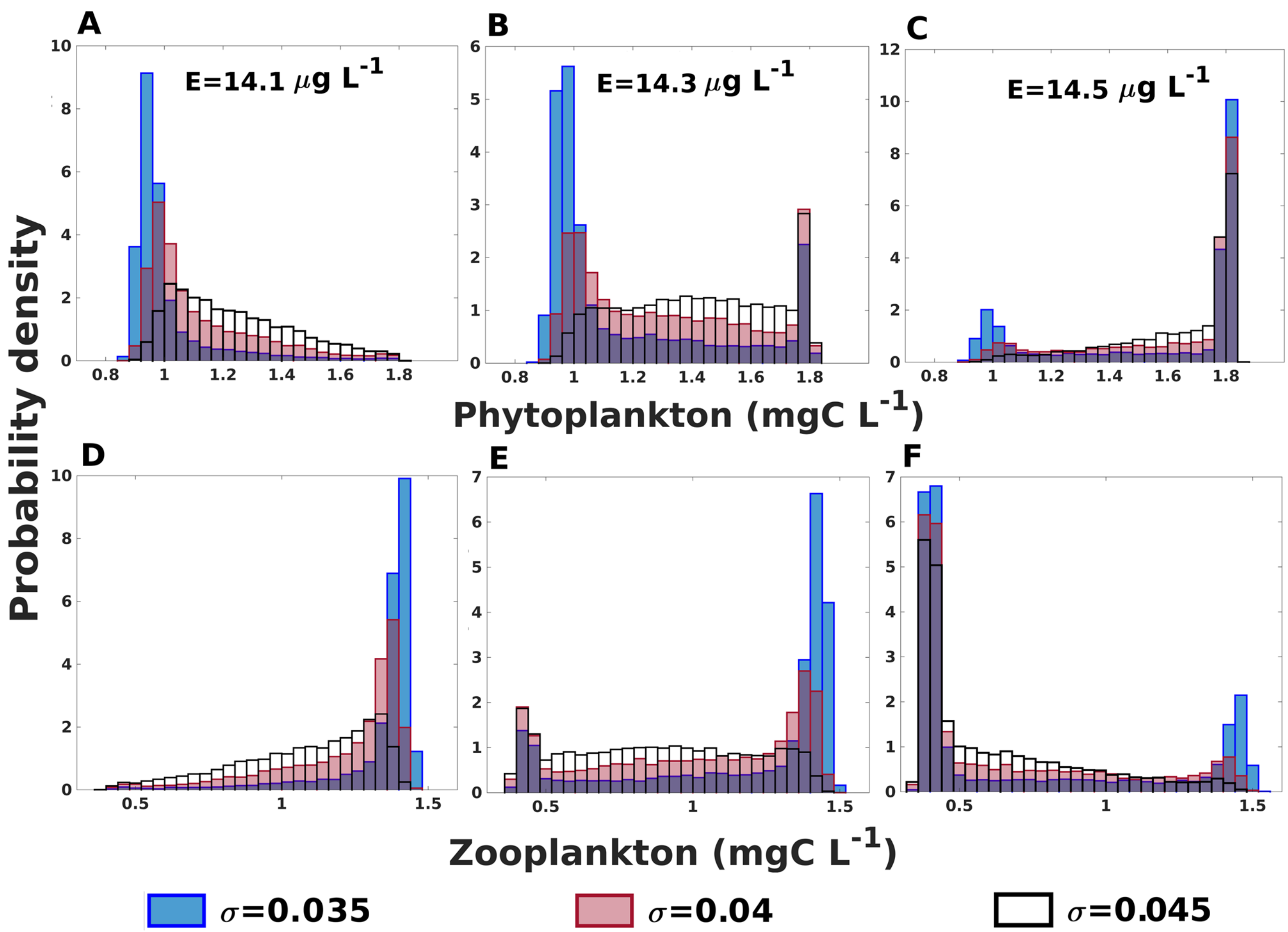

Fig. 5 Probability density estimates of the (**A, B, C**) phytoplankton and (**D, E, F**) zooplankton populations under three different external copper concentrations: 14.1 $\mu g L^{-1}$, 14.3 $\mu g L^{-1}$ and 14.5 $\mu g L^{-1}$; K=2 $mgCL^{-1}$

provide early warning of regime shifts in lake community composition (Pace et al. 2013). As such the simulated data of zooplankton density was considered for a stretch starting from 4200 days to 4960 days (Fig. 8A). Both the metric, autocorrelation lag-1 as well as standard deviation decreases with time thus being unable to provide any early warning to the regime shift which we know occurred immediately after this time segment. Next, we analyze a shorter time series segment from 4700 to 4960 days (Fig. 8B) denoted by darker yellow shade in Fig. 7B. Evidently, our analysis shows that the early warning signals performed much better in case of short time series segments.

Discussion

Abrupt transitions to phytoplankton-dominated turbid water are known to occur in lake ecosystems but the impact of chemical pollution on such state shifts is not well understood. Fish density has been known to be an important driver of regime shifts in plankton community. To this end, using the approach prescribed in Prosnier et al. (2015), we introduced here a new model which takes into account both sigmoidal functional response for zooplankton predation by fish and its alteration under variable copper concentrations. Our analyses leads to a comprehensive understanding of the ecological dynamics due to the interaction between copper contamination and fish density. Further, consideration of environmental fluctuations in the form of stochasticity led to a clearer insight into how changing copper concentration of lake water may influence sudden shift to phytoplankton domination.

Moving towards the extreme ends of the copper concentration axis, first the zooplankton ceases to exist followed by the phytoplankton. This is attributed to decreased consumption by zooplankton and the inhibition of phytoplankton growth in these ranges. Although this behavior exhibited by our model is consistent with the earlier works

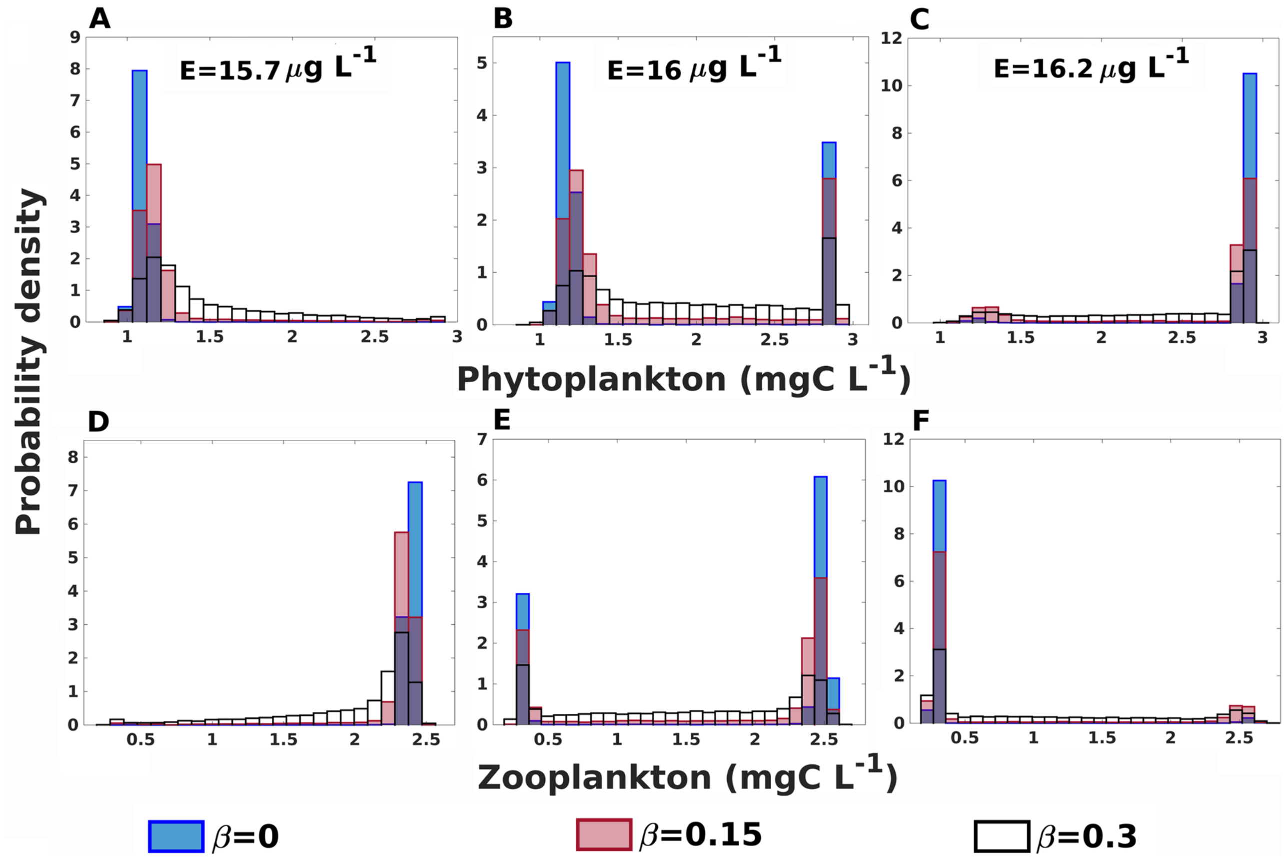

Fig. 6 Probability density estimates of the (**A, B, C**) phytoplankton and (**D, E, F**) zooplankton populations under three different external copper concentrations: 15.7 μgL^{-1}, 16 μgL^{-1} and 16.2 μgL^{-1}; K=3 $mgCL^{-1}$

(Prosnier et al. 2015; Banerjee et al. 2019), there is a notable change in plankton dynamics when both the functional groups coexist. Within such ranges, the earlier study by Banerjee et al. (2019) demonstrated that toxic or deficient copper concentration could lead to destabilization of the predator–prey dynamics. However, on incorporating the sigmoidal functional response for fish predation, we find no such destabilizing behavior in these ranges. Instead a

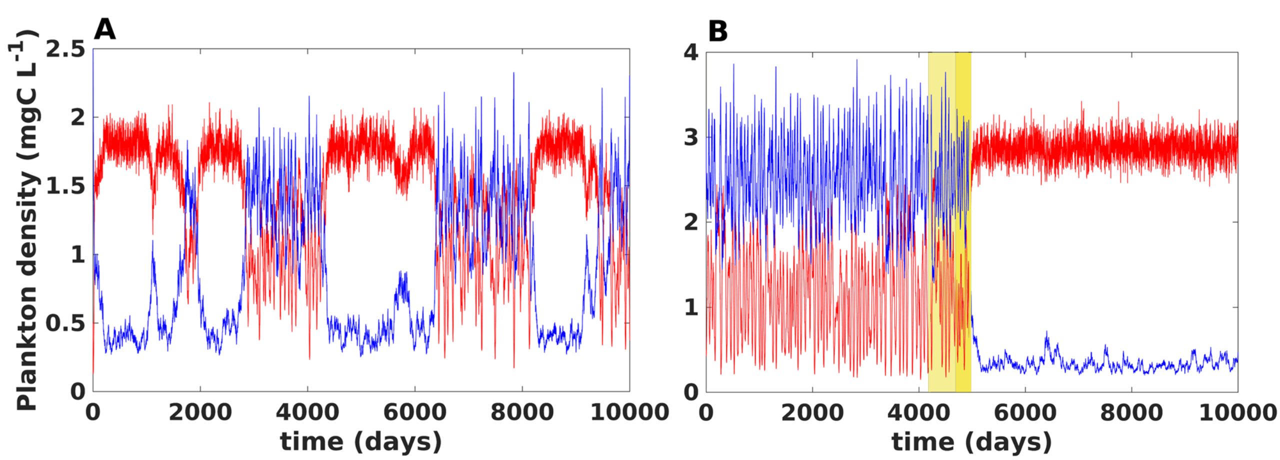

Fig. 7 Time series simulation of the stochastic model for **(A)** $K = 2$ $mgCL^{-1}$, $E = 14.3$ μgL^{-1} and **(B)** $K = 3$ $mgCL^{-1}$, $E = 16$ μgL^{-1}. The red and the blue line denotes the phytoplankton and the zooplankton densities respectively. Yellow shades represent the time segments that have been analyzed for early warning signals in Fig. 8

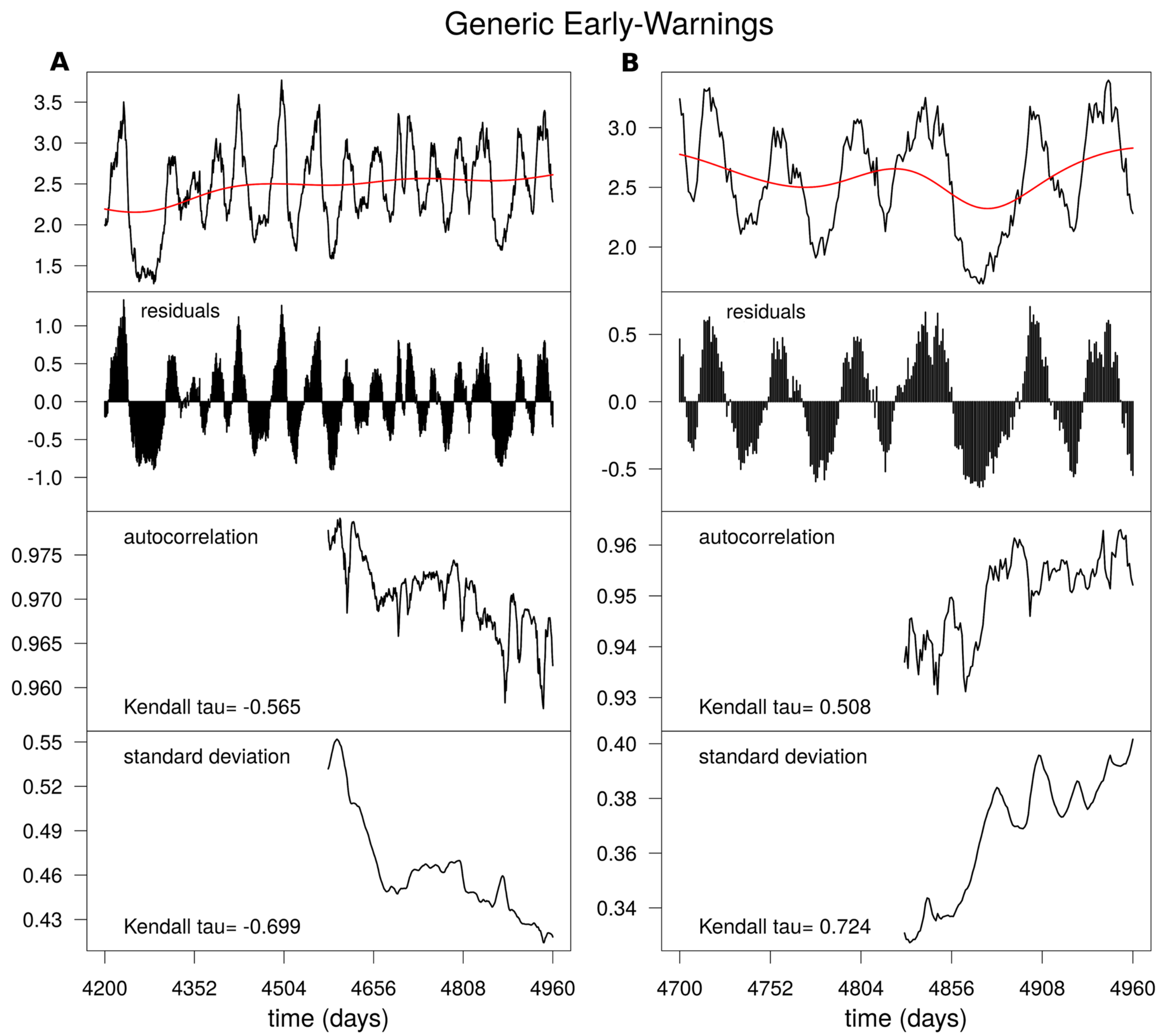

Fig. 8 Early warning signals for a simulation of the stochastic model. Two time segments of different lengths **(A)** 4200–4960 days and **(B)** 4700–4960 days which precedes the regime shift from zooplankton-dominated state to phytoplankton-dominated state were analyzed

bistable scenario is observed where the system can switch to a phytoplankton-dominated state (Fig. 2). This is counterintuitive as fish predation decreases in these ranges and so zooplankton dominance is expected. However, it must be noted that consumption by zooplankton also decreases in toxic or deficient concentrations thus leading to decline in its density and transition to phytoplankton-dominated state. In the intermediate regimes, the stable coexistence equilibrium is characterized by low phytoplankton and high zooplankton density because of increased zooplankton predation. When carrying capacity is increased here, the system may retain a relatively low phytoplankton density but only via population cycles (Fig. 2). Such destabilization of the system occurs due to increase in energy flux from the phytoplankton to the zooplankton relative to the zooplankton's loss rate, as indicated by the ecological theory on stability (Rip and McCann 2011). Although oscillatory dynamics in intermediate ranges have been observed in earlier studies of copper enrichment (Prosnier et al. 2015; Banerjee et al. 2019), here it resulted in bistability between population cycles and phytoplankton-dominated steady state which was not reported earlier.

The complexity of the dynamics exhibited by the system can be better understood by studying the interaction between fish density and copper enrichment (Fig. 4). The above-mentioned bistability which was observed at specific levels of copper enrichment, vanishes when fish density is comparatively high. Increase in zooplankton mortality at higher fish predation leads to stabilization of population cycles and phytoplankton domination across all copper concentrations. At intermediate fish density, the oscillatory dynamics may lead to collapse of the zooplankton population due to food shortage (Scheffer et al. 2000). Mathematically this occurs via homoclinic bifurcation resulting in phytoplankton domination being the only stable state in the middle ranges of copper concentration. This is significant from an ecological point of view because under such parameteric ranges, once the system reaches the condition of phytoplankton domination, changing copper concentrations has no effect on the ecosystem state. However, maintaining copper concentration at proper levels, the chance of switch to a phytoplankton-dominated equilibrium can be reduced (Fig. 3). When fish density is very low, the oscillations ceases and coexistence equilibrium is stable for a large range of copper concentration. This can be attributed to the diffusive inflow term which is stabilizing in nature (Fig. 4).

When stochasticity is added to the system, the bistability is weakened as the dynamics spends most of the time near the phytoplankton-dominated state. In fact, starting from a zooplankton-dominated condition, the system may become phytoplankton-dominated much prior to the fold bifurcation. Only a very small range of copper concentration parameter demonstrates bimodality in the probability density of the observed values. This bimodality is lost on increasing noise intensity or redness. It is interesting to note here that, for a higher carrying capacity value, the bimodality is more prominent as the system can only be at the two extremes which in the deterministic set up represent a population cycle near lower phytoplankton equilibrium and a phytoplankton-dominated equilibrium (see Fig. 2). At any point of time after a long run, the probability that the system displays intermediate values is very low. This happens mainly because for high carrying capacity, the boundary separating the basin of attractions is sufficiently distant from the two equilibria. As a result, once the system has switched to an alternate equilibrium, it is unable to switch back and continue in the same state unless the system is perturbed by noise of sufficiently large strength. In contrast, when the carrying capacity is comparatively low, both the phytoplankton-dominated and zooplankton-dominated equilibria are close to borderline separating the two basin of attractions thus allowing a frequent switch back and forth (Fig. 7 A, B and Appendix, Fig. 10).

Analyzing the time series prior to such regime shift, we find that generic measures like autocorrelation and variance failed to indicate the approaching state shift. This is not remarkably unexpected since it has already been argued that such measures were primarily developed to predict bifurcations and not stochasticity induced state shift (Boettiger and Hastings 2013). Nevertheless, the early warning indicators performed relatively well where a shorter time segment was analyzed. Similar results were reported in other bistable ecological systems which demonstrate noise induced regime shift (Sharma et al. 2015). However, it has been argued that it is not appropriate to conclude that the signals were successful because they failed to predict the upcoming transitions longer ahead. This failure to predict impending shifts further highlights the importance of the present study.

Summing up, our work reveals how both copper pollution as well as deficiency of copper can bring about regime shifts in lake ecosystems. Thereby, we want to stress the importance of deeper understanding of how human driven factors like nutrient enrichment, fishing and chemical pollution can interact with the complex ecosystem dynamics to bring about undesirable outcomes. The study also points to the importance of considering stochasticity in such modeling efforts as noise can influence the outcome which might be quite different from what is predicted from the deterministic model. Our results suggest that more efforts to understand the nonlinearity involving complex anthropogenic changes and their interaction with stochasticity is required to get a better insight into the present day scenario.

Appendix

Effect of stochasticity in low copper concentrations

Deficient copper concentrations also lead to bistable system dynamics resulting in planktonic regime shifts. The effect of stochasticity on such low ranges of copper concentration is examined when carrying capacity $K = 2$. Similar to the toxic concentration case, the system switches to phytoplankton-dominated state prior to the fold bifurcation. The probability density of the observed values from the simulation is unimodal with mode around zooplankton-dominated equilibrium at copper concentration 5.1 $\mu g L^{-1}$. Subsequent small decrease of copper results in the system demonstrating bimodality at concentration 5.095 $\mu g L^{-1}$ and unimodal mode around phytoplankton-dominated state at concentration 5.085 $\mu g L^{-1}$ (see Fig. 9). Increased intensity of noise leads to decreased skewness of the probability densities.

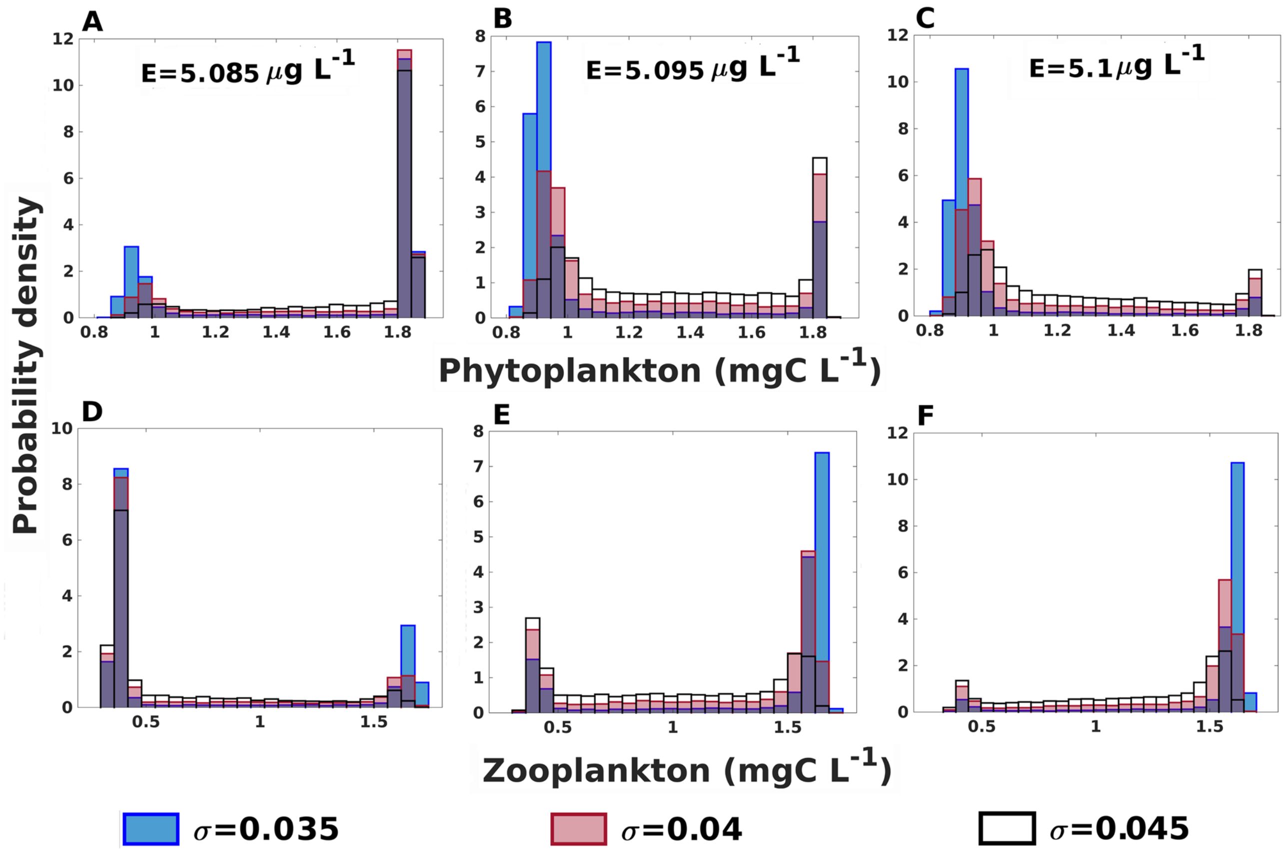

Fig. 9 Probability density estimates of the (**A, B, C**) phytoplankton and (**D, E, F**) zooplankton populations under three different external copper concentrations: 5.085 μgL^{-1}, 5.095 μgL^{-1} and 5.1 μgL^{-1}; $K = 2\, mgCL^{-1}$

Basin of attraction for the alternative stable states

The stochastic switch between the attractors in Fig. 7 can be understood with the help of basin of attraction for the two equilibria under different carrying capacities. When $K = 2$, the boundary separating the basin of attraction is very close to both the phytoplankton and zooplankton-dominated equilibrium which facilitates multiple stochastic switching. On the other hand, the boundary is relatively farther away from the two attractor in case of higher carrying capacity, i.e., $K = 3$ resulting in very infrequent switch.

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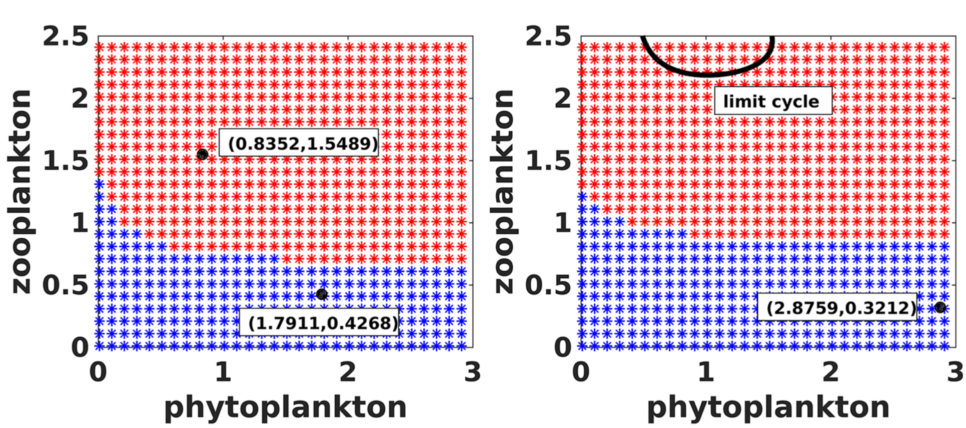
Fig. 10 Basin of attraction for the bistable scenario for different carrying capacities. Left panel: $K = 2$, $E = 14.3\ \mu gL^{-1}$; Right panel: $K = 3$, $E = 16\ \mu gL^{-1}$. The red and the blue points denote initial conditions for which the system converges to the zooplankton-dominated and phytoplankton-dominated equilibrium respectively



Author Contributions SB and BS conceived the idea; SB, BS, MR, MB, and JC refined it; SB and BS designed the simulations; SB programmed the simulations and ran the experiments; SB wrote the first draft; All authors commented on the previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflicts of interest The authors have no competing interest to declare that are relevant to the content of this article.

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