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Copper Contamination Effects on Phytoplankton-Zooplankton System within Deterministic and Stochastic Environments

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Abstract Since the aquatic organisms are very sensitive to the increasing copper contamination in water, this paper focuses on investigating the effects of copper contamination on the interaction between phytoplankton and zooplankton species within both deterministic and stochastic environments. We first construct a deterministic phytoplankton-zooplankton interaction model coupled with the copper concentration and analyze its dynamics, including existence and stability of equilibria, as well as the existence of Hopf bifurcation. A new stochastic model is derived in the form of continuous-time Markov chain (CTMC), and branching process theory is applied to the CTMC model to estimate the extinction probability of zooplankton species. Analytical and numerical findings show that the destiny of species is closely related to the copper concentration, and the predictions of the deterministic and stochastic models may be different in some cases.

Keywords Phytoplankton-zooplankton system, copper contamination, CTMC model, extinction probability

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1. Introduction

Almost all aquatic life is based upon plankton, which is the most abundant form of life floating freely near the surfaces of all aquatic environments, namely, lakes, rivers, estuaries and oceans [1, 37]. The plant forms of plankton community are known as phytoplankton, which is a vital role in ecological systems since nearly half of the world's carbon dioxide is absorbed by them, and they also provide valuable oxygen resources and are important nutrients for a large number of aquatic species [31]. The animals in the plankton community are known as zooplankton. They consume the phytoplankton and can be a highly favourable food source for fish and other aquatic animals [37]. In past years, numerous works have been done towards analyzing the dynamics of phytoplankton-zooplankton system, see Refs. [7, 18–20, 24, 33, 38] and the references therein. Besides, some researchers used Daphnia as the test organism on plankton ecosystem [27, 28, 34], because it constitutes a central component in aquatic food web structure and is sensitive to a multitude of xenobiotics (organophosphates, heavy metals, organochlorines, pyrethroids *etc.*) [5].

As a receptor of urban wastewater, industrial and mine effluents, agricultural

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runoff, and atmospheric pollution, aquatic ecosystems are prone to copper pollution. As an unusual micronutrient, copper is involved in many cellular reactions such as oxygen and iron acquisition [26] as well as denitrification [15], which results in bacteria and phytoplankton having an essential copper requirement. However, a high concentration of copper in water can also induce toxic effects with a deleterious impact on growth [8, 35]. The copper with high concentration can inhibit the photosynthesis of phytoplankton (algae) [16], and then decrease the concentrations of glucides, proteins, amino-acids, chlorophyll and alkaline phosphatase activity in the algal cells [11, 12, 44]. The direct effects of copper on zooplankton (such as, Daphnia) include a decrease in fecundity, survival, body length, weight, and carbon uptake, as well as a delay in maturation [4, 21, 22]. Moreover, the Daphnia's swimming velocity, filtration rate, and ingestion rate are optimal for an intermediate copper range [14, 41].

Mathematical modeling has already proved a useful tool to help predict the effects of pollutant (including copper) on aquatic ecosystems [5,6,10,32,40,42]. For example, in order to predict the effects of copper on a plant-herbivore interaction in a freshwater ecosystem Prosnier *et al.* [32] built a model that focuses on the interaction between algas and herbivores. Theoretical and numerical results showed that the herbivore may be more affected by copper pollution when community interactions are taken into account, and the copper pollution may stabilize the alga-herbivore interaction at the community level. More recently, based on the deterministic model in Ref. [32], Camara *et al.* [6] considered the environmental stochastic effects on the phytoplankton-zooplankton dynamics and proposed a stochastic alga-Daphnia model with white noises in Itô's sense. They supposed that the species lives in an environment subject to random fluctuations which affect the growth rate. The growth rate can be rewritten as an average growth plus an error term which can be approximated by a white noise (see Ref. [6] for more details).

We should point out that, except for the white noise, there are other tools which can be used to describe the environmental fluctuations. Specifically, some scholars formulated stochastic population or epidemic systems by using the continuous-time Markov chain (CTMC) [2,9,17,25,45]. For example, a CTMC model was developed for the dynamics of a viral infection and an immune response during the early stages of infection in Ref. [45]. It was found that the CTMC model can provide new insights, distinct from the basic deterministic model. In the case of $R_0 > 1$, the deterministic model predicts that the viral infection persists in the host, but for the CTMC model, there is a positive probability of viral extinction. Hu *et al.* [17] formulated a CTMC model for a predator-prey species system with disease in the predator. By applying the branching process theory to the CTMC model, the authors estimated the probabilities for disease outbreaks or successful invasions of prey species when the basic reproduction number is greater than the threshold value.

Motivated by the above works, we will devote ourself to investigating the copper contamination effects on phytoplankton-zooplankton system in deterministic and stochastic environments respectively. In Section 2, by considering that the maximum uptake rate of zooplankton is influenced by the copper contamination, we first construct and analyze a deterministic copper-dependence Scenedesmus-Daphnia model. In Section 3, we formulate a CTMC model based on the deterministic model and estimate the extinction probability of Daphnia species by applying the branching process theory. Our results are briefly summarized and discussed in

Section 4.

2. Formulation of copper-dependence model

The model considered in our analysis is based on a simple freshwater ecosystem consisting of two compartments, phytoplankton and zooplankton, with the general Scenedesmus and Daphnia chosen as model organisms for these compartments. The Scenedesmus-Daphnia interaction is described through the Rosenzweig-MacArthur model [36] based on logistic growth for Scenedesmus and on a type II functional response for Daphnia [29,30]:

$$\begin{cases} \frac{\mathrm{d}S}{\mathrm{d}t} = rS\left(1-\frac{S}{K}\right) - \frac{ISD}{S+h}, \\ \frac{\mathrm{d}D}{\mathrm{d}t} = \left(\frac{eIS}{S+h} - m\right)D, \end{cases} \tag{2.1}$$

where $S = S(t)$ and $D = D(t)$ represent Scenedesmus and Daphnia densities at time t, respectively. Parameters r is the Scenedesmus intrinsic rate of natural increase, K is the Scenedesmus carrying capacity, I is the maximum take rate of Daphnia, h is the half-saturation constant of Daphnia, e is the conversion efficiency and m is the mortality rate of Daphnia.

To explore the effect of copper on the dynamic behavior of plankton system, we consider copper dependent parameters. We first determine the internal concentration (Cu_{int}) as a function of the external concentration for each population. This can be derived with the following biodynamic model [32]:

$$Cu_{\text{int}} = \left(\frac{k_m}{k_c + Cu} \cdot Cu + AE \cdot IR \cdot Cu_F\right) \cdot \frac{1}{k_e},$$

where Cu is the external concentration, k_m is the maximal intake rate and k_c is the half-saturation constant. Cu_F is the copper concentration in food, AE is the assimilation efficiency, IR is the ingestion rate and k_e is the constant loss rate. Consequently, the internal copper concentrations for Scenedesmus(C_S) and Daphnia(C_D) as a function of external concentration(Cu) are as follows [5,6,32]:

$$C_S(Cu) = \left(\frac{Cu \cdot k_{mS}}{Cu + k_{cS}}\right) \cdot \frac{1}{k_{eS}}, \tag{2.2}$$

$$C_D(Cu) = \left(\frac{Cu \cdot k_{mD}}{Cu + k_{cD}} + \frac{eIS}{S+h} \cdot C_S\right) \cdot \frac{1}{k_{eD}}, \tag{2.3}$$

where k_{mS} and k_{mD} are the maximum ingestion rates of Scenedesmus and Daphnia, respectively. k_{cS} and k_{cD} are their half-satiation constants, k_{eS} and k_{eD} are their constant loss rates, respectively.

It is common to represent copper dose-response relationships by a sigmoid curve that captures only the effect of copper as a pollutant at high concentration. Thus, Prosnier *et al* [32] introduced the following asymmetric double sigmoid function with two thresholds, deficiency and toxicity:

$$\begin{aligned} Cu_x = (a+c) - \frac{1}{2}(a-e)\tanh\left[d_x\left(C_x(Cu) - C_x(V_x)\right)\right] \\ + \frac{1}{2}(a-c)\tanh\left[b_x\left(C_x(Cu) - C_x(U_x)\right)\right], \end{aligned} \tag{2.4}$$

Table 1. Values of the parameters for model (2.6).

Parameters	Values	Units	Parameters	Values	Units
r	1.2	d^{-1}	k_{mD}	15	$\mu\mathrm{g}\mathrm{g}^{-1}\mathrm{d}^{-1}$
K	0.1-5	mgCL^{-1}	k_{cD}	7	$\mu\mathrm{gL}^{-1}$
h	0.164	mgCL^{-1}	k_{eD}	1	$\mu\mathrm{gd}^{-1}$
e	0.6	–	V_I	5	$\mu\mathrm{gL}^{-1}$
m	0.35	d^{-1}	U_I	16.8	$\mu\mathrm{gL}^{-1}$
Cu	0-100	$\mu\mathrm{gL}^{-1}$	d_I	5	–
I	1.8	d^{-1}	b_I	1	–

where Cu_x is the effect of copper on parameter x, $(a+c)$ is the minimal value of the effect, $(a-e)$ is the amplitude of the effect, V_x and U_x are copper concentrations that cause deficiency and toxicity in 50% of individuals, d_x and b_x the lower and higher slopes of the curve, respectively.

The effect of copper on predation is between none effect on predation at intermediate concentrations and total inhibition of predation at low and high concentrations. Thus, by taking $a=-0.5$ and $c=e=0.5$ and assuming that C_S in Eq. (2.3) is a constant, we get from Eqs. (2.3) and (2.4):

$$\begin{aligned} Cu_I = & \frac{1}{2}\tanh\left[\frac{d_I}{k_{eD}}\left(\frac{Cu\cdot k_{mD}}{Cu+k_{cD}}-\frac{V_I\cdot k_{mD}}{V_I+k_{cD}}\right)\right] \\ & -\frac{1}{2}\tanh\left[\frac{b_I}{k_{eD}}\left(\frac{Cu\cdot k_{mD}}{Cu+k_{cD}}-\frac{U_I\cdot k_{mD}}{U_I+k_{cD}}\right)\right], \end{aligned} \tag{2.5}$$

and the maximum uptake rate of Daphnia under the influence of copper is $I\left(Cu\right)=Cu_I\cdot I$. Introducing the copper effect into model (2.1) leads to the following equations:

$$\begin{cases} \frac{\mathrm{d}S}{\mathrm{d}t}=rS\left(1-\frac{S}{K}\right)-\frac{I(Cu)SD}{S+h}, \\ \frac{\mathrm{d}D}{\mathrm{d}t}=\left(\frac{eI(Cu)S}{S+h}-m\right)D. \end{cases} \tag{2.6}$$

Parameter values in model (2.6) derived from Refs. [5,6] are given in Table 1.

3. Qualitative analysis of deterministic model (2.6)

For model (2.6), the trivial equilibrium $E^0=(0,0)$ and boundary equilibrium $E^1=(K,0)$ are always feasible, the positive equilibrium $E^*=(S^*,D^*)$ is feasible if and only if $I(Cu)>\frac{m(K+h)}{eK}$, where

$$S^*=\frac{mh}{eI(Cu)-m},\quad D^*=\frac{r}{I(Cu)}\left(1-\frac{S^*}{K}\right)\left(S^*+h\right).$$

To investigate the stability of the above equilibria, we have to consider the following Jacobian matrix of model (2.6):

$$J(S,D)=\begin{pmatrix} r(1-\frac{2S}{K})-\frac{I(Cu)Dh}{(S+h)^2} & -\frac{I(Cu)S}{S+h} \\ \frac{eI(Cu)h}{(S+h)^2}D & \frac{eI(Cu)S}{S+h}-m \end{pmatrix}.$$

At the trivial equilibrium $E^0=(0,0)$, the Jacobian matrix takes the form

$$J_{E^0}=\begin{pmatrix} r & 0 \\ 0 & -m \end{pmatrix}.$$

The corresponding eigenvalues are $\lambda_1=r>0$ and $\lambda_2=-m<0$, thus E^0 is a saddle. At the boundary equilibrium $E^1=(K,0)$, the Jacobian matrix takes the form

$$J_{E^1}=\begin{pmatrix} -r & -\frac{I(Cu)K}{K+h} \\ 0 & \frac{eI(Cu)K}{K+h}-m \end{pmatrix}.$$

The corresponding eigenvalues are $\lambda_1=-r<0$ and $\lambda_2=\frac{eI(Cu)K}{K+h}-m$. If $I(Cu)<\frac{m(K+h)}{eK}$, then E^1 is a stable node; if $I(Cu)>\frac{m(K+h)}{eK}$, then E^1 is a saddle.

At the positive equilibrium $E^*=(S^*,D^*)$, the Jacobian matrix takes the form

$$J_{E^*}=\begin{pmatrix} r(1-\frac{2S^*}{K})-\frac{I(Cu)D^*h}{(S^*+h)^2} & -\frac{I(Cu)S^*}{S^*+h} \\ \frac{eI(Cu)h}{(S^*+h)^2}D^* & 0 \end{pmatrix},$$

and

$$\mathrm{Det}(J_{E^*})=\frac{ehI^2(Cu)S^*D^*}{(S^*+h)^3}>0,$$

$$\mathrm{Trace}(J_{E^*})=r(1-\frac{2S^*}{K})-\frac{I(Cu)D^*h}{(S^*+h)^2}=\frac{I(Cu)D^*S^*}{(K-S^*)(S^*+h)^2}(K-2S^*-h).$$

According to Routh-Hurwitz criterion, we know that E^* is stable if $K<2S^*+h$, and unstable if $K>2S^*+h$. Furthermore, in the case of $K=2S^*+h$, we know that $\mathrm{Trace}(J_{E^*})=0$ and the following transversality condition for Hopf bifurcation is satisfied:

$$\frac{\mathrm{d}}{\mathrm{d}K}\mathrm{Trace}(J_{E^*})|_{K=2S^*+h}=\frac{rS^*}{(2S^*+h)^2}(2-\frac{h}{S^*+h})\neq 0.$$

Therefore, we can conclude from [39] that model (2.6) undergoes a Hopf bifurcation at the positive equilibrium E^* as K passes through the critical value $2S^*+h$.

Summarizing the above discussions, we obtain the following theorems.

Theorem 3.1. *For model* (2.6)*, there exists the trivial equilibrium* E^0 *and boundary equilibrium* E^1*.* E^0 *is always unstable;* E^1 *is stable if* $I(Cu)<\frac{m(K+h)}{eK}$*, whereas it is unstable if* $I(Cu)>\frac{m(K+h)}{eK}$*.*

Theorem 3.2. *For model* (2.6)*, there exists the positive equilibrium* E^* *in the case of* $I(Cu)>\frac{m(K+h)}{eK}$*.* E^* *is stable if* $K<2S^*+h$ *and unstable if* $K>2S^*+h$*, and Hopf bifurcation occurs when* $K=2S^*+h$*. That is, a limit cycle* Γ *will bifurcate from* E^* *as* K *passes through the critical value* $2S^*+h$*.*

To visualize the dynamics of model (2.6), in Fig. 1, we show the stability domains in (Cu, K) plane by taking the other parameter values in Table 1, where

$$L_1 : I(Cu) = \frac{m(K+h)}{eK}, \quad L_2 : K = 2S^* + h.$$

Specifically, boundary equilibrium E^1 is stable in the case of $(Cu, K) \in D_0$, positive equilibrium E^* is stable in the case of $(Cu, K) \in D_1$, and there exists a stable limit cycle in the case of $(Cu, K) \in D_2$. One can see from Fig. 1 that if $K < 0.1174$, E^1 is always stable for any concentration of Cu. If $K \in (0.1174, 0.3985)$, E^1 is stable for low and high concentrations of Cu, whereas E^* is stable for middle concentration of Cu. If $K > 0.3985$, the model dynamics will experience four transitions as the concentration of Cu increases. Let $K = 0.45$, and we obtain that the four critical concentrations of Cu are 4.9425, 5.2455, 11.6912 and 15.0906. The orbits of model (2.6) will converge to the boundary equilibrium E^1 in the cases of $Cu < 4.9425$ or $Cu > 15.0906$, as shown in Fig. 2, i.e., the Scenedesmus species survives and the Daphnia species goes to extinction. The orbits will converge to the positive equilibrium E^* in the cases of $Cu \in (4.9425, 5.2455)$ or $Cu \in (11.6912, 15.0906)$, as shown in Fig. 3, i.e., the two species survive in the form of constant. The orbits will converge to the limit cycle Γ in the case of $Cu \in (5.2455, 11.6912)$, as shown in Fig. 4, i.e., the two species survive in the form of oscillation.

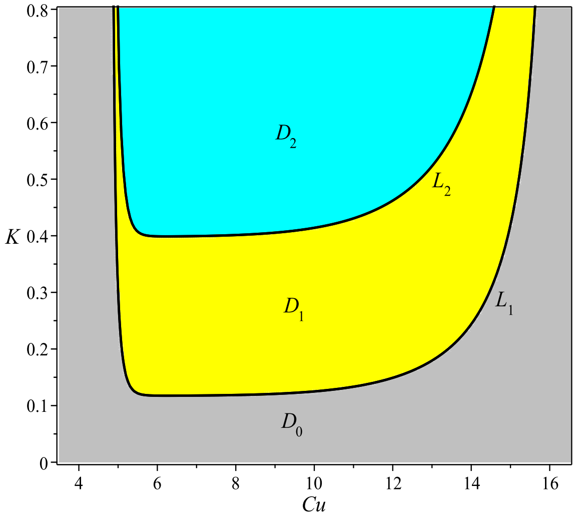

Figure 1. Stability domains in (Cu, K) plane for model (2.6) with fixed parameters showed in Table 1.

4. Extinction probability analysis based on CTMC model

To gain an understanding of the probability of Daphnia species extinction, a time-homogenous CTMC model can be formulated based on the infinitesimal probabilities. We first construct a CTMC model for the Scenedesmus-Daphnia interaction based on the ODE model (2.6). Define a CTMC by the discrete random vector

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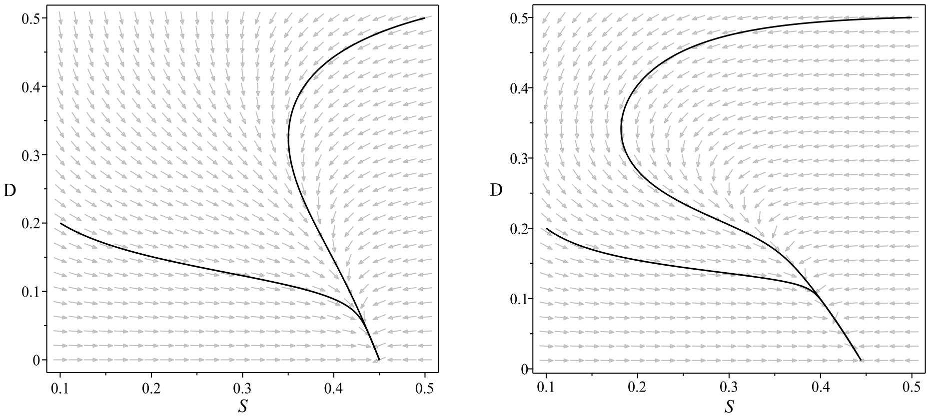

Figure 2. Phase portraits of model (2.6) with $K = 0.45$, $Cu = 4.5$ (left) and $Cu = 15.5$ (right).

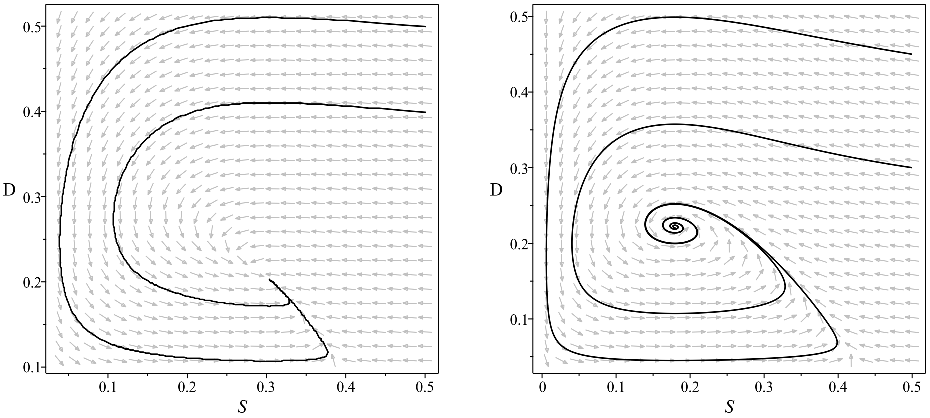

Figure 3. Phase portraits of model (2.6) with $K = 0.45$, $Cu = 5$ (left) and $Cu = 13$ (right).

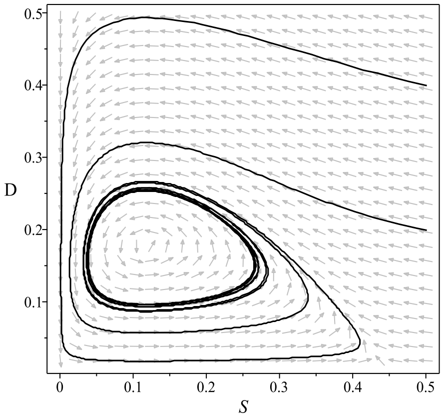

Figure 4. Phase portraits of model (2.6) with $K = 0.45$, $Cu = 6.5$.

Table 2. State transitions and the infinitesimal probabilities for the CTMC model

Description	State transition $a \to b$	Rate $P(a,b)$
Increase of S due to the birth	$(S,D) \to (S+1,D)$	$P_1 = rS(1-\frac{S}{K})$
Decrease of S due to the predation	$(S,D) \to (S-1,D)$	$P_2 = \frac{I(Cu)SD}{S+h}$
Increase of D due to the predation	$(S,D) \to (S,D+1)$	$P_3 = \frac{eI(Cu)SD}{S+h}$
Decrease of D due to the death	$(S,D) \to (S,D-1)$	$P_4 = mD$
No change	$(S,D) \to (S,D)$	$1-\sum_{i=1}^{4} P_i$

$Y(t) = (S(t), D(t))$ which takes values in a set $\mathbb{K} \subset \mathbb{N}_0^2$, where $\mathbb{N}_0$ is the set of non-negative integers. For simplicity, the same notations for the random variables are used as in deterministic model (2.6). The infinitesimal transition probabilities for the process $Y(t)$ are given by

$$\text{Prob}\,\{Y(t+\Delta t) = b|\ Y(t) = a\} = P(a,b)\Delta t + o(\Delta t), \tag{4.1}$$

where the transitions and their rates are summarized in Table 2.

In the following, we will derive the extinction probability of Daphnia species based on the branching process theory [3]. In order to derive the extinction probability, we apply the branching process theory to approximate the Markov chain process (listed in Table 2) near the deterministic boundary equilibrium $E^1 = (K,0)$ with a small initial number of Daphnia species. Given $D(0) = i$, the branching process has a limiting probability of extinction

$$P_0 = \lim_{t\to\infty} \text{Prob}\,\{D(t) = 0\},$$

which can be estimated by the offspring probability-generating function (pgf) of $D(t)$, one can see Refs. [17, 25, 45] for more details about the offspring pgf.

In the continuous-time process, a birth is not related to a death. Hence, the offspring pgf for Daphnia species D given the initial numbers $S(0) = K$ and $I(0) = 1$ is

$$f(u) = p_0 + p_2 u^2,$$

where

$$p_0 = \frac{P_4}{P_3+P_4} = \frac{m}{\frac{eI(Cu)K}{K+h} + m} = \frac{m(K+h)}{eI(Cu)K + m(K+h)}$$

is the probability of decrease of a Daphnia individual, and

$$p_2 = \frac{P_3}{P_3+P_4} = \frac{\frac{eI(Cu)K}{K+h}}{\frac{eI(Cu)K}{K+h} + m} = \frac{eI(Cu)K}{eI(Cu)K + m(K+h)}$$

is the probability of increase of a Daphnia individual.

The mean number of offspring per Daphnia individual is given by

$$m_D = f'(1) = 2p_2 = \frac{2eI(Cu)K}{eI(Cu)K + m(K+h)}.$$

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By the theory of Galton-Watson branching process, we know that

$$P_0 = \lim_{t\to\infty} \text{Prob}\,\{D(t) = 0\} = 1$$

in the case of $m_D < 1$ (i.e., $I(Cu) < \frac{m(K+h)}{eK}$). Biologically speaking, the extinction probability of Daphnia species is one in that case. If $m_D > 1$ (i.e., $I(Cu) > \frac{m(K+h)}{eK}$), then

$$P_0 = \lim_{t\to\infty} \text{Prob}\,\{D(t) = 0\} = \frac{m(K+h)}{eI(Cu)K},$$

and the extinction probability of Daphnia species is approximately $\frac{m(K+h)}{eI(Cu)K}$.

When the initial number $D(0) = i$, we get the following conclusion.

Theorem 4.1. *For model* (4.1)*, the extinction probability of Daphnia species is one in the case of* $I(Cu) < \frac{m(K+h)}{eK}$*, and is approximately* $\left(\frac{m(K+h)}{eI(Cu)K}\right)^i$ *in the case of* $I(Cu) > \frac{m(K+h)}{eK}$*, where i is the initial number of Daphnia species.*

Remark 4.1. One can see from Theorem 3.2 and Theorem 4.1 that the properties of CTMC model are totally different to the ODE model. Specifically, when $I(Cu) > \frac{m(K+h)}{eK}$, the ODE model predicts that the Daphnia species can survive, whereas the CTMC model predicts that the Daphnia species has a probability of extinction which is approximately $\left(\frac{m(K+h)}{eI(Cu)K}\right)^i$ with $D(0) = i$.

By fixing $D(0) = i = 1$, $K = 0.45$ and the other parameter values in Table 1, we show the curve of the extinction probability as a function of Cu in Fig. 5. It indicates that the curve of extinction probability P_0 exhibits a nadir structure. The extinction probability will decreases monotonically to 0.5692 when the concentration of Cu is less than 6.2446, but increases monotonically when the concentration of Cu is more than 6.2446.

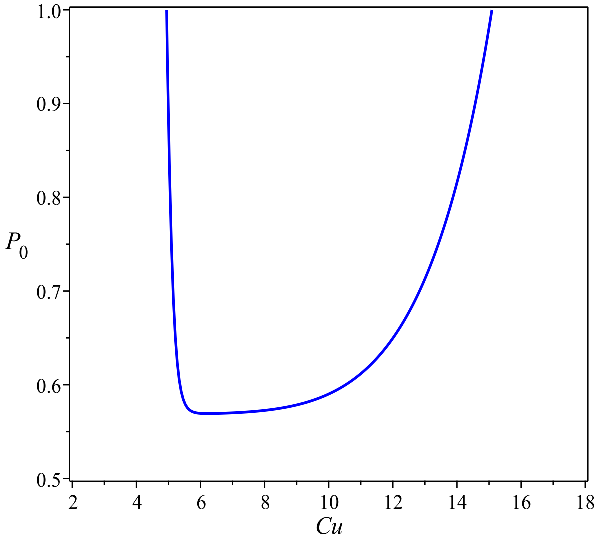

Figure 5. Extinction probability as a function of Cu with $D(0) = i = 1$, $K = 0.45$

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5. Conclusion and discussion

In this paper, we mainly investigated how the concentration of copper affects the phytoplankton-zooplankton dynamics in the freshwater ecosystem, through the model on interactions between Scenedesmus and Daphnia in deterministic and stochastic environments respectively.

By considering the maximum take rate of Daphnia as a function of copper concentration, we first constructed a Scenedesmus-Daphnia interaction model coupled with the copper concentration. For this model, we established the existence and stability conditions of the equilibria and proved the existence of Hopf bifurcation. We found that for different concentrations, the Scenedesmus-Daphnia interaction system may exhibit different dynamics: the Scenedesmus species survives and the Daphnia species goes to extinction, and the two species survive in the form of constant or in the form of oscillation.

To understand the effect of stochastic environment on the destiny of species, we used the CTMC to model the interaction between Scenedesmus and Daphnia. Applying the branching process theory, the approximate extinction probability of Daphnia species was obtained for the CTMC model. The results revealed that the Daphnia species will go to extinction in a positive probability, even if it can survive in the deterministic environment. Besides, this probability is closely related to the concentration of copper.

Note that the predictions of deterministic model and stochastic model are different in some cases, and some researches have used other stochastic processes to model the stochastic factors in ecosystems (see Refs. [13, 23, 43, 46] and the references therein). Therefore, in our future works, we will construct and study the Scenedesmus-Daphnia interaction models driven by other stochastic processes, such as standard Wiener process and mean-reverting Ornstein-Uhlenbeck process.

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