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¹ The time delays influence on the dynamical complexity of algal blooms
² in the presence of bacteria

³ Pankaj Kumar Tiwari^a, Sudip Samanta^b, Francesca Bona^c, Ezio Venturino^d, Arvind Kumar Misra ^{1e}

⁴ *^aDepartment of Mathematics, University of Kalyani, Kalyani - 741 235, West Bengal, India*

⁵ *^bDepartment of Mathematics, Faculty of Science & Arts - Rabigh, King Abdulaziz University, Rabigh-25732, Saudi Arabia*

⁶ *^cDBIOS, University of Turin, via Accademia Albertina 13, 10123 Turin, Italy*

⁷ *^dDipartimento di Matematica "Giuseppe Peano", via Carlo Alberto 10, 10123 Torino, Università di Torino, Italy;
Member of the INdAM research group GNCS*

⁸ *^eDepartment of Mathematics, Institute of Science, Banaras Hindu University, Varanasi 221005, India*

¹¹ **Abstract**

¹² Bacteria associated with oceanic algal blooms are acknowledged to play important roles in carbon,
¹³ nitrogen, and sulfur cycling. They influence the climate, mediate primary production, participate in bio-
¹⁴ geochemical cycles, and maintain ecological balance. A greater insight on the control of the interactions
¹⁵ between microalgae and other microorganisms, particularly bacteria, would be helpful in exploring the
¹⁶ role of bacteria on algal blooms in lakes. The present study is to investigate the effects of bacteria on the
¹⁷ occurrence of algal blooms in lakes. We propose a nonlinear mathematical model by taking into account
¹⁸ interactions among nutrients, algae, detritus and bacteria in a lake. We assume that bacteria enhance
¹⁹ the growth of algal biomass through remineralization only. Equilibria are analyzed for feasibility and
²⁰ stability, substantiated via numerical simulations. Increase in uptake rate of nutrients by algae and bac-
²¹ teria death rate generates transcritical bifurcations. We perform a global sensitivity analysis to identify
²² the important parameters of the model having a significant impact on the densities of algae and bacteria
²³ in the lake. Our findings show that massive algal production might occur in the presence of bacteria,
²⁴ and microalgae-bacteria interactions can be beneficial to the massive production of microalgae. Further,
²⁵ the effect of time delays involved in the bacterial decomposition conversion of detritus into nutrients is
²⁶ studied. Chaotic oscillations may arise via equilibrium destabilization on increasing the values of the
²⁷ time lag. To support chaos occurrence, the Poincaré map is drawn and the Lyapunov exponents are
²⁸ also computed. The findings, critically important for lake restoration, indicate that hypoxia in the lake
²⁹ can be prevented if detritus removal is performed on a regular basis, at time intervals smaller than the
³⁰ critical threshold in the delay with which detritus is decomposed into nutrients.

³¹ **Key words:** Mathematical model, Nutrients, Algae-bacteria interactions, Delay, Chaos, Lyapunov
³² exponent, Global sensitivity.

³³ **1. Introduction**

³⁴ In marine and freshwater ecosystems, phytoplankton transform inorganic carbon of water into organic
³⁵ matter that enters the food web or sinks to the sediments. Approximately one-half of such matter is
³⁶ directly utilized by heterotrophic bacteria, through the water column and at the level of sediments,
³⁷ and newly converted into inorganic compounds: CO₂ and nutrients (1). Seasonally in sea and lakes,
³⁸ phytoplankton increase in number determining the so-called blooms, and their requirement of CO₂
³⁹ and nutrients, such as nitrogen and phosphorous, increases consequently (2). Blooms of algae, that

¹ Corresponding author. Email: akmisra@bhu.ac.in

40 are sometimes a signal of dangerous eutrophication of waters, are even correlated with a subsequent
41 increase in activity of heterotrophic bacteria that convert algal organic production into bacterial biomass,
42 releasing CO₂ and regenerating nutrients associated with algal organic matter (3). With more food
43 available as a consequence of algal blooms, bacteria grow and use up the dissolved oxygen in the water
44 (3). Thus, the content of dissolved oxygen decreases and create hypoxic areas where aquatic life is not
45 longer possible (4). Indeed algal blooms are considered one of the most critical emergence affecting
46 water bodies across the world (5; 6; 7; 8; 9; 10). Moreover, under eutrophic conditions harmful species of
47 phytoplankton such as toxic cyanobacteria are facilitated and can cause serious adverse effects on animals
48 and humans. They have been reported to kill aquatic life, taint drinking water, contaminate fish and
49 shellfish, making catch inedible (11; 12; 13; 14). Eutrophication negatively affects local economies and
50 ecosystem services such as fishing, tourism, recreation and real estate (15; 16).

51 Phytoplankton and bacterioplankton interact continuously: their communities are closely interre-
52 lated in terms of abundance and functions (17). Moreover, heterotrophic bacteria satisfy their carbon
53 requirement not only by using phytoplankton derived matter but also by degrading all organic com-
54 pounds released into the aquatic ecosystems by human activities, and therefore nutrients produced by
55 bacteria from sewage are another resource supporting the algal growth (3). Bacteria can also compete
56 with planktonic algae for the same inorganic resources, principally at the earliest and terminal stages
57 of a bloom when nutrients are become limiting (3). Clearly, phytoplankton blooms create environmen-
58 tal conditions favouring the increase in the bacterial growth and production (18). Bacterial and algal
59 biomasses are generally correlated at the height of the bloom, while algae prevail during the earliest stage
60 when nutrients are scarce. Bacteria remain abundant when blooms decline as they continue to utilize the
61 organic substances released by dying and dead algae (19). Two distinct phases can be recognized in the
62 release of organic compounds by phytoplankton. In the earliest stages of a bloom, algae release soluble,
63 low molecular weight compounds which can act as chemical attractants for bacteria. In the declining
64 stage, phytoplankton release higher molecular weight macromolecules such as polysaccharides, proteins
65 and lipids, that can be assimilated by bacteria.

66 Heterotrophic bacteria assimilate and remineralize the organic matter firstly by converting it to the
67 dissolved phase thanks to the action of their extracellular and cell-surface enzymes. Then such dissolved
68 molecules are readily transported across the cell wall and transformed into bacterial biomass. In lab
69 cultures flavobacteria and roseobacter have been seen to directly attack viable algal cells (20). However,
70 their interactions with phytoplankton are essentially mutualistic, as they provide algae with nutrients,
71 vitamins and growth promoting factors, such as the auxins. But at the end of a bloom when nutrients
72 become limiting, symbiosis can be converted in competition as roseobacteria in particular produce al-
73 gicidal compounds favouring the decline of algae community (21). The interactions between these two
74 communities are areas of recent studies (22; 23), which shed light on the complex role of heterotrophic
75 bacteria in algal growth and survival. They not only decompose organic matter allowing the nutrient
76 recycling, but also promote algal growth by complex communication mechanisms and nutrient exchange
77 (24). Indeed not only macro-nutrients such as nitrogen, phosphorus and carbon are exchanged between
78 them but also micro-nutrients such as vitamins and other growth-promoting molecules (25; 26).

79 Several studies have been conducted to explore the role of nutrients on the bloom of algae in
80 lakes/ponds (6; 7; 8; 9; 10). Deeper insights into the role of heterotrophic bacteria may have important
81 applications in the strategies to control algal blooms in aquatic ecosystems. Moreover, nowadays algaeb-
82 bacteria interactions are considered as promising in biotechnology, as recent studies highlighted the pos-
83 tive role of bacteria for massive algal cultivation for biotechnological applications (20; 22; 23; 27; 28; 29).
84 However, in (6; 7; 8; 9; 10) models on the recycling of detritus into nutrients do not explicitly account for
85 the role of bacteria. It is well documented that bacteria play a potentially important role in structuring

86 algal species (30). Thus, the possible effects of bacteria on the population dynamics of algal species
87 must be considered in the modelling process. Therefore, in this paper, our aim is to assess the effect of
88 algae-bacteria interactions on the dynamics of algal population.

89 In many processes of real phenomena, the present dynamics of the state variables depends not only
90 on the present state of the processes but also on their past history (31). These processes are generally
91 modeled by time delays which are known to trigger instabilities (32; 33). The potential effects of nutrient
92 recycling on the ecosystem has been studied (6; 34; 35), but it is not an instantaneous process. The time
93 needed by bacteria to transform the mass of dead algae into nutrients has not been explicitly taken into
94 account, in general, but it should, in order to represent a complete nutrient cycle (36). Plankton-nutrient
95 interaction models with both instantaneous and delayed nutrient recycling show that the stability of the
96 positive equilibrium is lost after the input rate of nutrient crosses a threshold value and oscillations
97 emerges through Hopf bifurcation (37). A planktonic resource-consumer model exhibiting a temporal
98 delay in the formation of nutrients from the dead plankton is presented in (38), where the nutrient inflows
99 at a constant rate. The system may destabilize due to this temporal lag. Other similar investigations
100 involve e.g. delays on nutrient cycling in phytoplankton-zooplankton interactions in an estuarine system
101 (39), discrete time delays in the conversion of detritus into nutrients, for which upon crossing a threshold,
102 the system may switch finitely many times back and forth from stability to instability, but eventually
103 becoming unstable (40). Control measures have therefore been considered in (41): the presence of two
104 time delays may produce a stabilizing effect on the system dynamics. In view of these considerations,
105 here we study the effects of time delays on the algae-bacteria interactions, due to the time lags needed
106 for the bacterial conversion of detritus into nutrients (36; 38; 40; 41). The possibility of Hopf-bifurcation
107 is explored by taking the time delay as a bifurcation parameter.

108 The rest of the paper is organized as follows: in the next section, we formulate the model. In Section
109 3, we study the dynamics of nutrients-algae system only, while in Section 4, we include detritus also,
110 then in Section 5, we consider the input rate of nutrients from external sources as zero. In Section 6, we
111 analyze the full model, and in Section 7, we show that system's equilibria are related via transcritical
112 bifurcations. In Section 8, we consider the modified model to account for time delays in the decomposition
113 and regeneration processes. Hopf-bifurcation at the coexistence equilibrium are studied in Section 9.
114 In Section 10, we validate our analytical findings through numerical simulations. A global sensitivity
115 analysis is performed to identify the most influential model parameters that have significant impact on
116 algae and bacteria. We conclude with a wrap-up discussion.

117 2. The mathematical model

118 Currently there are more than 500 hypoxic systems covering over 2,40,000 km² around the globe
119 (42). In China, several lakes such as lake Chaohu, Lake Taihu and Dianchi had been examined and
120 data showed that they were in eutrophication (43). Algae, heterotrophic bacteria and Archea are the
121 primary producers and decomposers, respectively, making them the structural pillars of the ecosystem
122 and its foremost functional entities. *Pseudomonas diminuta* and *Pseudomonas vesicularis*, two obligate
123 aerobes, stimulated the growth of the green microalgae *Scenedesmus bicellularis* and *Chlorella sp.*, with-
124 out releasing any growth-promoting substance (44). Indeed, under controlled conditions with a limited
125 concentration of inorganic carbon, Mouget et al. (44) found that the presence of *P. diminuta* stimulated
126 the photosynthetic activity of *S. bicellularis*. These authors suggest that aerobic bacteria can enhance
127 algal productivity by attenuating the photosynthetic oxygen tension around algal cells. Moreover, bac-
128 teria may become an important source of carbon from algal growth, especially under conditions of CO₂
129 limitation (45). Finally, they can promote algal growth by releasing vitamins and other growth factors
130 or by modifying some physico-chemical property of the aquatic environment such as the pH (46). In

most cases the association between algae and bacteria leads to mutual interactions (47). Indeed algae provide oxygen and organic molecules to support bacteria growth, despite in some phases of algal bloom their interaction may include resource (e.g. nutrients) competition. However, most types of interactions between algae and bacteria in the planktonic zone are scarcely studied. The ones studied often reflect the importance of undertaking such studies (3). Here, we consider the growth of algae due to bacteria only via nutrient regeneration on decomposition of organic matter, no other mode is considered (3; 44).

Consider a lake which is being eutrophied due to overgrowth of algae and other biological species caused by discharge of nutrients from domestic drainage as well as from water run off, etc., and also from nutrients formed from detritus upon bacterial decomposition. We consider four dependent variables in the lake, namely; concentration of nutrients (nitrogen, phosphorus, etc.), N ($\mu\text{g}/\text{L}$), density of algal populations, A ($\mu\text{g}/\text{L}$), density of detritus (formed due to death of algae), D ($\mu\text{g}/\text{L}$), and density of bacteria, B ($\mu\text{g}/\text{L}$), at any time $t > 0$. Algae in lakes consist of diverse assemblage of all major taxonomic groups. Many of these forms have different physiological requirements and differ in their response to light, temperature and concentration of nutrients. Here, we do not consider the effects of light and temperature on the algal growth and assume that the algal population fully depends on the availability of nutrients in the lake. It is assumed that nutrients are continuously discharged into the lake from different sources (domestic drainage, water run off from agricultural fields, etc.) at a constant rate, being naturally depleted and utilized by algae. The utilization rate of nutrients by algae is assumed in the form of a Holling type-II term and the growth rate of algal populations is proportional to the same interaction term. Algae are removed by natural death, higher predation and intraspecific competition and then are turned into detritus which either naturally depletes or is decomposed by the bacterial pool, this being expressed once more via a Holling type-II function. Depletion of detritus occurs due to biochemical processes performed by anaerobic and aerobic bacteria that convert it into nutrients. Conversion by anaerobic bacteria does not need dissolved oxygen (DO), but the latter is required in the aerobic processes for nutrient degradation. This results in the depletion of DO level in the water body. However, in this paper the bacteria decomposition process is considered without explicitly writing an equation for DO level. After decomposition by bacteria, detritus are recycled into nutrients (remineralization) and the bacterial population increases due to this conversion process. Further, the density of bacteria increases in the aquatic environment due to other types of detritus, different from the algal one. Bacteria natural mortality is taken into account as well as due to other causes, such as enzymatic attack, temperature variations, UV radiation, photo-oxidation, etc. (48).

Algal bloom has pushed the problem of the quality and quantity of water available for consumption to alarming levels, so that nowadays the existence of aquatic life is threatened (10; 49; 50). Large amounts of decaying biological materials in the water bodies lead to oxygen depletion, and this results in fish population collapse, as the oxygen saturation level has an effect on growth and feed conversion ratios of fish. Due to low levels of DO, frequently associated with phenomena such as heat waves, cloudy weather, organic overload, algae die-offs, or heavy thunderstorms (51), the whole aquatic ecosystem is significantly affected and survival of the aquatic species is threatened. Incorporating fish populations and DO levels in the model formulation would be more realistic, but would by far increase the complexity of the model and therefore is not considered here. Other related studies have in part considered these issues, see (52; 53).

The schematic diagram for the interactions among nutrients, algae, detritus and bacteria is depicted in Fig. 1. The resulting system, in which all the parameters are assumed to be positive and constant,

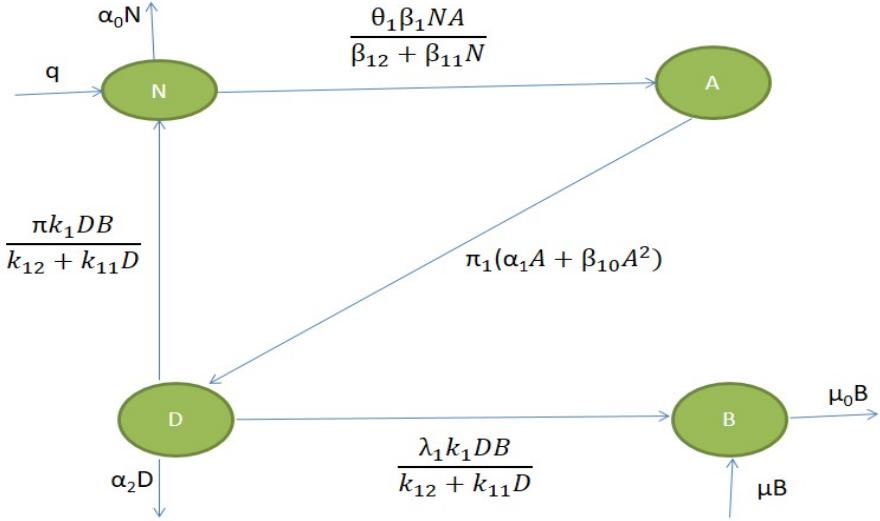


Figure 1: Schematic diagram for the interactions among nutrients, algae, detritus and bacteria.

¹⁷⁴ reads:

$$\begin{aligned}
 \frac{dN}{dt} &= q - \alpha_0 N - \frac{\beta_1 N A}{\beta_{12} + \beta_{11} N} + \frac{\pi k_1 D B}{k_{12} + k_{11} D}, \\
 \frac{dA}{dt} &= \frac{\theta_1 \beta_1 N A}{\beta_{12} + \beta_{11} N} - \alpha_1 A - \beta_{10} A^2, \\
 \frac{dD}{dt} &= \pi_1 (\alpha_1 A + \beta_{10} A^2) - \alpha_2 D - \frac{k_1 D B}{k_{12} + k_{11} D}, \\
 \frac{dB}{dt} &= \mu B - \mu_0 B + \frac{\lambda_1 k_1 D B}{k_{12} + k_{11} D}.
 \end{aligned} \tag{2.1}$$

¹⁷⁵ The biological meaning of the parameters involved in the system (2.1) and their values used for
¹⁷⁶ numerical simulations are given in Table 1. The constant π_1 represents the conversion of dead algae into
¹⁷⁷ detritus due to natural death, higher predation and intraspecies competition (6; 54). For the biological
¹⁷⁸ soundness (i.e. boundedness of the trajectories) of the model, the bacteria natural death rate is assumed
¹⁷⁹ to be higher than its growth rate due to detritus types other than algal one, i.e., $\mu_0 - \mu$ is positive. Also,
¹⁸⁰ the following two conditions must hold

$$\theta_1 \beta_1 - \beta_{11} \alpha_1 > 0, \tag{2.2}$$

$$\lambda_1 k_1 - k_{11}(\mu_0 - \mu) > 0. \tag{2.3}$$

¹⁸¹ Biologically, to satisfy condition (2.2), the total benefit to the algal biomass on consumption of nutrients
¹⁸² must exceed the natural death rate of algae. If this condition fails, the growth rate of algae becomes
¹⁸³ negative and thus as time increases algae disappear. Similarly, condition (2.3) means that the bacteria

184 population growth caused by detritus decomposition must be greater than the difference between the
 185 natural death rate of bacteria and the bacterial population growth due to other types of detritus. If the
 186 condition does not hold, then the bacteria population declines, and eventually vanishes as time increases.
 187 To have a meaningful model, the algal and bacterial populations must thrive, thus the conditions (2.2)
 188 and (2.3) must hold.

Table 1: Parameter values (hypothetical) in the system (2.1)

Names	Description	Unit	Value	Reference
q	Input rate of nutrients to the lake from domestic drainage and water run off from agricultural fields	$\mu\text{g/L/day}$	0.05	(8)
α_0	Per capita loss rate of nutrient due to sinking from the epilimnion down to the hypolimnion and thus making these nutrients unavailable for algae uptake	1/day	0.01	(10)
β_1	Maximum uptake rate of nutrients by algae	1/day	0.85	
β_{12}	Half saturation constant	$\mu\text{g/L/day}$	1	
β_{11}	Proportionality constant	—	10	
π	Remineralization of detritus into nutrients	—	0.3	
k_1	Maximum decomposition rate of detritus by bacteria	1/day	0.5	
k_{12}	Half saturation constant	$\mu\text{g/L/day}$	1	
k_{11}	Proportionality constant	—	0.3	
θ_1	Algal growth due to nutrients uptake	—	5	
α_1	Natural mortality and higher predation of algae	1/day	1/3	
β_{10}	Algal mortality due to intraspecific competition	$\text{L}/\mu\text{g/day}$	0.01	
π_1	Algal conversion into detritus	—	0.2	
α_2	Sinking rate of detritus to the bottom of the lake, being buried into the sediments at the lake bottom	1/day	0.006	
μ	Bacterial growth due to other types of detritus	1/day	1.85	
μ_0	Natural death rate of bacteria	1/day	2	
λ_1	Bacterial growth due to detritus	—	0.5	

189

190 3. Ecosystem with nutrients and algae only

191 Considering a special case of system (2.1) where only the dynamics of nutrients and algae is taken
 192 into account, then we have the following subsystem

$$\begin{aligned}
 \frac{dN}{dt} &= q - \alpha_0 N - \frac{\beta_1 N A}{\beta_{12} + \beta_{11} N}, \\
 \frac{dA}{dt} &= \frac{\theta_1 \beta_1 N A}{\beta_{12} + \beta_{11} N} - \alpha_1 A - \beta_{10} A^2.
 \end{aligned} \tag{3.1}$$

193 3.1. Boundedness

194 The feasible region for system (3.1) is given in the following lemma.

195 **Lemma 3.1.** *The region of attraction for all solutions of system (1) initiating in the positive quadrant
 196 is given by (55):*

$$\Omega_1 = \{(N, A) \in \mathbb{R}_+^2 : 0 < N + P \leq q/\delta_m\},$$

197 where $\delta_m = \min\{\alpha_0, \alpha_1\}$. The region Ω_1 is closed and bounded in the positive quadrant of the two
 198 dimensional plane. Consequently, the system (3.1) is dissipative and any solution is defined for $t \geq 0$.

199 3.2. Equilibria

200 System (3.1) has two feasible equilibria: (i) The algae-free equilibrium $\bar{E}_0 = (q\alpha_0^{-1}, 0)$, always feasible,
 201 and (ii) The interior equilibrium $\bar{E}^* = (\bar{N}^*, \bar{A}^*)$, where $\bar{N}^* = \frac{\beta_{12}(\alpha_1 + \beta_{10}\bar{A}^*)}{(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}\bar{A}^*}$ and \bar{A}^* is a
 202 positive root of the following equation:

$$f(A) = \left[q - \frac{A(\alpha_1 + \beta_{10}A)}{\theta} \right] [(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}A] - \beta_{10}\alpha_0(\alpha_1 + \beta_{10}A). \quad (3.2)$$

203 From equation (3.2), we note the following

204 1. $f(0) = q(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{12}\alpha_1\alpha_0$, which is positive provided

$$q(\theta_1\beta_1 - \beta_{11}\alpha_1) > \beta_{12}\alpha_1\alpha_0. \quad (3.3)$$

205 2. $f(\bar{A}) < 0$, where $\bar{A} = \frac{\theta_1\beta_1 - \beta_{11}\alpha_1}{\beta_{11}\beta_{10}}$.

206 3. $f'(A) < 0$, $\forall A \in (0, \bar{A})$.

207 Thus, equation (3.2) has exactly one positive root in the interval $(0, \bar{A})$ and the interior equilibrium \bar{E}^*
 208 is feasible provided condition (3.3) holds.

209 3.3. Stability

210 3.3.1. Local stability

211 The Jacobian of system (3.1) is

$$\bar{J} = \begin{pmatrix} -\left(\alpha_0 + \frac{\beta_1\beta_{12}A}{(\beta_{12} + \beta_{11}N)^2}\right) & -\frac{\beta_1N}{\beta_{12} + \beta_{11}N} \\ \frac{\theta_1\beta_1\beta_{12}A}{(\beta_{12} + \beta_{11}N)^2} & \frac{\theta_1\beta_1N}{\beta_{12} + \beta_{11}N} - \alpha_1 - 2\beta_{10}A \end{pmatrix}.$$

At equilibrium \bar{E}_0 , the eigenvalues are

$$-\alpha_0, \quad \frac{\theta_1\beta_1q}{\beta_{12}\alpha_0 + \beta_{11}q} - \alpha_1.$$

212 One eigenvalue is negative while the other is negative if condition (3.3) does not hold. Thus, the
 213 equilibrium \bar{E}_0 is related via transcritical bifurcation to the equilibrium \bar{E}^* .

214 The characteristic equation at the equilibrium \bar{E}^* is

$$\begin{aligned} \lambda^2 + \lambda \left(\alpha_0 + \beta_{10}\bar{A}^* + \frac{\beta_1\beta_{12}\bar{A}^*}{(\beta_{12} + \beta_{11}\bar{N}^*)^2} \right) + \beta_{10}\bar{A}^* \left(\alpha_0 + \frac{\beta_1\beta_{12}\bar{A}^*}{(\beta_{12} + \beta_{11}\bar{N}^*)^2} \right) \\ + \frac{\theta_1\beta_1\beta_{12}\bar{A}^*}{(\beta_{12} + \beta_{11}\bar{N}^*)^2} \frac{\beta_1\bar{N}^*}{\beta_{12} + \beta_{11}\bar{N}^*} = 0. \end{aligned}$$

215 Since the linear and constant terms are positive, in view of Routh-Hurwitz criterion, the roots are either
 216 negative or have negative real parts. Thus, the equilibrium \bar{E}^* is unconditionally stable.

217 The results can be summarized in the following theorem.

218 **Theorem 3.1.** 1. The algae-free equilibrium \bar{E}_0 is related to the interior equilibrium \bar{E}^* via a trans-
 219 critcal bifurcation.

220 2. The interior equilibrium \bar{E}^* , if feasible, is unconditionally locally asymptotically stable.

221 3.3.2. Global stability

222 As far as global stability of the equilibrium \bar{E}^* is concerned, we have the following result.

223 **Theorem 3.2.** *The coexistence equilibrium \bar{E}^* , if feasible, is globally asymptotically stable inside the
224 region of attraction Ω_1 provided the following condition holds:*

$$\left[\frac{\beta_1 \beta_{11} q}{(\beta_{12} \delta_m + \beta_{11} q)(\beta_{12} + \beta_{11} \bar{N}^*)} \right]^2 \bar{N}^* < \frac{4 \beta_{10} \alpha_0}{\theta_1}. \quad (3.4)$$

225 *Proof.* We consider the following as a Lyapunov function candidate

$$U = \frac{1}{2}(N - \bar{N}^*)^2 + m_1 \left(A - \bar{A}^* - \bar{A}^* \ln \frac{A}{\bar{A}^*} \right), \quad (3.5)$$

226 where m_1 is a positive constant to be determined. The time derivative of U along the solutions trajectory
227 of the system (3.1) is

$$\begin{aligned} \dot{U} = & - \left[\alpha_0 + \frac{\beta_1 \beta_{12} A}{(\beta_{12} + \beta_{11} N)(\beta_{12} + \beta_{11} \bar{N}^*)} \right] (N - \bar{N}^*)^2 - m_1 \beta_{10} (A - \bar{A}^*)^2 \\ & + \left[\frac{m_1 \theta_1 \beta_1 \beta_{12}}{(\beta_{12} + \beta_{11} N)(\beta_{12} + \beta_{11} \bar{N}^*)} - \frac{\beta_1 \bar{N}^*}{\beta_{12} + \beta_{11} \bar{N}^*} \right] (N - \bar{N}^*)(A - \bar{A}^*). \end{aligned}$$

228 Set $m_1 = \bar{N}^*/\theta_1$, \dot{U} is negative definite inside Ω_1 provided condition (3.4) holds. ■

229 4. Ecosystem behavior in the absence of bacteria

230 If we consider the case when no bacteria is present in the aquatic environment, then system (2.1)
231 takes the following form

$$\begin{aligned} \frac{dN}{dt} &= q - \alpha_0 N - \frac{\beta_1 N A}{\beta_{12} + \beta_{11} N}, \\ \frac{dA}{dt} &= \frac{\theta_1 \beta_1 N A}{\beta_{12} + \beta_{11} N} - \alpha_1 A - \beta_{10} A^2, \\ \frac{dD}{dt} &= \pi_1 (\alpha_1 A + \beta_{10} A^2) - \alpha_2 D. \end{aligned} \quad (4.1)$$

232 4.1. Boundedness

233 The feasible region for system (4.1) is given in the following lemma.

234 **Lemma 4.1.** *The region of attraction for all solutions of system (4.1) initiating in the positive octant
235 is given by (55):*

$$\Omega_2 = \{(N, A, D) \in \mathbb{R}_+^3 : 0 < N + P + D \leq q/\delta_n\},$$

236 where $\delta_n = \min\{\alpha_0, (1-\pi)\alpha_1, \alpha_2\}$. The region Ω_2 is closed and bounded in the positive cone of the three
237 dimensional space. Consequently, the system (4.1) is dissipative and any solution is defined for $t \geq 0$.

²³⁸ 4.2. Equilibria

System (4.1) has two feasible equilibria: (i) The algae-detritus-free equilibrium $\hat{E}_0 = (q\alpha_0^{-1}, 0, 0)$, always feasible, and (ii) The interior equilibrium $\hat{E}^* = (\hat{N}^*, \hat{A}^*, \hat{D}^*)$, where

$$\hat{N}^* = \frac{\beta_{12}(\alpha_1 + \beta_{10}\hat{A}^*)}{(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}\hat{A}^*}, \quad \hat{D}^* = \frac{\pi_1\hat{A}^*(\alpha_1 + \beta_{10}\hat{A}^*)}{\alpha_2}$$

²³⁹ and \hat{A}^* is a positive root of the following equation:

$$g(A) = \left[q - \frac{A(\alpha_1 + \beta_{10}A)}{\theta} \right] [(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}A] - \beta_{10}\alpha_0(\alpha_1 + \beta_{10}A). \quad (4.2)$$

²⁴⁰ From (3.2), we have

²⁴¹ 1. $g(0) = q(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{12}\alpha_1\alpha_0$, which is positive provided

$$q(\theta_1\beta_1 - \beta_{11}\alpha_1) > \beta_{12}\alpha_1\alpha_0. \quad (4.3)$$

²⁴² 2. $g(\bar{A}) < 0$, where $\bar{A} = \frac{\theta_1\beta_1 - \beta_{11}\alpha_1}{\beta_{11}\beta_{10}}$.

²⁴³ 3. $g'(A) < 0, \forall A \in (0, \bar{A})$.

²⁴⁴ Thus, the equation (4.2) has exactly one positive root in the interval $(0, \bar{A})$. Thus, the interior equilibrium ²⁴⁵ \hat{E}^* is feasible provided condition (4.3) holds.

²⁴⁶ 4.3. Stability

²⁴⁷ 4.3.1. Local stability

²⁴⁸ The Jacobian of system (4.1) is

$$\bar{J} = \begin{pmatrix} -\left(\alpha_0 + \frac{\beta_1\beta_{12}A}{(\beta_{12} + \beta_{11}N)^2}\right) & -\frac{\beta_1N}{\beta_{12} + \beta_{11}N} & 0 \\ \frac{\theta_1\beta_1\beta_{12}A}{(\beta_{12} + \beta_{11}N)^2} & \frac{\theta_1\beta_1N}{\beta_{12} + \beta_{11}N} - \alpha_1 - 2\beta_{10}A & 0 \\ 0 & \pi_1(\alpha_1 + 2\beta_{10}A) & -\alpha_2 \end{pmatrix}.$$

At equilibrium \hat{E}_0 , the eigenvalues are

$$-\alpha_0, \frac{\theta_1\beta_1q}{\beta_{12}\alpha_0 + \beta_{11}q} - \alpha_1, -\alpha_2.$$

²⁴⁹ Two eigenvalues are negative while the other is negative if condition (4.3) does not hold. Thus, the ²⁵⁰ equilibrium \hat{E}_0 is related via transcritical bifurcation to the equilibrium \hat{E}^* .

²⁵¹ One eigenvalue at the equilibrium \hat{E}^* is $-\alpha_2$, while the other two are roots of the quadratic

$$\begin{aligned} \lambda^2 + \lambda \left(\alpha_0 + \beta_{10}\hat{A}^* + \frac{\beta_1\beta_{12}\hat{A}^*}{(\beta_{12} + \beta_{11}\hat{N}^*)^2} \right) + \beta_{10}\hat{A}^* \left(\alpha_0 + \frac{\beta_1\beta_{12}\hat{A}^*}{(\beta_{12} + \beta_{11}\hat{N}^*)^2} \right) \\ + \frac{\theta_1\beta_1\beta_{12}\hat{A}^*}{(\beta_{12} + \beta_{11}\hat{N}^*)^2} \frac{\beta_1\hat{N}^*}{\beta_{12} + \beta_{11}\hat{N}^*} = 0. \end{aligned}$$

²⁵² Since the linear and constant terms are positive, in view of Routh-Hurwitz criterion, the roots are either ²⁵³ negative or have negative real parts. Thus, the equilibrium \hat{E}^* is always stable.

²⁵⁴ Now, we summarize the results in the following theorem.

²⁵⁵ **Theorem 4.1.** 1. The algae-free equilibrium \hat{E}_0 is related to the interior equilibrium \hat{E}^* via a trans-²⁵⁶ critical bifurcation.

²⁵⁷ 2. The interior equilibrium \hat{E}^* , if feasible, is always locally asymptotically stable.

258 4.3.2. Global stability

259 For global stability of equilibrium \widehat{E}^* , we have the following result.

260 **Theorem 4.2.** *The interior equilibrium \widehat{E}^* , if feasible, is globally asymptotically stable inside the region
261 of attraction Ω_2 provided the following conditions hold*

$$\left[\frac{\beta_1 \beta_{11} q}{(\beta_{12} \delta_n + \beta_{11} q)(\beta_{12} + \beta_{11} \widehat{N}^*)} \right]^2 \widehat{N}^* < \frac{2\beta_{10}\alpha_0}{\theta_1}, \quad (4.4)$$

$$\pi_1^2 [\alpha_1 + \beta_{10}(q/\delta_n + \widehat{A}^*)]^2 < \frac{2\beta_{10}\alpha_2 \widehat{N}^*}{\theta_1}. \quad (4.5)$$

262 *Proof.* We consider the following as a Lyapunov function candidate

$$V = \frac{1}{2}(N - \widehat{N}^*)^2 + m_1 \left(A - \widehat{A}^* - \widehat{A}^* \ln \frac{A}{\widehat{A}^*} \right) + \frac{m_2}{2}(D - \widehat{D}^*)^2, \quad (4.6)$$

263 where m_1 and m_2 are positive constants to be determined. The time derivative of V along the solutions
264 trajectory of the system (4.1) is

$$\begin{aligned} \dot{V} = & - \left[\alpha_0 + \frac{\beta_1 \beta_{12} A}{(\beta_{12} + \beta_{11} N)(\beta_{12} + \beta_{11} \widehat{N}^*)} \right] (N - \widehat{N}^*)^2 - m_1 \beta_{10} (A - \widehat{A}^*)^2 - m_2 \alpha_2 (D - \widehat{D}^*)^2 \\ & + \left[\frac{m_1 \theta_1 \beta_1 \beta_{12}}{(\beta_{12} + \beta_{11} N)(\beta_{12} + \beta_{11} \widehat{N}^*)} - \frac{\beta_1 \widehat{N}^*}{\beta_{12} + \beta_{11} \widehat{N}^*} \right] (N - \widehat{N}^*)(A - \widehat{A}^*) \\ & + m_2 \pi_1 [\alpha_1 + \beta_{10}(A + \widehat{A}^*)](A - \widehat{A}^*)(D - \widehat{D}^*). \end{aligned}$$

265 Setting $m_1 = \overline{N}^*/\theta_1$ and $m_2 = 1$, \dot{V} is negative definite inside Ω_2 provided conditions (4.4) and (4.5)
266 are satisfied. ■

267 5. No nutrients input from external sources

268 In all the previous cases, as well as in the full model to be analyzed in the next section, the equilibria
269 always show a nonnegative value for the nutrients. This is evident mathematically and biologically,
270 as their continuous input from external sources prevents them to disappear. To better focus on this
271 situation, we now examine the case in which this inflow is prevented. It turns out anyway, that no
272 nutrient-free equilibrium can be achieved as it will be apparent from the analysis below. The biological
273 reason is that nutrients are replenished by the detritus decomposed by bacteria, and only if one of these
274 two population vanishes, they are also doomed. But in turn, the disappearance of either detritus or
275 bacteria is ultimately related to the total ecosystem collapse or no nutrients production: for no detritus
276 to be generated, the algae must vanish; if bacteria are absent, no conversion to nutrients occurs, and
277 detritus can only sink to the bottom layers of the lake. Assume therefore that nutrients present in the
278 lake are only due to recycling of detritus upon bacterial decomposition. In this particular case, we set
279 $q = 0$, and hence equation (2.1) reduces to

$$\begin{aligned} \frac{dN}{dt} &= \frac{\pi k_1 DB}{k_{12} + k_{11} D} - \alpha_0 N - \frac{\beta_1 NA}{\beta_{12} + \beta_{11} N}, \\ \frac{dA}{dt} &= \frac{\theta_1 \beta_1 NA}{\beta_{12} + \beta_{11} N} - \alpha_1 A - \beta_{10} A^2, \\ \frac{dD}{dt} &= \pi_1 (\alpha_1 A + \beta_{10} A^2) - \alpha_2 D - \frac{k_1 DB}{k_{12} + k_{11} D}, \\ \frac{dB}{dt} &= \mu B - \mu_0 B + \frac{\lambda_1 k_1 DB}{k_{12} + k_{11} D}. \end{aligned} \quad (5.1)$$

280 5.1. Equilibria

281 System (5.1) has two feasible equilibria:

- 282 1. The origin $\tilde{E}_0 = (0, 0, 0, 0)$, which is always feasible.
283 2. The interior equilibrium $\tilde{E}^* = (\tilde{N}^*, \tilde{A}^*, \tilde{D}^*, \tilde{B}^*)$, with

$$\begin{aligned}\tilde{N}^* &= \frac{\beta_{12}(\alpha_1 + \beta_{10}\tilde{A}^*)}{(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}\tilde{A}^*}, & \tilde{D}^* &= \frac{k_{12}(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)}, \\ \tilde{B}^* &= \frac{1}{\mu_0 - \mu} \left[\pi_1 \tilde{A}^*(\alpha_1 + \beta_{10}\tilde{A}^*) - \frac{k_{12}\alpha_2(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)} \right]\end{aligned}$$

284 and \tilde{A}^* is a positive root of the equation

$$c_3 A^3 + c_2 A^2 + c_1 A + c_0 = 0, \quad (5.2)$$

285 where

$$\begin{aligned}c_3 &= \beta_{10}^2 \beta_{11} (1 - \pi \pi_1 \theta_1) \{ \lambda_1 k_1 - k_{11}(\mu_0 - \mu) \}, \\ c_2 &= -\beta_{10} (1 - \pi \pi_1 \theta_1) \{ \lambda_1 k_1 - k_{11}(\mu_0 - \mu) \} (\theta_1 \beta_1 - 2\beta_{11}\alpha_1), \\ c_1 &= -k_{12}\alpha_2 \theta_1 \beta_{11}\beta_{10} + \{ \lambda_1 k_1 - k_{11}(\mu_0 - \mu) \} [\beta_{12}\beta_{10}\theta_1\alpha_0 + \alpha_1(1 - \pi \pi_1 \theta_1)(\theta_1 \beta_1 - \beta_{11}\alpha_1)], \\ c_0 &= -\theta_1 [k_{12}\alpha_2(\mu_0 - \mu)(\theta_1 \beta_1 - \beta_{11}\alpha_1) + \beta_{12}\alpha_1\alpha_0 \{ \lambda_1 k_1 - k_{11}(\mu_0 - \mu) \}].\end{aligned}$$

286 In view of assumptions (2.2) and (2.3), equation (5.2) has exactly one positive if the following condition
287 holds:

$$\theta_1 \beta_1 - 2\beta_{11}\alpha_1 > 0. \quad (5.3)$$

288 Clearly, \tilde{D}^* is positive in view of assumption (2.3), while \tilde{N}^* and \tilde{B}^* are positive if respectively the
289 following condition hold

$$(\theta_1 \beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}\tilde{A}^* > 0, \quad \pi_1 \tilde{A}^*(\alpha_1 + \beta_{10}\tilde{A}^*) - \frac{k_{12}\alpha_2(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)} > 0. \quad (5.4)$$

290 5.2. Local stability of equilibria

291 In this section, the local stability analysis of equilibria of the model (5.1) is performed. The Jacobian
292 of (5.1) is $\tilde{J} = [\tilde{J}_{ij}]$, $i, j = 1, 2, 3, 4$, with nonvanishing explicit entries given by

$$\begin{aligned}\tilde{J}_{11} &= -\left(\alpha_0 + \frac{\beta_1 \beta_{12} A}{(\beta_{12} + \beta_{11} N)^2} \right), \quad \tilde{J}_{12} = -\frac{\beta_1 N}{\beta_{12} + \beta_{11} N}, \quad \tilde{J}_{13} = \frac{\pi k_1 k_{12} B}{(k_{12} + k_{11} D)^2}, \\ \tilde{J}_{14} &= \frac{\pi k_1 D}{k_{12} + k_{11} D}, \quad \tilde{J}_{21} = \frac{\theta_1 \beta_1 \beta_{12} A}{(\beta_{12} + \beta_{11} N)^2}, \quad \tilde{J}_{22} = \frac{\theta_1 \beta_1 N}{\beta_{12} + \beta_{11} N} - \alpha_1 - 2\beta_{10} A, \\ \tilde{J}_{32} &= \pi_1 (\alpha_1 + 2\beta_{10} A), \quad \tilde{J}_{33} = -\left(\alpha_2 + \frac{k_1 k_{12} B}{(k_{12} + k_{11} D)^2} \right), \quad \tilde{J}_{34} = -\frac{k_1 D}{k_{12} + k_{11} D}, \\ \tilde{J}_{43} &= \frac{\lambda_1 k_1 k_{12} B}{(k_{12} + k_{11} D)^2}, \quad \tilde{J}_{44} = \frac{\lambda_1 k_1 D}{k_{12} + k_{11} D} - (\mu_0 - \mu).\end{aligned}$$

293 1. The Jacobian \tilde{J} evaluated at the equilibrium \tilde{E}_0 leads to the eigenvalues $-\alpha_0$, $-\alpha_1$, $-\alpha_2$ and
294 $-(\mu_0 - \mu)$. Since all the eigenvalues are negative, the equilibrium \tilde{E}_0 is stable.

295 2. The Jacobian \tilde{J} evaluated at \tilde{E}^* leads to the matrix $\tilde{J}_{\tilde{E}^*} = [\tilde{a}_{ij}]$, $i, j = 1, 2, 3, 4$. Some entries of
296 matrix $\tilde{J}_{\tilde{E}^*}$ simplify as follows: $(\tilde{J}_{\tilde{E}^*})_{22} = \tilde{a}_{22} = -\beta_{10}\tilde{A}^*$, $(\tilde{J}_{\tilde{E}^*})_{44} = \tilde{a}_{44} = 0$.

The associated characteristic equation is given by $\lambda^4 + \tilde{A}_1\lambda^3 + \tilde{A}_2\lambda^2 + \tilde{A}_3\lambda + \tilde{A}_4 = 0$, where

$$\begin{aligned}\tilde{A}_1 &= -(\tilde{a}_{11} + \tilde{a}_{22} + \tilde{a}_{33}), \quad \tilde{A}_2 = \tilde{a}_{11}(\tilde{a}_{22} + \tilde{a}_{33}) - \tilde{a}_{22}\tilde{a}_{33} - \tilde{a}_{34}\tilde{a}_{43} - \tilde{a}_{12}\tilde{a}_{21}, \\ \tilde{A}_3 &= \tilde{a}_{11}(\tilde{a}_{22}\tilde{a}_{33} + \tilde{a}_{34}\tilde{a}_{43}) + \tilde{a}_{22}\tilde{a}_{34}\tilde{a}_{43} + \tilde{a}_{21}(\tilde{a}_{12}\tilde{a}_{33} - \tilde{a}_{13}\tilde{a}_{32}), \\ \tilde{A}_4 &= \tilde{a}_{21}(\tilde{a}_{12}\tilde{a}_{34}\tilde{a}_{43} - \tilde{a}_{14}\tilde{a}_{34}\tilde{a}_{43}) - \tilde{a}_{11}\tilde{a}_{22}\tilde{a}_{34}\tilde{a}_{43}.\end{aligned}$$

Clearly, \tilde{A}_1 is positive. Employing Routh-Hurwitz criterion, we have the following theorem.

Theorem 5.1. 1. The equilibrium \tilde{E}_0 is always stable.

2. The equilibrium \tilde{E}^* , if feasible, is locally asymptotically stable provided the following conditions are satisfied:

$$\tilde{A}_4 > 0, \quad \tilde{A}_1\tilde{A}_2 - \tilde{A}_3 > 0, \quad \tilde{A}_3(\tilde{A}_1\tilde{A}_2 - \tilde{A}_3) - \tilde{A}_1^2\tilde{A}_4 > 0. \quad (5.5)$$

6. Mathematical analysis of full model (2.1)

6.1. Equilibrium analysis

System (2.1) has the following three equilibria:

1. The algae-detritus-bacteria-free (or nutrients-only) equilibrium, $E_0 = (q\alpha_0^{-1}, 0, 0, 0)$, which is always feasible.

2. The bacteria-free equilibrium, $E_1 = (N_1, A_1, D_1, 0)$, with

$$N_1 = \frac{\beta_{12}(\alpha_1 + \beta_{10}A_1)}{(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}A_1}, \quad D_1 = \frac{\pi_1(\alpha_1A_1 + \beta_{10}A_1^2)}{\alpha_2}$$

and A_1 is positive root of the equation

$$F(A) = \left[q - \frac{(\alpha_1 + \beta_{10}A)A}{\theta_1} \right] [(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}A] - \beta_{12}\alpha_0(\alpha_1 + \beta_{10}A) = 0. \quad (6.1)$$

Note that in equation (6.1), $F(0) > 0$ if

$$(\theta_1\beta_1 - \beta_{11}\alpha_1)q - \beta_{12}\alpha_1\alpha_0 > 0, \quad (6.2)$$

while setting

$$\bar{A} = \frac{\theta_1\beta_1 - \beta_{11}\alpha_1}{\beta_{11}\beta_{10}}$$

we find $F(\bar{A}) < 0$ and $F'(A) < 0$ for $A \in (0, \bar{A})$. This implies that there exists a unique positive root

$A = A_1$ of equation (6.1) in the interval $(0, \bar{A})$. Hence feasibility of E_1 reduces to asking condition (6.2).

3. The interior equilibrium, $E^* = (N^*, A^*, D^*, B^*)$, with

$$\begin{aligned}N^* &= \frac{\beta_{12}(\alpha_1 + \beta_{10}A^*)}{(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}A^*}, \quad D^* = \frac{k_{12}(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)}, \\ B^* &= \frac{1}{\mu_0 - \mu} \left[\pi_1(\alpha_1 A^* + \beta_{10} A^{*2}) - \frac{k_{12}\alpha_2(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)} \right]\end{aligned}$$

and A^* is positive root of the equation

$$\begin{aligned}G(A) &= \left[q_1 + \left(\pi\pi_1 - \frac{1}{\theta_1} \right) \alpha_1 A + \left(\pi\pi_1 - \frac{1}{\theta_1} \right) \beta_{10} A^2 \right] [(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}A] \\ &\quad - \beta_{12}\alpha_0(\alpha_1 + \beta_{10}A) = 0,\end{aligned} \quad (6.3)$$

³¹³ where $q_1 = q - \frac{k_{12}\alpha_2(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)}$.

³¹⁴ Positivity of N^* and B^* imply respectively the feasibility conditions

$$(\theta_1\beta_1 - \beta_{11}\alpha_1)q_1 - \beta_{12}\alpha_1\alpha_0 > 0, \quad (6.4)$$

$$\pi_1(\alpha_1 A^* + \beta_{10} A^{*2}) - \frac{k_{12}\alpha_2(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)} > 0. \quad (6.5)$$

³¹⁵ In addition, requiring

$$q[\lambda_1 k_1 - k_{11}(\mu_0 - \mu)] - k_{12}\pi\alpha_2(\mu_0 - \mu) > 0, \quad (6.6)$$

ensures that $D^* > 0$ and together with (6.4) implies that $G(0) > 0$. Further, letting

$$\bar{A} = \frac{\theta_1\beta_1 - \beta_{11}\alpha_1}{\beta_{11}\beta_{10}}$$

³¹⁶ we find $G(\bar{A}) < 0$ and $G'(A) < 0$ for $A \in (0, \bar{A})$.

³¹⁷ Thus there exists a unique positive root $A = A^*$ of equation (6.3) in the interval $(0, \bar{A})$.

³¹⁸ 6.2. Local stability of equilibria

³¹⁹ In this section, the local stability analysis of equilibria of the model (2.1) is performed. The Jacobian
³²⁰ of (2.1) is $J = [J_{ij}]$, $i, j = 1, 2, 3, 4$, with nonvanishing explicit entries given by

$$\begin{aligned} J_{11} &= -\left(\alpha_0 + \frac{\beta_1\beta_{12}A}{(\beta_{12} + \beta_{11}N)^2}\right), \quad J_{12} = -\frac{\beta_1N}{\beta_{12} + \beta_{11}N}, \quad J_{13} = \frac{\pi k_1 k_{12}B}{(k_{12} + k_{11}D)^2}, \\ J_{14} &= \frac{\pi k_1 D}{k_{12} + k_{11}D}, \quad J_{21} = \frac{\theta_1\beta_1\beta_{12}A}{(\beta_{12} + \beta_{11}N)^2}, \quad J_{22} = \frac{\theta_1\beta_1 N}{\beta_{12} + \beta_{11}N} - \alpha_1 - 2\beta_{10}A, \\ J_{32} &= \pi_1(\alpha_1 + 2\beta_{10}A), \quad J_{33} = -\left(\alpha_2 + \frac{k_1 k_{12}B}{(k_{12} + k_{11}D)^2}\right), \quad J_{34} = -\frac{k_1 D}{k_{12} + k_{11}D}, \\ J_{43} &= \frac{\lambda_1 k_1 k_{12}B}{(k_{12} + k_{11}D)^2}, \quad J_{44} = \frac{\lambda_1 k_1 D}{k_{12} + k_{11}D} - (\mu_0 - \mu). \end{aligned}$$

³²¹ **Theorem 6.1.** 1. The equilibrium E_0 is unstable whenever the equilibrium E_1 is feasible.

³²² 2. The equilibrium E_1 is unstable whenever the equilibrium E^* is feasible.

³²³ 3. The equilibrium E^* , if feasible, is locally asymptotically stable provided the following conditions are
³²⁴ satisfied, where the relevant quantities are defined in the proof:

$$A_4 > 0, \quad A_1 A_2 - A_3 > 0, \quad A_3(A_1 A_2 - A_3) - A_1^2 A_4 > 0. \quad (6.7)$$

Proof. 1. The Jacobian J evaluated at the equilibrium E_0 leads to the following eigenvalues:

$$-\alpha_0, \quad \frac{\theta_1\beta_1 q}{\beta_{12}\alpha_0 + \beta_{11}q} - \alpha_1, \quad -\alpha_2, \quad -(\mu_0 - \mu).$$

³²⁵ The second one is negative (or positive) provided condition (6.2) does not hold (or hold). Thus, the
³²⁶ equilibrium E_0 is stable (or unstable) whenever the equilibrium E_1 is not feasible (or feasible).

³²⁷ 2. The Jacobian J evaluated at the equilibrium E_1 immediately gives two eigenvalues

$$-\alpha_2, \quad \frac{\lambda_1 k_1 (\pi_1 \alpha_1 A_1 + \pi_2 \beta_{10} A_1^2)}{k_{12}\alpha_2 + k_{11}\pi_1(\alpha_1 A_1 + \beta_{10} A_1^2)} - (\mu_0 - \mu)$$

³²⁸ while the remaining two are roots of the following equation with all positive coefficients:

$$\lambda^2 + \left(\beta_{10}A_1 + \alpha_0 + \frac{\beta_1\beta_{12}A_1}{(\beta_{12} + \beta_{11}N_1)^2} \right) \lambda + \beta_{10}A_1 + \frac{\theta_1\beta_1\beta_{12}A_1}{(\beta_{12} + \beta_{11}N_1)^2} \beta_1N_1\beta_{12} + \beta_{11}N_1 = 0. \quad (6.8)$$

³²⁹ Clearly, roots of equation (6.8) are either negative or with negative real parts. Thus, the matrix J_{E_1} has
³³⁰ three eigenvalues which are either negative or with negative real parts and one eigenvalue is negative (or
³³¹ positive) provided condition (6.5) is not satisfied (or satisfied). Therefore, the equilibrium E_1 is stable
³³² (or unstable) whenever the equilibrium E^* is not feasible (or feasible).

³³³ 3. The Jacobian J evaluated at E^* leads to the matrix $J_{E^*} = [a_{ij}]$, $i, j = 1, 2, 3, 4$. Some entries of
³³⁴ matrix J_{E^*} simplify as follows: $(J_{E^*})_{22} = a_{22} = -\beta_{10}A^*$, $(J_{E^*})_{44} = a_{44} = 0$.

³³⁵ The associated characteristic equation is given by $\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0$, where

$$\begin{aligned} A_1 &= -(a_{11} + a_{22} + a_{33}), \quad A_2 = a_{11}(a_{22} + a_{33}) - a_{22}a_{33} - a_{34}a_{43} - a_{12}a_{21}, \\ A_3 &= a_{11}(a_{22}a_{33} + a_{34}a_{43}) + a_{22}a_{34}a_{43} + a_{21}(a_{12}a_{33} - a_{13}a_{32}), \\ A_4 &= a_{21}(a_{12}a_{34}a_{43} - a_{14}a_{34}a_{43}) - a_{11}a_{22}a_{34}a_{43}. \end{aligned}$$

³³⁶ Clearly, A_1 is positive. Using the Routh-Hurwitz criterion, roots of the characteristic equation are either
³³⁷ negative or have negative real parts iff conditions (6.7) are satisfied. ■

³³⁸ 7. Transcritical bifurcation

³³⁹ Considering E_0 and E_1 taking β_1 as a bifurcation parameter, then at $\beta_1 = \beta_1^*$, an exchange of
³⁴⁰ feasibility and stability properties between these two equilibria occurs. This is a clear indication of the
³⁴¹ presence of a transcritical bifurcation at the critical threshold β_1^* . We now rigorously prove that indeed
³⁴² this is the case.

³⁴³ Observe that the eigenvalues of the Jacobian matrix

$$J(E_0, \beta_1^*) = \begin{pmatrix} -\alpha_0 & -\frac{\beta_1 q}{\beta_{12}\alpha_0 + \beta_{11}q} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & \pi_1\alpha_1 & -\alpha_2 & 0 \\ 0 & 0 & 0 & -(\mu_0 - \mu) \end{pmatrix},$$

are given by

$$\eta_1 = -\alpha_0, \quad \eta_2 = 0, \quad \eta_3 = -\alpha_2 \text{ and } \eta_4 = -(\mu_0 - \mu).$$

³⁴⁴ Thus, $\eta_2 = 0$ is a simple zero eigenvalue and the other ones are real and negative. Hence, at $\beta_1 = \beta_1^*$
³⁴⁵ the equilibrium E_0 is non-hyperbolic and the assumption (A1) of Theorem 4.1 in (56) is verified.

³⁴⁶ Now, denote by $\mathbf{w} = (w_1, w_2, w_3, w_4)^T$ a right eigenvector associated with the zero eigenvalue $\eta_2 = 0$,
³⁴⁷ explicitly given by

$$w_1 = -\frac{\beta_1 q}{\alpha_0(\beta_{12}\alpha_0 + \beta_{11}q)}, \quad w_2 = 1, \quad w_3 = \frac{\pi_1\alpha_1}{\alpha_2} \text{ and } w_4 = 0.$$

³⁴⁸ Furthermore, the left eigenvector $\mathbf{v} = (v_1, v_2, v_3, v_4)$ is $\mathbf{v} = (0, 1, 0, 0)$, so that $\mathbf{w} \cdot \mathbf{v} = 1$.

Now, the coefficients a and b defined in Theorem 4.1 of (56)

$$a = \sum_{k,i,j=1}^4 v_k w_i w_j \frac{\partial^2 f_k}{\partial x_i \partial x_j}(E_0, \beta_1^*), \quad b = \sum_{k,i=1}^4 v_k w_i \frac{\partial^2 f_k}{\partial x_i \partial \beta_1}(E_0, \beta_1^*),$$

³⁴⁹ may be explicitly computed. Taking into account system (2.1), it follows that

$$a = \frac{\beta_{12}\alpha_0\alpha_1}{\theta_1 q^2(\beta_{12}\alpha_0 + \beta_{11}q)} - 2\beta_{10}, \quad b = \frac{\theta_1 q}{\beta_{12}\alpha_0 + \beta_{11}q} > 0. \quad (7.1)$$

Now $a > 0$ if and only if

$$\frac{\beta_{12}\alpha_0\alpha_1}{\theta_1 q^2(\beta_{12}\alpha_0 + \beta_{11}q)} > 2\beta_{10}.$$

³⁵⁰ In view of previous considerations, we have the following theorem.

³⁵¹ **Theorem 7.1.** Consider system (2.1) and let a and b as given by (7.1), where $b > 0$. The local dynamics
³⁵² of system (2.1) around the equilibrium E_0 are totally determined by the sign of a .

³⁵³ (i) If $a < 0$, when $\beta_1 < \beta_1^*$ with $\beta_1 \approx \beta_1^*$, E_0 is locally asymptotically stable, and there exists a negative
³⁵⁴ unstable equilibrium E_1 ; when $\beta_1 > \beta_1^*$ with $\beta_1 \approx \beta_1^*$, E_0 is unstable, and there exists a positive locally
³⁵⁵ asymptotically stable equilibrium E_1 .

³⁵⁶ (ii) If $a > 0$, when $\beta_1 < \beta_1^*$ with $\beta_1 \approx \beta_1^*$, E_0 is locally asymptotically stable, and there exists a positive unstable equilibrium E_1 ; when $\beta_1 > \beta_1^*$ with $\beta_1 \approx \beta_1^*$, E_0 is unstable, and there exists a negative locally
³⁵⁷ asymptotically stable equilibrium E_1 .

³⁵⁸ *Proof.* It follows from (56) Theorem 4.1 pp. 373, and Remark 1 pp. 375. ■

³⁶⁰ **Corollary 7.1.** Consider the model (2.1) and let a and b as given by (7.1) where $b > 0$. At $\beta_1 = \beta_1^*$,
³⁶¹ the system (2.1) undergoes a transcritical bifurcation. If $a < 0$ the bifurcation at $\beta_1 = \beta_1^*$ is supercritical
³⁶² (or forward). On the other hand, if $a > 0$, the bifurcation at $\beta_1 = \beta_1^*$ is subcritical (or backward)
³⁶³ bifurcation.

³⁶⁴ *Proof.* It is a straightforward application of Theorem 7.1. ■

³⁶⁵ **Remark 1.** Taking μ_0 as a bifurcation parameter, we can prove the existence of a transcritical
³⁶⁶ bifurcation between equilibria E_1 and E^* of the system (2.1) using the same approach as above.

³⁶⁷ In Table 2, we listed the equilibria of the systems (2.1), (3.1), (4.1) and (5.1), and the conditions for
³⁶⁸ their feasibility and stability.

Table 2: Equilibria and conditions for their feasibility and stability

Models	Equilibria	Feasibility conditions	Conditions for LAS
(3.1)	$E_0 = (q\alpha_0^{-1}, 0, 0)$ $E^* = (N^*, A^*)$	Always feasible $q(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{12}\alpha_1\alpha_0 > 0$	$q(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{12}\alpha_1\alpha_0 < 0$ Always stable
(4.1)	$\tilde{E}_0 = (q\alpha_0^{-1}, 0, 0)$ $\tilde{E}^* = (\tilde{N}^*, \tilde{A}^*, \tilde{D}^*)$	Always feasible $q(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{12}\alpha_1\alpha_0 > 0$	$q(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{12}\alpha_1\alpha_0 < 0$ Always stable
(5.1)	$\tilde{E}_0 = (0, 0, 0, 0)$ $\tilde{E}^* = (\tilde{N}^*, \tilde{A}^*, \tilde{D}^*, \tilde{B}^*)$	Always feasible $\pi_1\tilde{A}^*(\alpha_1 + \beta_{10}\tilde{A}^*) - \frac{k_{12}\alpha_2(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)} > 0$ $(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{11}\beta_{10}A^* > 0$ $\theta_1\beta_1 - 2\beta_{11}\alpha_1 > 0$	Always stable $\tilde{A}_4 > 0, \tilde{A}_1\tilde{A}_2 - \tilde{A}_3 > 0$ $\tilde{A}_3(\tilde{A}_1\tilde{A}_2 - \tilde{A}_3) - \tilde{A}_1^2\tilde{A}_4 > 0$
(2.1)	$E_0 = (q\alpha^{-1}, 0, 0, 0)$ $E_1 = (N_1, A_1, D_1, 0)$ $E^* = (N^*, A^*, D^*, B^*)$	Always feasible $q(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{12}\alpha_1\alpha_0 > 0$ $\pi_1(\alpha_1 A^* + \beta_{10}A^{*2}) - \frac{k_{12}\alpha_2(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)} > 0$ $(\theta_1\beta_1 - \beta_{11}\alpha_1)q_1 - \beta_{12}\alpha_1\alpha_0 > 0$ $q[\lambda_1 k_1 - k_{11}(\mu_0 - \mu)] - k_{12}\pi\alpha_2(\mu_0 - \mu) > 0$	$q(\theta_1\beta_1 - \beta_{11}\alpha_1) - \beta_{12}\alpha_1\alpha_0 < 0$ $\pi_1(\alpha_1 A_1 + \beta_{10}A_1^2) < \frac{k_{12}\alpha_2(\mu_0 - \mu)}{\lambda_1 k_1 - k_{11}(\mu_0 - \mu)}$ $A_4 > 0, A_1 A_2 - A_3 > 0,$ $A_3(A_1 A_2 - A_3) - A_1^2 A_4 > 0$

³⁶⁹

370 **Remark 2.** Since the inflow rate of nutrients in the aquatic system plays an important role in
 371 determining the dynamics of the system, Table 2 allows to assess how system dynamics is affected by
 372 changes in the input rate of nutrients. Note that the equilibrium \tilde{E}_0 is always feasible and stable while
 373 the equilibrium \tilde{E}^* is feasible if conditions (5.3) and (5.4) are satisfied, and is stable provided conditions
 374 in (5.5) hold. That is, if conditions (5.3), (5.4) and (5.5) are satisfied, the equilibria \tilde{E}_0 and \tilde{E}^* are
 375 feasible and stable simultaneously. This ensures bistability. The bistability behavior of system (5.1) is
 376 shown in Fig. 2. Thus, by completely stopping the input rate of nutrients in the lake, we may achieve
 377 the algae-free system or algae-persistent system depending on the current value of the algal density.
 378 Recall that when $q \neq 0$, the algae-free equilibrium is stable only when the algae-persistent equilibrium is
 379 not feasible. Overall, in order to preserve the aquatic system, the inflow rate of the nutrients coming
 380 from various sources must be controlled. Moreover, for the systems without bacteria, (i.e. systems (3.1)
 381 and (4.1)), the coexistence equilibrium is always locally asymptotically stable and globally asymptotically
 382 stable under certain conditions.

383 8. Effect of time delay

384 In this section, we modify our model (2.1) by incorporating a discrete time delay which represents
 385 the time lag involved in the conversion of detritus into nutrients due to bacterial decomposition and the
 386 corresponding growth in the bacterial population. For instance, we consider the same lag (τ) in these
 387 two processes. With this modification, we have the following system of delay differential equations:

$$\begin{aligned}
 \frac{dN(t)}{dt} &= q - \alpha_0 N(t) - \frac{\beta_1 N(t)A(t)}{\beta_{12} + \beta_{11}N(t)} + \frac{\pi k_1 D(t - \tau)B(t)}{k_{12} + k_{11}D(t - \tau)}, \\
 \frac{dA(t)}{dt} &= \frac{\theta_1 \beta_1 N(t)A(t)}{\beta_{12} + \beta_{11}N(t)} - \alpha_1 A(t) - \beta_{10} A^2(t), \\
 \frac{dD(t)}{dt} &= \pi_1 (\alpha_1 A(t) + \beta_{10} A^2(t)) - \alpha_2 D(t) - \frac{k_1 D(t)B(t)}{k_{12} + k_{11}D(t)}, \\
 \frac{dB(t)}{dt} &= \mu B(t) - \mu_0 B(t) + \frac{\lambda_1 k_1 D(t - \tau)B(t)}{k_{12} + k_{11}D(t - \tau)}.
 \end{aligned} \tag{8.1}$$

388 The initial conditions for the system (8.1) take the form

$$N(\phi) = \psi_1(\phi), \quad P(\phi) = \psi_2(\phi), \quad A(\phi) = \psi_3(\phi), \quad D(\phi) = \psi_4(\phi), \quad -\tau \leq \phi \leq 0,$$

389 where $\psi = (\psi_1, \psi_2, \psi_3, \psi_4)^T \in \mathcal{C}_+$ such that $\psi_i(\phi) \geq 0$, $i = 1, 2, 3, 4 \forall \phi \in [-\tau, 0]$ and \mathcal{C}_+ denotes the
 390 Banach space $\mathcal{C}_+([-\tau, 0], \mathbf{R}_{+0}^4)$ of continuous functions mapping the interval $[-\tau, 0]$ into \mathbf{R}_{+0}^4 . The norm
 391 of an element ψ in \mathcal{C}_+ is denoted by $\|\psi\| = \sup_{-\tau \leq \phi \leq 0} \{|\psi_1(\phi)|, |\psi_2(\phi)|, |\psi_3(\phi)|, |\psi_4(\phi)|\}$. For biological
 392 feasibility, we further assume that $\psi_i(0) \geq 0$ for $i = 1, 2, 3, 4$.

393 In the following, we carry out the local stability analysis for the interior equilibrium E^* and show
 394 that the system (8.1) undergoes a Hopf-bifurcation around this equilibrium.

395 9. Hopf-bifurcation analysis

396 To study the stability behavior of the equilibrium E^* in the presence of time delay, we linearize the
 397 system (8.1) about the equilibrium E^* and get

$$\frac{dY}{dt} = LY(t) + MY(t - \tau), \tag{9.1}$$

³⁹⁸ where

$$L = \begin{pmatrix} V_{11} & V_{12} & 0 & V_{14} \\ V_{21} & V_{22} & 0 & 0 \\ 0 & V_{32} & V_{33} & V_{34} \\ 0 & 0 & 0 & 0 \end{pmatrix}, M = \begin{pmatrix} 0 & 0 & M_{13} & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & M_{43} & 0 \end{pmatrix} \text{ and } Y(\cdot) = \begin{pmatrix} n(\cdot) \\ a(\cdot) \\ d(\cdot) \\ b(\cdot) \end{pmatrix},$$

³⁹⁹ with

$$\begin{aligned} V_{11} &= -\left(\alpha_0 + \frac{\beta_1 \beta_{12} A^*}{(\beta_{12} + \beta_{11} N^*)^2}\right), \quad V_{12} = -\frac{\beta_1 N^*}{\beta_{12} + \beta_{11} N^*}, \quad V_{14} = \frac{\pi k_1 D^*}{k_{12} + k_{11} D^*}, \\ V_{21} &= \frac{\theta_1 \beta_1 \beta_{12} A^*}{(\beta_{12} + \beta_{11} N^*)^2}, \quad V_{22} = -\beta_{10} A^*, \quad V_{32} = \pi_1 (\alpha_1 + 2\beta_{10} A^*), \\ V_{33} &= -\left(\alpha_2 + \frac{k_1 k_{12} B^*}{(k_{12} + k_{11} D^*)^2}\right), \quad V_{34} = -\frac{k_1 D^*}{k_{12} + k_{11} D^*}, \quad M_{13} = \frac{\pi k_1 k_{12} B^*}{(k_{12} + k_{11} D^*)^2}, \quad M_{43} = \frac{\lambda_1 k_1 k_{12} B^*}{(k_{12} + k_{11} D^*)^2}. \end{aligned}$$

⁴⁰⁰ Here, n , a , d and b are small perturbations around the equilibrium E^* . The characteristic equation for ⁴⁰¹ the linearized system (9.1) is given by

$$\lambda^4 + A_3 \lambda^3 + A_2 \lambda^2 + A_1 \lambda + (B_2 \lambda^2 + B_1 \lambda + B_0) e^{-\lambda \tau} = 0, \quad (9.2)$$

⁴⁰² where

$$\begin{aligned} A_3 &= -(V_{11} + V_{22} + V_{33}), \quad A_2 = V_{11} V_{22} + V_{22} V_{33} + V_{11} V_{33} - V_{12} V_{21}, \\ A_1 &= V_{12} V_{21} V_{33} - V_{11} V_{22} V_{33}, \quad B_2 = -V_{34} M_{43}, \\ B_1 &= V_{22} V_{34} M_{43} + V_{11} V_{34} M_{43} - V_{21} V_{33} M_{13}, \quad B_0 = V_{12} V_{21} V_{34} M_{43} + V_{14} V_{21} V_{32} M_{43} - V_{11} V_{22} V_{34} M_{43}. \end{aligned}$$

⁴⁰³ Equation (9.2) is transcendental in λ , so that it has infinitely many complex roots. To understand the ⁴⁰⁴ local stability behavior of the equilibrium E^* , we need to assess the signs of real parts of the roots of ⁴⁰⁵ equation (9.2). This is a complicated task in the presence of the time delay. Therefore, equation (9.2) ⁴⁰⁶ is first analyzed in the absence of time delay and then conditions for local asymptotic stability behavior ⁴⁰⁷ of the equilibrium E^* are deduced when time delay is present.

⁴⁰⁸ For $\tau = 0$, Theorem 6.1 provides the conditions under which all the roots of equation (9.2) are either ⁴⁰⁹ negative or with negative real parts. For $\tau > 0$ by Rouche's Theorem and continuity in τ , the sign of ⁴¹⁰ roots of equation (9.2) will change across the imaginary axis, i.e., if equation (9.2) has purely imaginary ⁴¹¹ roots. Hence, putting $\lambda = i\omega$ ($\omega > 0$) in equation (9.2) and separating real and imaginary parts, we get

$$w^4 - A_2 \omega^2 = -(B_0 - B_2 \omega^2) \cos(\omega \tau) - B_1 \omega \sin(\omega \tau), \quad (9.3)$$

$$A_3 \omega^3 - A_1 \omega = -(B_0 - B_2 \omega^2) \sin(\omega \tau) + B_1 \omega \cos(\omega \tau). \quad (9.4)$$

⁴¹² Squaring and adding equations (9.3) and (9.4), we obtain

$$(w^4 - A_2 \omega^2)^2 + (A_3 \omega^3 - A_1 \omega)^2 = (B_0 - B_2 \omega^2)^2 + B_1^2 \omega^2. \quad (9.5)$$

⁴¹³ Simplifying equation (9.5) and substituting $\omega^2 = \psi$, we get the following equation in ψ :

$$\Psi(\psi) = \psi^4 + C_3 \psi^3 + C_2 \psi^2 + C_1 \psi + C_0 = 0, \quad (9.6)$$

⁴¹⁴ where

$$C_3 = -2A_2 + A_3^2, \quad C_2 = A_2^2 - 2A_1 A_3 - B_2^2, \quad C_1 = A_1^2 + 2B_2 B_0 - B_1^2, \quad C_0 = -B_0^2.$$

⁴¹⁵ The existence of positive roots of equation (9.6) is addressed in the following lemma, whose proof follows
⁴¹⁶ by Descartes' rule, (57).

⁴¹⁷ **Lemma 2.** The polynomial equation (9.6) has

⁴¹⁸ (1) at least one positive root if

- (a) $C_3 > 0, C_2 < 0, C_1 > 0, C_0 < 0.$
- (b) $C_3 < 0, C_2 < 0, C_1 > 0, C_0 < 0.$
- (c) $C_3 < 0, C_2 > 0, C_1 > 0, C_0 < 0.$
- (d) $C_3 < 0, C_2 > 0, C_1 < 0, C_0 < 0.$

⁴¹⁹ (2) exactly one positive root if

- (a) $C_3 < 0, C_2 < 0, C_1 < 0, C_0 < 0.$
- (b) $C_3 > 0, C_2 < 0, C_1 < 0, C_0 < 0.$
- (c) $C_3 > 0, C_2 > 0, C_1 < 0, C_0 < 0.$
- (d) $C_3 > 0, C_2 > 0, C_1 > 0, C_0 < 0.$

⁴²⁰ For other choices of the coefficients of equation (9.6), the positive root cannot be guaranteed.

⁴²¹ Now, we can characterize the system behavior:

Theorem 9.1. Assume that the equilibrium E^* is locally asymptotically stable for $\tau = 0$ and that one of the conditions (1) or (2) given in Lemma 2 holds. Let $\psi_0 = \omega_0^2$ be a positive root of (9.6). Then, there exists $\tau = \tau_0$ such that the equilibrium E^* is asymptotically stable when $0 \leq \tau < \tau_0$ and unstable for $\tau > \tau_0$, where

$$\tau_k = \frac{1}{\omega_0} \tan^{-1} \left[\frac{B_1 \omega_0 (\omega_0^4 - A_2 \omega_0^2) + (B_0 - B_2 \omega_0^2)(A_3 \omega_0^3 - A_1 \omega_0)}{(B_0 - B_2 \omega_0^2)(\omega_0^4 - A_2 \omega_0^2) - B_1 \omega_0 (A_3 \omega_0^3 - A_1 \omega_0)} \right] + \frac{k\pi}{\omega_0},$$

⁴²² for $k = 0, 1, 2, 3, \dots$. Furthermore, the system will undergo a Hopf-bifurcation at E^* when $\tau = \tau_0$ provided
⁴²³ $\Psi'(\omega_0^2) > 0$.

⁴²⁴ *Proof.* Since $\psi = \omega_0^2$ is a solution of the equation (9.6), the characteristic equation (9.2) has pair of
⁴²⁵ purely imaginary roots $\pm i\omega_0^2$. It follows from equations (9.3) and (9.4) that τ_k is a function of ω_0^2 for
⁴²⁶ $k = 0, 1, 2, 3, \dots$. Therefore, the system will be locally asymptotically stable at E^* for $\tau = 0$, if the
⁴²⁷ conditions (6.7) hold. In that case by *Butler's lemma*, the equilibrium E^* will remain stable for $\tau < \tau_0$,
⁴²⁸ such that $\tau_0 = \min_{k \geq 0} \tau_k$ and unstable for $\tau \geq \tau_0$, provided that the transversality condition holds. The
⁴²⁹ transversality condition is given as

$$sgn \left[\frac{d(Re(\lambda))}{d\tau} \right]_{\tau=\tau_0}^{-1} = \left[\frac{\Psi'(\omega_0^2)}{B_1^2 \omega_0^2 + (B_0 - B_2 \omega_0^2)^2} \right]. \quad (9.7)$$

⁴³⁰ Note that $\Psi'(\omega_0^2) \neq 0$ if Lemma 2 holds. Hence, the transversality condition is satisfied and a Hopf
⁴³¹ bifurcation occurs at $\tau = \tau_0$ i.e., a family of periodic solutions emanate from the equilibrium E^* as the
⁴³² delay parameter, τ , passes through its critical value, τ_0 , (31). ■

⁴³³

⁴³⁴ 10. Numerical simulations

⁴³⁵ Here, we report the simulations performed to investigate the system behavior using the Matlab
⁴³⁶ variable step Runge-Kutta solver ode45. In spite of importance of clean water on the Earth, quantitative

437 data on water pollution are scanty and, therefore, we are unable to check the validity of the model and
 438 its outcome with the field data. However, to visualize different analytical results and to have some
 439 insights from it, we have numerically simulated the system (2.1). The (hypothetical) parameter values
 440 are chosen within ranges defined in the existing literature (6; 9; 40).

441 First of all, we choose some important parameters of the model (2.1) and see their effects on the
 442 equilibrium values of nutrients, algae, detritus and bacteria in the lake. For our purpose, we select q , β_1 ,
 443 β_{10} , k_1 , μ and μ_0 and analyze the behavior of model's variables by varying two parameters at a time viz.
 444 (q, k_1) , (μ_0, β_{10}) and (μ, β_1) integrating up to time $t = 100$ days, when the system is stabilized. In each
 445 figure, the surface represents the value of the population at a (dynamic) equilibrium, i.e. steady state or
 446 persistent oscillation. When two surfaces are shown, they indicate the maximum and minimum values
 447 that these variables attain in the limit cycle. When they collide, it means that a stable equilibrium is
 448 attained, while when they differ, the solution oscillates.

449 Fig. 3 shows the system behavior as functions of q and k_1 . On increasing the input rate of nutrients
 450 in the lake, the equilibrium values of all the populations increase. In this case, sustained oscillations in
 451 time are found (34; 58). For low values of k_1 , the bacteria vanish but this population increases with an
 452 increase in k_1 . On the other hand, the detritus is high for low values of k_1 , but as k_1 increases, bacteria
 453 decompose it at a high rate leading to a detritus-free environment.

454 In Fig. 4, we vary μ_0 and β_{10} . For low values of the bacteria mortality rate μ_0 , the bacterial
 455 population is at high level but disappears on increasing the values of μ_0 . Consequently the density of
 456 detritus increases at a high rate. On increasing the algae intraspecific competition rate β_{10} , the algal
 457 population decreases to a very low level while the nutrients increase as there are less algae that utilize
 458 them. Here too persistent oscillations are observed in all the panels.

459 Fig. 5 considers the parameters μ and β_1 . Increase in β_1 causes a significant decrease in the
 460 concentration of nutrients but an opposite behavior for algae and detritus. For low values of β_1 , these
 461 populations vanish altogether. Bacteria thrive only for larger values of μ and increase more with an
 462 increase in β_1 . Again, we can observe persistent oscillations for all variables of the model.

463 We show the transcritical bifurcation between the equilibria E_0 and E_1 also numerically, varying the
 464 uptake rate of nutrients by algae, β_1 , in Fig. 6(a). For low values of β_1 (i.e., no nutrients consumed
 465 by algae), the nutrients remains at a fixed level but their concentration suddenly drops as β_1 crosses its
 466 critical value. Also, there is a transcritical bifurcation between the equilibria E_1 and E^* , shown varying
 467 the natural death rate of bacteria, μ_0 , in Fig. 6(b). Actually, the coexistence equilibrium E^* can stably
 468 achieved for the parameters values as given in Table 1, not shown.

469 To see the effect of the delay involved in the conversion of detritus into nutrients and the growth
 470 of bacterial populations, we set the system at a stable focus in the absence of time delay ($\tau = 0$). We
 471 gradually increase the value of time delay τ and observe the solution trajectories that still produce a
 472 stable focus at $\tau = 10$ days, not shown. By increasing the time delay to $\tau = 15.2$ days, the system
 473 (8.1) exhibits limit cycles, Fig. 7. Next, we increase the values of time delay to $\tau = 20$ days and found
 474 that the system exhibits period doubling solutions, Fig. 8. The system shows chaotic behavior for
 475 further increase in time delay ($\tau = 21.5$ days), Fig. 9. For better visualization, we draw the bifurcation
 476 diagram of the system (8.1) by varying the bifurcation parameter $\tau \in [10, 22]$, Fig. 10. It is clear from
 477 the figure that the chaotic regime is reached via a stable focus for $\tau < 14.5$, limit cycle behaviour for
 478 $14.5 \leq \tau \leq 15.9$, period doubling oscillations for $15.9 \leq \tau \leq 20.2$, and higher periodic and chaotic
 479 oscillations for $\tau \geq 20.2$. However, we could not provide bifurcation diagram for $\tau > 22$, because the
 480 solutions trajectories of the system (2.1) blow up after $\tau > 22$. Recall that systems in the absence of
 481 bacteria (systems (3.1) and (4.1)) are bounded while the systems in the presence of bacteria (systems
 482 (2.1) and (5.1)) are unbounded. Further, we draw the Poincaré map of the system (8.1) in the $A - D - B$

483 space fixing $N = 0.8$, for $\tau = 21.5$ days, Fig. 11. The scattered distribution of the sampling points
 484 implies the chaotic behavior of the system. We also draw the maximum Lyapunov exponent of the
 485 system (8.1) for $\tau = 21.5$ days, Fig. 12. To draw the maximum Lyapunov exponent, we first simulate
 486 the delayed system (8.1). Then considering the times series solutions of each component, we compute the
 487 Lyapunov exponents by using the algorithm of (59; 60). In the figure, positive values of the maximum
 488 Lyapunov exponent indicates the chaotic regime of the system. Therefore, we can conclude that the
 489 system (8.1) shows chaotic behavior for $\tau = 21.5$ days.

490 10.1. Sensitivity analysis

491 We perform the global sensitivity analysis following the techniques of (61; 62) to identify the most
 492 influential parameters that have significant impact on some important output variables of the system
 493 (2.1). We calculate partial rank correlation coefficients (PRCCs) between the parameters $q, \beta_1, k_1, \pi, \theta_1,$
 494 λ_1, μ and μ_0 from system (2.1) with algae and bacteria in the lake as output. Nonlinear and monotone
 495 relationships were observed with the input parameters of the model (2.1), which is a prerequisite for
 496 computing PRCCs. Using the Latin Hypercube Sampling (LHS), we drawn 200 samples from the
 497 biologically feasible regions of the parameters of interest. The bar diagram of the PRCC values of
 498 the densities of algae and bacteria against these parameters is depicted in Fig. 13. PRCC values of
 499 these parameters with the responses suggest that the parameters $q, \beta_1, \theta_1, \mu$ and μ_0 have significant
 500 correlations with the density of algae, Fig. 13(a). The parameter θ_1 has maximum positive correlation
 501 with the density of algae. The bacteria mortality has negative correlation with the density of algae while
 502 other parameters have positive correlations. For the density of bacteria, the significant parameters are
 503 $\beta_1, \theta_1, \lambda_1, \mu$ and μ_0 , Fig. 13(b). The growth rate of bacteria due to detritus of other type than algal
 504 one, μ , has maximum positive correlation with bacteria. The death rate of bacteria, μ_0 , has negative
 505 correlation with bacteria whereas other parameters have positive correlations.

506 11. Discussion

507 Marine microbes play important roles in aquatic systems, especially marine ones. They influence
 508 the climate, mediate primary production, participate in biogeochemical cycles, and maintain ecological
 509 balance (63). The microbes that make up harmful algal blooms are being studied closely by scientists
 510 (64). Because of high diversity and complexity, the interaction between algae and bacteria has become the
 511 concern of many researchers. Scientists have explored the relationships between algae and bacteria from
 512 different perspectives, including the physical, biological, environmental and chemical processes involved
 513 (64). Microbes, which exist as free-living forms as well as securely attached to algal cells, have now
 514 been demonstrated to modulate algal growth rates and transitions between life history stages, influence
 515 toxin production, and even induce the rapid lysis of algal cells (65). However, given the complex array
 516 of interactions that have evolved between them, some ecological functions and related mechanisms have
 517 not yet been fully elucidated.

518 In this paper, we have investigated the effect of bacteria on the dynamics of algal blooms in lakes.
 519 A nonlinear mathematical model has been proposed by taking nutrients, algae, detritus and bacteria as
 520 state variables. The model exhibits three non-negative equilibria; E_0 , E_1 and E^* that are related to
 521 each other via transcritical bifurcations. Equilibria E_0 and E_1 are linked on varying the parameter β_1 ,
 522 the latter arising when the bifurcation parameter β_1 crosses from below its critical value. On the other
 523 hand, the equilibria E_1 and E^* are tied by the parameter μ_0 , the former arising when the bifurcation
 524 parameter μ_0 crosses from below its critical value. For higher values of μ_0 , bacteria vanish and hence the
 525 density of algae in the lake increases up to a limit value. The partial rank correlation coefficient (PRCC)
 526 technique is performed to assess the sensitivity of the ecosystem with respect to the model parameters.

527 The main parameters influencing the system behavior appear to be q , β_1 , k_1 , π , θ_1 , λ_1 and μ . They
528 present positive correlations with the densities of algae and bacterial population.

529 The effect of time delay on algal bloom into the lake has also been investigated. The time delay has
530 been introduced to model more realistically the formation of nutrients from detritus and the subsequent
531 growth of bacteria, that are not instantaneous processes. Previous studies show the occurrence of limit
532 cycle oscillations through a Hopf-bifurcation by varying the delay parameter (9; 40). However, to the
533 best of our knowledge, in the context of algal bloom models no study is carried out for the delayed
534 systems showing chaotic dynamics. In the present investigation, we found that as the delay parameter
535 increases, the system (8.1) exhibits a transition from stable focus to limit cycle oscillations to period
536 doubling oscillations to chaotic dynamics. The density of algae in the lake may increase drastically and
537 in that case a massive death of fishes may occur as a consequence of low levels of dissolved oxygen. To
538 avoid this unpleasant outcome, the detritus of the lake should be removed before the critical value of
539 delay parameter is reached. Longer delay in this action may cause fluctuations in the density of algae
540 for a long time and cause hypoxia in the lake. These findings are thus of critical importance for the
541 practice of lake restoration.

542 The role of space in ecological interactions has been identified as an important factor (66). Spatial
543 patterns are ubiquitous in nature and modify the stability properties of ecosystems at a range of spatial
544 scales. Spatial variability of algae is very common in aquatic ecosystems. Several attempts have been
545 made to explain such spatial variation using different types of mathematical models (67; 68). To further
546 extrapolate the results of the present study, extensions of the model presented here might be worth
547 investigating, incorporating perhaps diffusion and advection, that play a crucial role in the spatial
548 movement of algae in water bodies. A second issue concerns the parameter values used. Here they are
549 taken as hypothetical, but tuning them using real data would be a very interesting step. At present
550 however, for lack of the field results, is not possible. This investigation might be undertaken in future
551 researches.

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558 References

- 559 [1] D.M. Sigman, M.P. Hain, The biological productivity of the ocean. Nature Education Knowledge
560 3(10) (2012) 21.
- 561 [2] J. Lv, H. Wu, M. Chen, Effects of nitrogen and phosphorus on phytoplankton composition and
562 biomass in 15 subtropical, urban shallow lakes in Wuhan, China. Limnologica, 41(1) (2011) 48-56.
- 563 [3] R. Ramanan et al., Algae-bacteria interactions: evolution, ecology and emerging applications.
564 Biotechnology advances, 34(1) (2016) 14-29.
- 565 [4] The Effects: Dead Zones and Harmful Algal Blooms. <https://www.epa.gov/nutrientpollution/effects-dead-zones-and-harmful-algal-blooms>

- 566 [5] D. Anderson, HABs in a changing world: a perspective on harmful algal blooms, their impacts, and
 567 research and management in a dynamic era of climatic and environmental change, *Harmful Algae*
 568 2012 (2014) 3-17.
- 569 [6] J.B. Shukla, A.K. Misra, P. Chandra, Modeling and analysis of the algal bloom in a lake caused by
 570 discharge of nutrients, *Appl. Math. Comp.* 196(2) (2008) 782-790.
- 571 [7] A.K. Misra, Modeling the depletion of dissolved oxygen in a lake due to submerged macrophytes,
 572 *Nonlinear Anal. Model. Control* 15(2) (2010) 185-198.
- 573 [8] A.K. Misra, P.K. Tiwari, E. Venturino, Modeling the impact of awareness on the mitigation of algal
 574 bloom in a lake, *J. Biol. Phys.* 42(1) (2016) 147-165.
- 575 [9] P.K. Tiwari, A.K. Misra, E. Venturino, The role of algae in agriculture: A mathematical study, *J.
 576 Biol. Phys.* 43(2) (2017) 297-314.
- 577 [10] S. Chakraborty et al., Effects of fertilizers used in agricultural fields on algal blooms, *Eur. Phys. J.
 578 Special Topics* 226 (2017) 2119-2133.
- 579 [11] R.J. Diaz, R. Rosenberg, Spreading dead zones and consequences for marine ecosystems, *Science*
 580 321 (2008) 926-929.
- 581 [12] X. Gao, J.C. Ren, Z.X. Zong, Studies on the nutrient energetics of *Microcystis aeruginosa*, *Acta
 582 Scientiarum Naturalium* 30(4) (1994) 461-469.
- 583 [13] N.N. Rabalais et al., Dynamics and distribution of natural and human-caused hypoxia, *Biogeosciences*
 584 7 (2010) 585-619.
- 585 [14] W. Carmichael, Cyanobacterial harmful algal blooms: state of the science and research needs,
 586 Springer (2008).
- 587 [15] Interview: Raising awareness about global toxic algae bloom.
 588 [http://www.digitaljournal.com/news/environment/interview-raising-awareness-about-global-toxic-al...](http://www.digitaljournal.com/news/environment/interview-raising-awareness-about-global-toxic-al)
- 589 [16] Water quality standards. <https://www.pca.state.mn.us/water/water-quality-standards>.
- 590 [17] H. Sarmento, J.M. Gasol, Use of phytoplankton-derived dissolved organic carbon by different types
 591 of bacterioplankton, *Environ. Microbiol.* 14 (2012) 2348-2360.
- 592 [18] Y. Aota, H. Nakajima, Mutualistic relationships between phytoplankton and bacteria caused by
 593 carbon excretion from phytoplankton, *Ecol. Res.* 16 (2001) 289-299.
- 594 [19] L. Riemann, G.F. Steward, F. Azam, Dynamics of bacterial community composition and activity
 595 during a mesocosm diatom bloom, *Appl. Environ. Microbiol.* 66 (2000) 578-587.
- 596 [20] M.R. Seyedsayamdst et al., The Jekyll and Hyde chemistry of *Phaeobacter gallaciensis*, *Nature
 597 Chem.* 3 (2011) 331-335.
- 598 [21] A.M. Amaro et al., Identification and characterization of potentially algal-lytic marine bacteria
 599 strongly associated with the toxic dinoflagellate *Alexandrium catenella*, *J. Eukaryot. Microbiol.* 52
 600 (2005) 191-200.
- 601 [22] S.A. Amin et al. Interaction and signalling between a cosmopolitan phytoplankton and associated
 602 bacteria, *Nature* 522 (2015) 98-101.

- 603 [23] M. Landa et al., Shifts in bacterial community composition associated with increased carbon cycling
604 in a mosaic of phytoplankton blooms, ISME J. 10 (2015) 39-50.
- 605 [24] L. Philippot et al., Going back to the roots: the microbial ecology of the rhizosphere. Nat. Rev.
606 Microbiol. 11 (2013) 789-799.
- 607 [25] M.T. Croft et al., Algae acquire vitamin B12 through a symbiotic relationship with bacteria, Nature
608 438 (2005) 90-93.
- 609 [26] M. Teplitski, S. Rajamani, Signal and nutrient exchange in the interactions between soil algae and
610 bacteria, In biocommunication in soil microorganisms; Witzany, G., Ed.; Springer: Berlin, Germany
611 (2011) 413-426.
- 612 [27] L.E. Gonzalez, Y. Bashan, Increased growth of the microalga Chlorella vulgaris when co-
613 immobilized and co-cultured in alginate beads with the plant-growth-promoting bacterium Azospir-
614 illum brasiliense, Appl. Environ. Microbiol. 66 (2000) 1527-1531.
- 615 [28] B.H. Kim et al., Role of Rhizobium, a plant growth promoting bacterium, in enhancing algal biomass
616 through mutualistic interaction, Biomass Bioenerg. 69 (2014) 95-105.
- 617 [29] R. Ramanan et al., Phycosphere bacterial diversity in green algae reveals an apparent similarity
618 across habitats, Algal Res. 8 (2015) 140-144.
- 619 [30] G.J. Doucette, Interactions between bacteria and harmful algae: a review, Nat. Toxins 3(2) (1995)
620 65-74.
- 621 [31] K. Gopalsamy, Stability and oscillations in delay differential equations of population dynamics,
622 Mathematics and its applications. Kluwer Academic Pub. Dordrecht 74 (1992).
- 623 [32] S. Ruan, J. Wei, Stability and bifurcation in a neural network model with two delays, Physica D
624 130 (1999) 255-272.
- 625 [33] S. Ruan, J. Wei, On the zeros of transcendental functions with applications to stability of delay
626 differential equations with two delays, Dyn. Contin. Disc. Impul. Syst. Ser. A Math. Anal. 10 (2003)
627 863-874.
- 628 [34] T. Amemiya et al., Stability and dynamical behavior in a lake-model and implications for regime
629 shifts in real lakes, Ecol. Model. 206 (2007) 54-62.
- 630 [35] A.K. Misra, Modeling the depletion of dissolved oxygen due to algal bloom in a lake by taking
631 Holling type-III interaction, Appl. Math. Comput. 217, (2011) 8367-8376.
- 632 [36] R.H. Whittaker, Communities and Ecosystems. Macmillan, New York (1975).
- 633 [37] S. Ruan, Oscillations in plankton models with nutrient recycling, J. Theor. Biol. 208 (2001) 15-26.
- 634 [38] M. Gao, H. Shi, Z. Li, A planktonic resourceconsumer model with a temporal delay in nutrient
635 recycling, J. Math. Anal. Appl. 339 (2008) 511-516.
- 636 [39] K. Das, S. Ray, Effect of delay on nutrient cycling in phytoplankton-zooplankton interactions in
637 estuarine system, Ecol. Model. 215 (2008) 69-76.
- 638 [40] A.K. Misra, P. Chandra, V. Raghavendra, Modeling the depletion of dissolved oxygen in a lake due
639 to algal bloom: Effect of time delay, Adv. Water Res. 34 (2011) 1232-1238.

- 640 [41] A.K. Misra, P.K. Tiwari, P. Chandra, Modeling the control of algal bloom in a lake by applying some
641 external efforts with time delay, Differ. Equ. Dyn. Syst. DOI 10.1007/s12591-017-0383-5 (2017).
- 642 [42] R. Diaz, N.N. Rabalais, D.L. Breitburg, Agriculture's impact on aquaculture: hypoxia and eutrophication
643 in marine waters, <https://www.oecd.org/tad/sustainable-agriculture/49841630.pdf>,
644 (2012).
- 645 [43] Y. Li, Effect of N, P concentration on growth rate, Acta Ecologica Sinica 26 (2006) 317-325.
- 646 [44] J.L. Mouget et al., Algal growth enhancement by bacteria: is consumption of photosynthetic oxygen
647 involved?. FEMS Microbiology Ecology, 18(1) (1995) 35-44.
- 648 [45] K.C. Marshall, Cyanobacterial-heterotrophic bacterial interactions. In: Microbials Mats-
649 Physiological Ecology of Benthic Microbial Communities (Y. Cohen, E. Rosenberg Eds.), American
650 Society for Microbiology, Washington DC. (1989) 239-245.
- 651 [46] R. Ukeles, J. Bishop, Enhancement of phytoplankton growth by marine bacteria, J. Phycol. 11
652 (1975) 142-149.
- 653 [47] A.K. Jones, The interaction of algae and bacteria. In: Microbial Interactions and Communities
654 (Bull, A.T. and Slater, J.H., Eds.), Academic Press, New York, (1982) 189-247.
- 655 [48] E. Beretta, Y. Kuang, Modeling and analysis of a marine bacteriophage infection, Math. Biosci.
656 149 (1998) 57-76.
- 657 [49] A.K. Misra, P. Chandra, J.B. Shukla, Mathematical modeling and analysis of the depletion of
658 dissolved oxygen in water bodies. Nonlinear Anal. RWA. 7 (2006) 980-996.
- 659 [50] J.B. Shukla, A.K. Misra, P. Chandra, Mathematical modeling of the survival of a biological species
660 in polluted water bodies, Diff. Equ. Dyn. Syst. 15(3/4) (2007) 209-230.
- 661 [51] P. Hohener, O. Atteia, Multidimensional analytical models for isotope ratios in groundwater pol-
662 lutant plumes of organic contaminants undergoing different biodegradation kinetics, Adv. Water.
663 Resour. 33 (2010) 740-751.
- 664 [52] P.K. Tiwari et al., Modeling the direct and indirect effect of pollutants on the fish survival in water
665 bodies, J. Biol. Syst. 25(03) (2017) 521-543.
- 666 [53] P.K. Tiwari et al., Human population effects on the Ulsoor lake fish survival, J. Biol. Syst. 26(04)
667 (2018) 603-632.
- 668 [54] S. Rinaldi et al., Modeling and control of river quality, McGraw-Hill Inc., U.K. (1979).
- 669 [55] H.I. Freedman, J.W.H. So, Global stability and persistence of simple food chains, Math. Biosci. 76
670 (1985) 69-86.
- 671 [56] C. Castillo-Chavez, B. Song, Dynamical models of tuberculosis and their applications, Math. Biosci.
672 Eng. 1 (2004) 361-404.
- 673 [57] X. Wang, A simple proof of Descartes's rule of signs, Am. Math. Mon. 111(6) (2004) 525-526.
- 674 [58] A. Huppert, B. Blasius, L. Stone, A model of phytoplankton blooms. Am. Nat. 159(2) (2002)
675 156-171.

- 676 [59] T. Park, A matlab version of the Lyapunov exponent esti-
677 mation algorithm of wolf et al. physica 16d, 1985. (2014).
678 <https://www.mathworks.com/matlabcentral/fileexchange/48084-lyapunov-exponent-estimation-from-a-time-series>
- 679 [60] A. Wolf et al., Determining Lyapunov exponents from a time series, Physica D Nonlinear Phenomena
680 16 (1985) 285-317.
- 681 [61] S.M. Blower, H. Dowlatabadi, Sensitivity and uncertainty analysis of complex models of disease
682 transmission: an HIV model, as an example, Int. Stat. Rev. 62 (1994) 229-243.
- 683 [62] S. Marino et al., A methodology for performing global uncertainty and sensitivity analysis in systems
684 biology, J. Theor. Biol. 254(1) (2008) 178-196.
- 685 [63] Climate Change and Harmful Algal Blooms. <https://www.epa.gov/nutrientpollution/climate-change-and-harmful-algal-blooms>
- 686 [64] J. Zhou et al., A review of the relationship between algae and bacteria in harmful algal blooms,
687 Acta Ecol. Sin. 34 (2014) 269-281.
- 688 [65] J.L. Fuentes et al., Impact of microalgae-bacteria interactions on the production of algal biomass
689 and associated compounds, Marine drugs 14(5) (2016) 100.
- 690 [66] H. Malchow, S. Petrovskii, E. Venturino, Spatiotemporal patterns in Ecology and Epidemiology,
691 CRC, 2008.
- 692 [67] S. Chakraborty et al., Spatial dynamics of a nutrient-phytoplankton system with toxic effect on
693 phytoplankton, Math. Biosci. 264 (2015) 94-100.
- 694 [68] P.K. Tiwari et al., Effect of cross-diffusion on the patterns of algal bloom in a lake: A nonlinear
695 analysis, Nonlinear Studies, 21(3) (2014) 443-462.

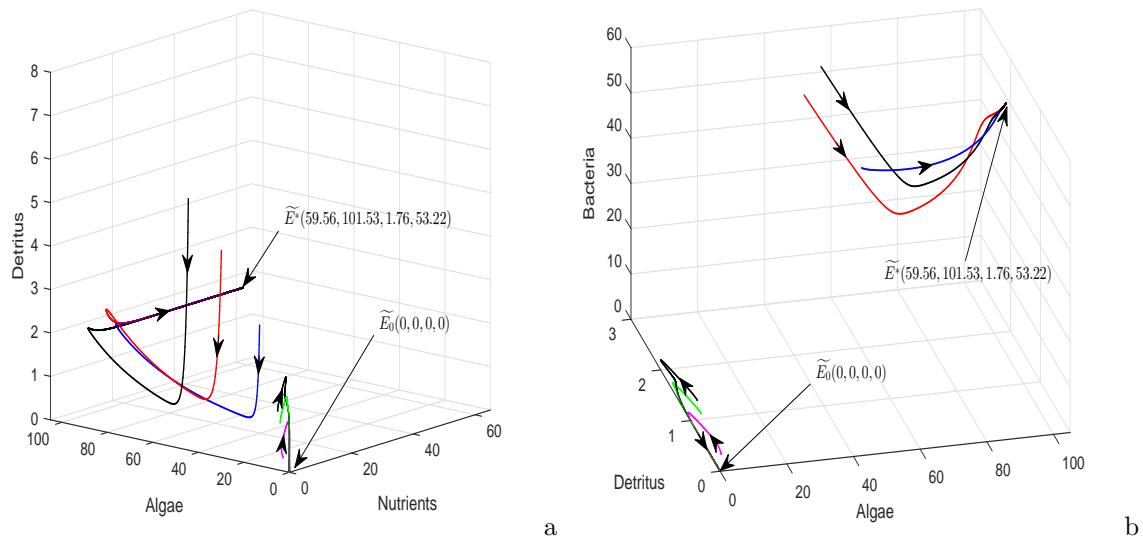


Figure 2: Figure shows bi-stability behavior of the system (5.1). The trajectories with different initial conditions lead to different attractors. Parameters values are same as in Table 1 except $\theta_1 = 15.5$, $\alpha_1 = 0.3$, $\pi_1 = 0.23$ and $\lambda_1 = 0.26$.

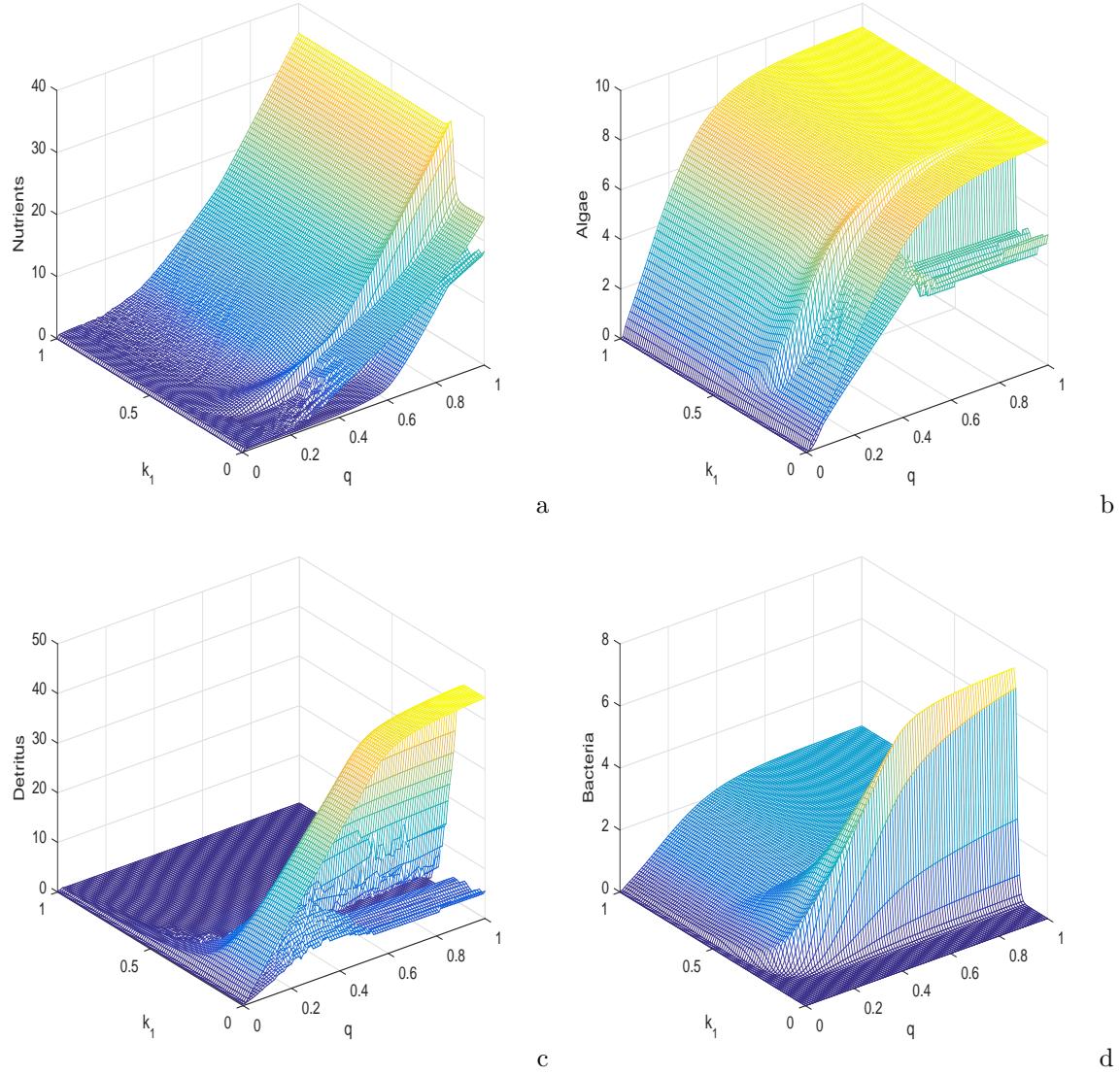


Figure 3: The equilibrium values of nutrients, algae, detritus and bacteria as functions of q and k_1 with initial conditions $(0.12, 1.15, 0.1, 0.06)$. Rest of the parameters values are same as in Table 1.

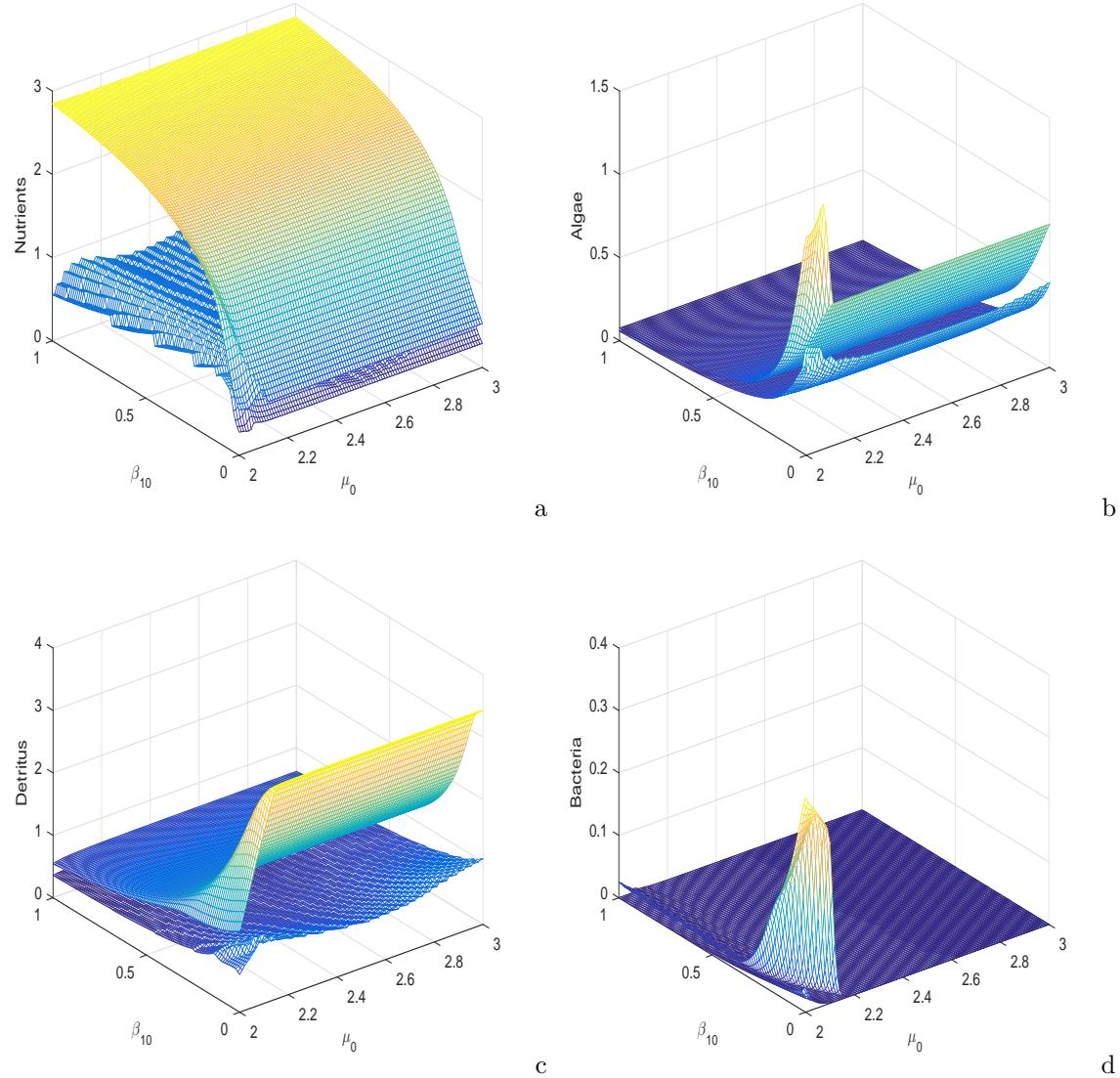


Figure 4: The equilibrium values of nutrients, algae, detritus and bacteria as functions of μ_0 and β_{10} with initial conditions $(0.12, 1.15, 0.1, 0.06)$. Rest of the parameters values are same as in Table 1.

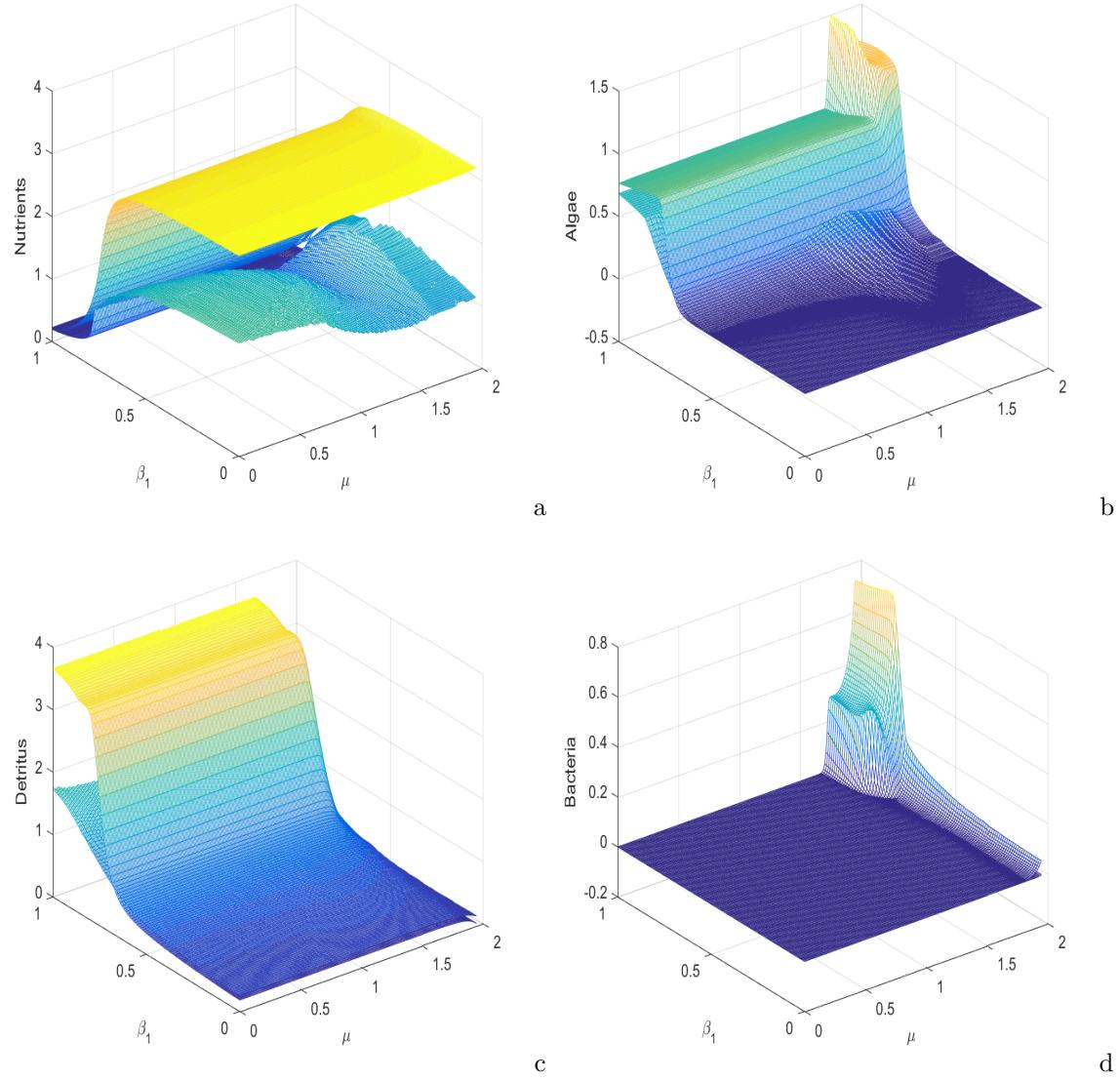


Figure 5: The equilibrium values of nutrients, algae, detritus and bacteria as functions of μ and β_1 with initial conditions $(0.12, 1.15, 0.1, 0.06)$. Rest of the parameters values are same as in Table 1.

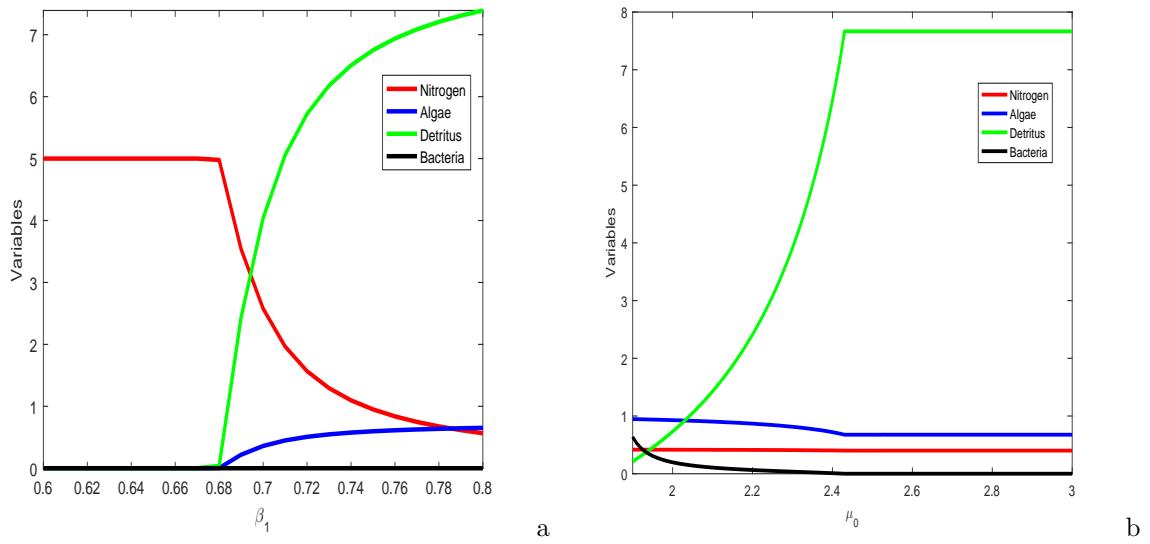


Figure 6: Transcritical bifurcations between equilibria (a) E_0 and E_1 , left to right, when $\mu = 0.8$ and (b) E^* and E_1 , left to right, when $\mu = 1.85$ and the other parameters values are same as in Table 1. Initial conditions are chosen as $(0.12, 1.15, 0.1, 0.06)$.

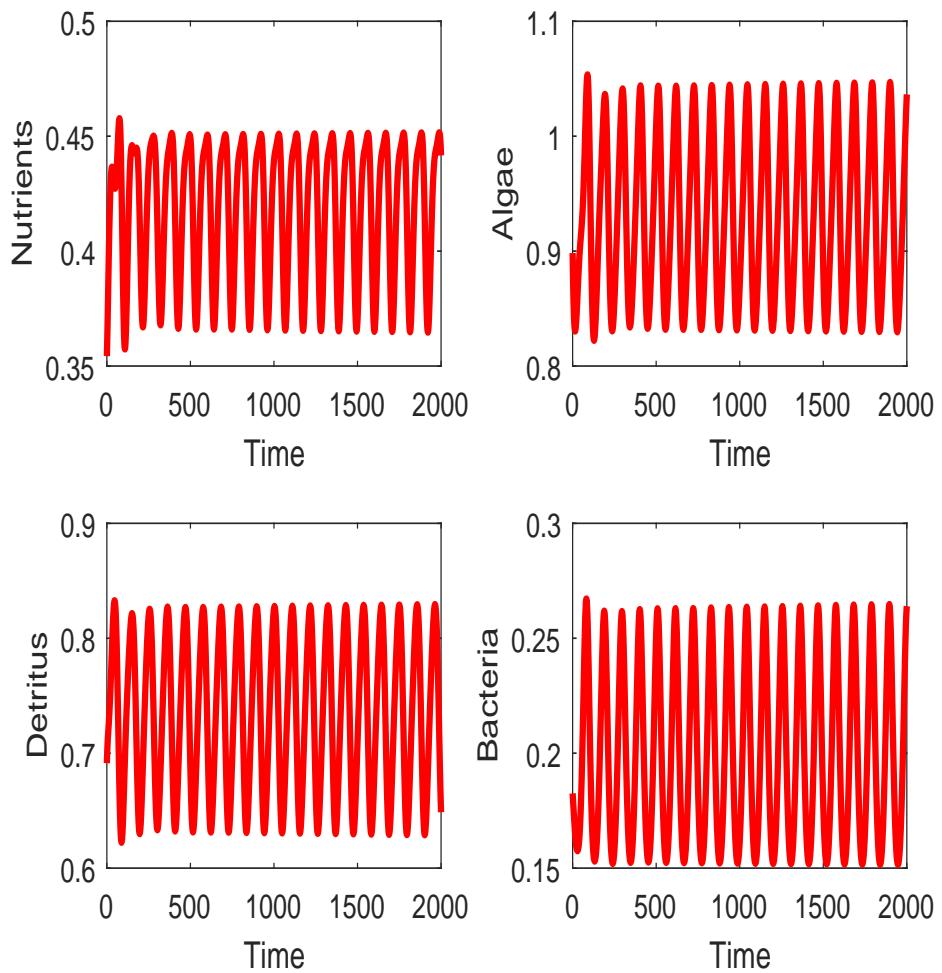


Figure 7: System (8.1) shows limit cycle oscillation for $\tau = 15.2$ days. Initial conditions are chosen as $(0.3543, 0.8983, 0.6913, 0.1825)$. Parameters values are same as in Table 1.

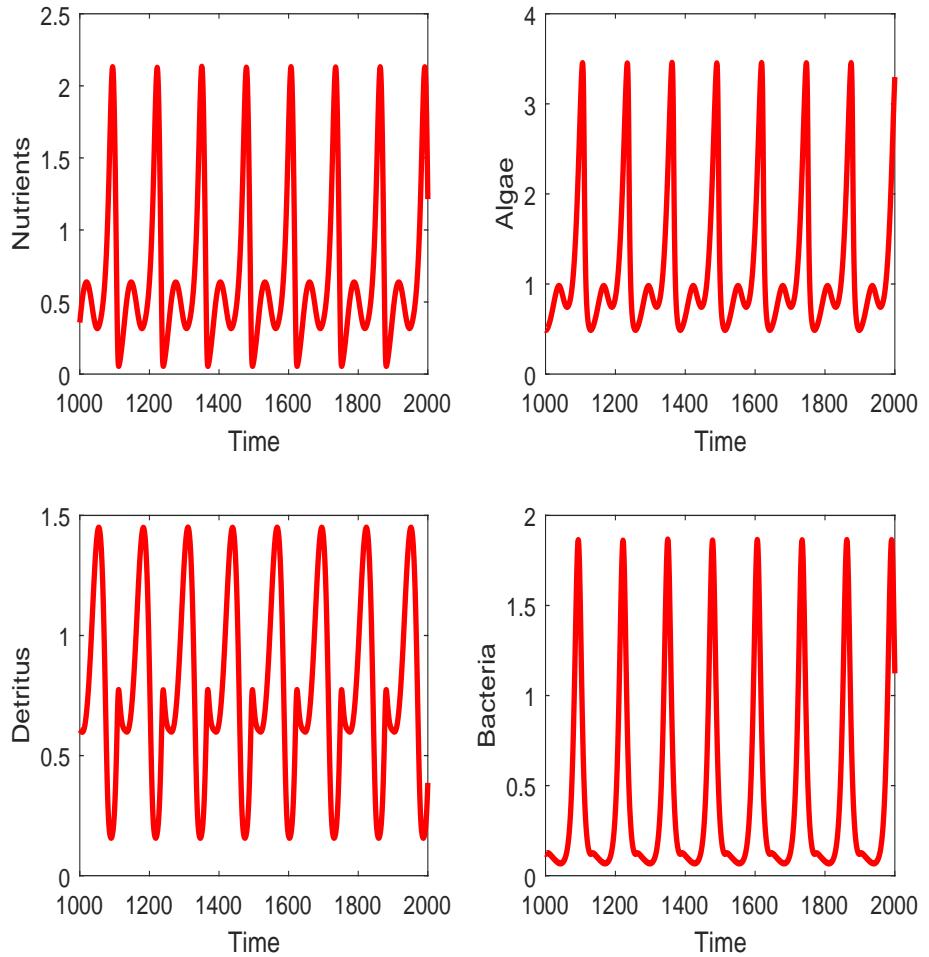


Figure 8: System (8.1) shows 2-periodic solutions for $\tau = 20$ days. Initial conditions are chosen as $(0.3543, 0.8983, 0.6913, 0.1825)$. Parameters values are same as in Table 1.

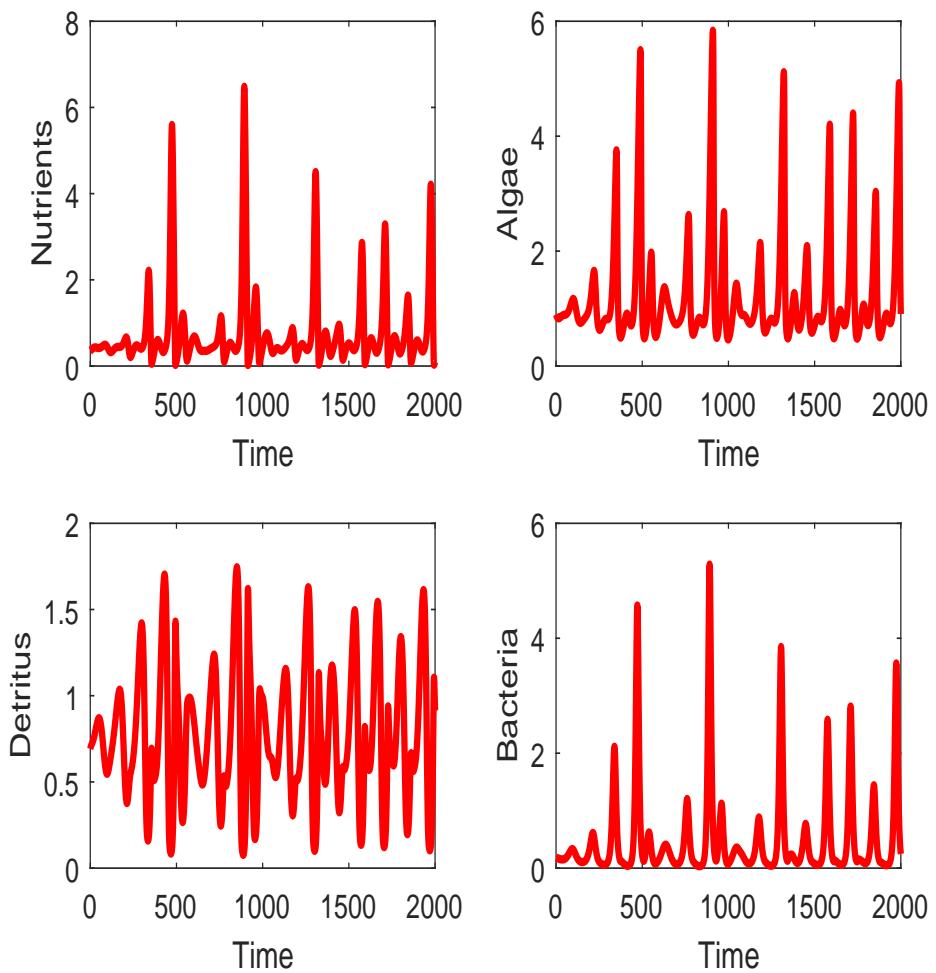


Figure 9: System (8.1) shows chaotic oscillations for $\tau = 21.5$ days. Initial conditions are chosen as $(0.3543, 0.8983, 0.6913, 0.1825)$. Parameters values are same as in Table 1.

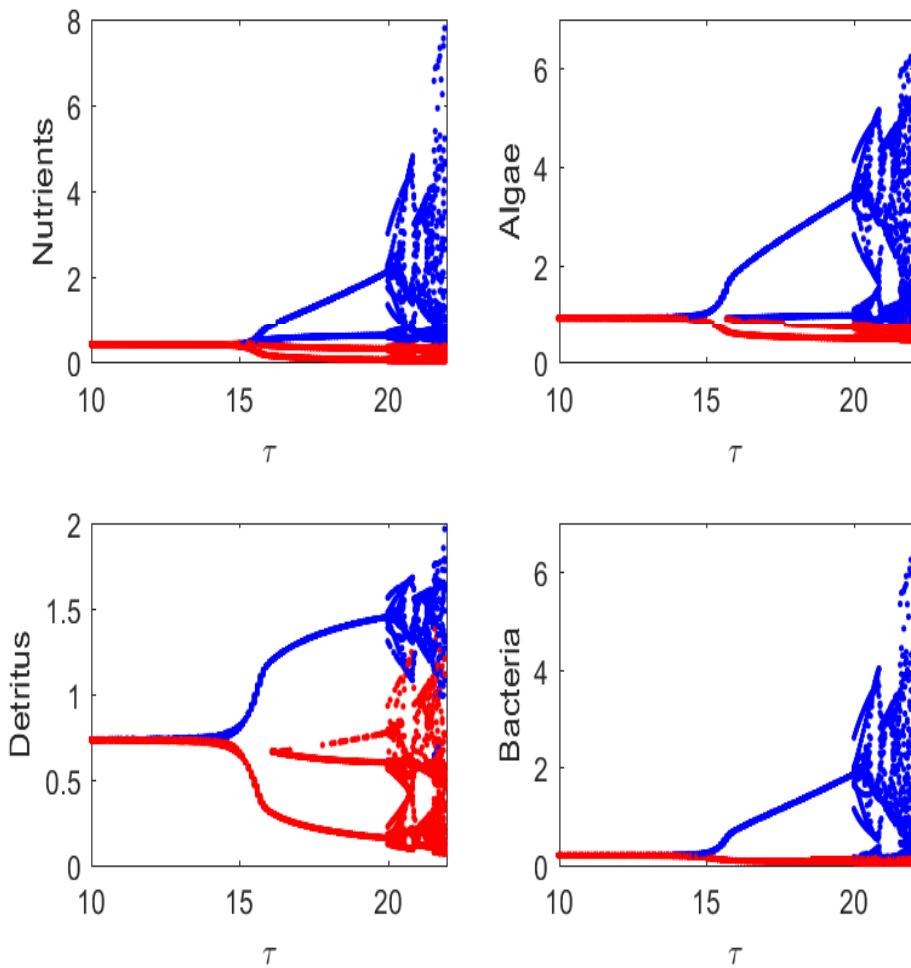


Figure 10: Bifurcation diagram of the system (8.1) with respect to $\tau \in [10, 22]$. Here, the maximum and minimum values of the oscillations are plotted in blue and red colors, respectively. Initial conditions are chosen as $(0.3543, 0.8983, 0.6913, 0.1825)$. Parameters values are same as in Table 1.

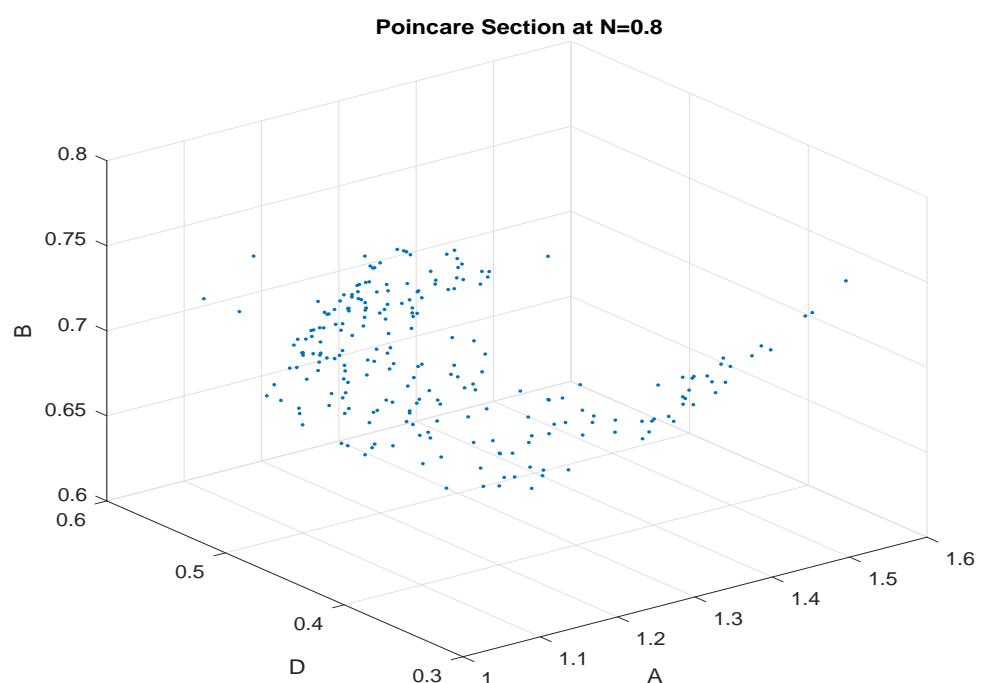


Figure 11: Poincare map of the system (8.1) in the $A-D-B$ space ($N = 10$) for $\tau = 21.5$ days. Initial conditions are chosen as $(0.3543, 0.8983, 0.6913, 0.1825)$. Parameters values are same as in Table 1.

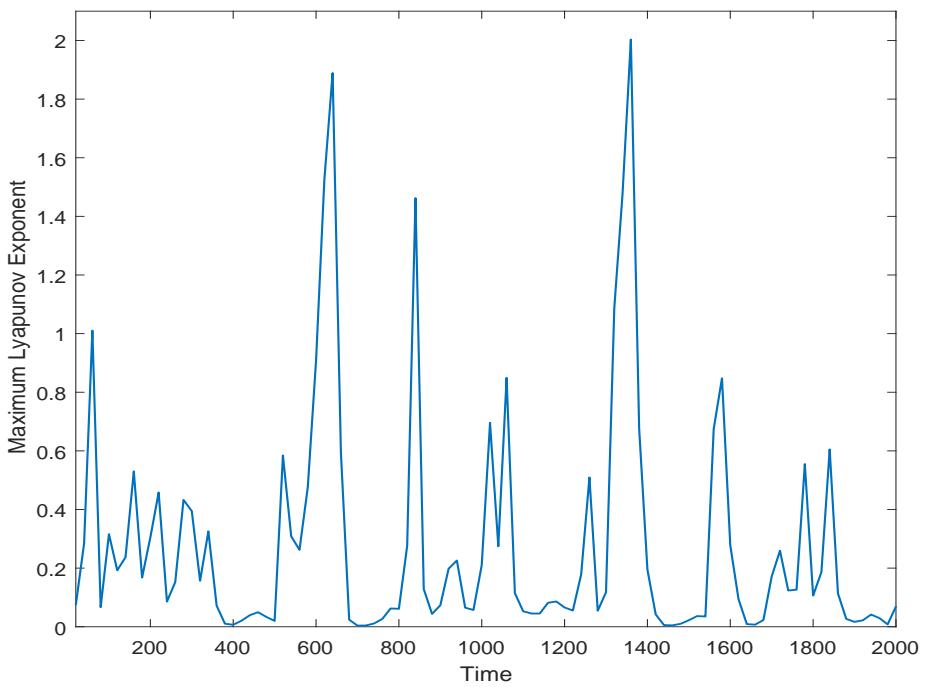


Figure 12: The maximum Lyapunov exponent of the system (8.1) for $\tau = 21.5$ days. Initial conditions are chosen as $(0.3543, 0.8983, 0.6913, 0.1825)$. Parameters values are same as in Table 1.

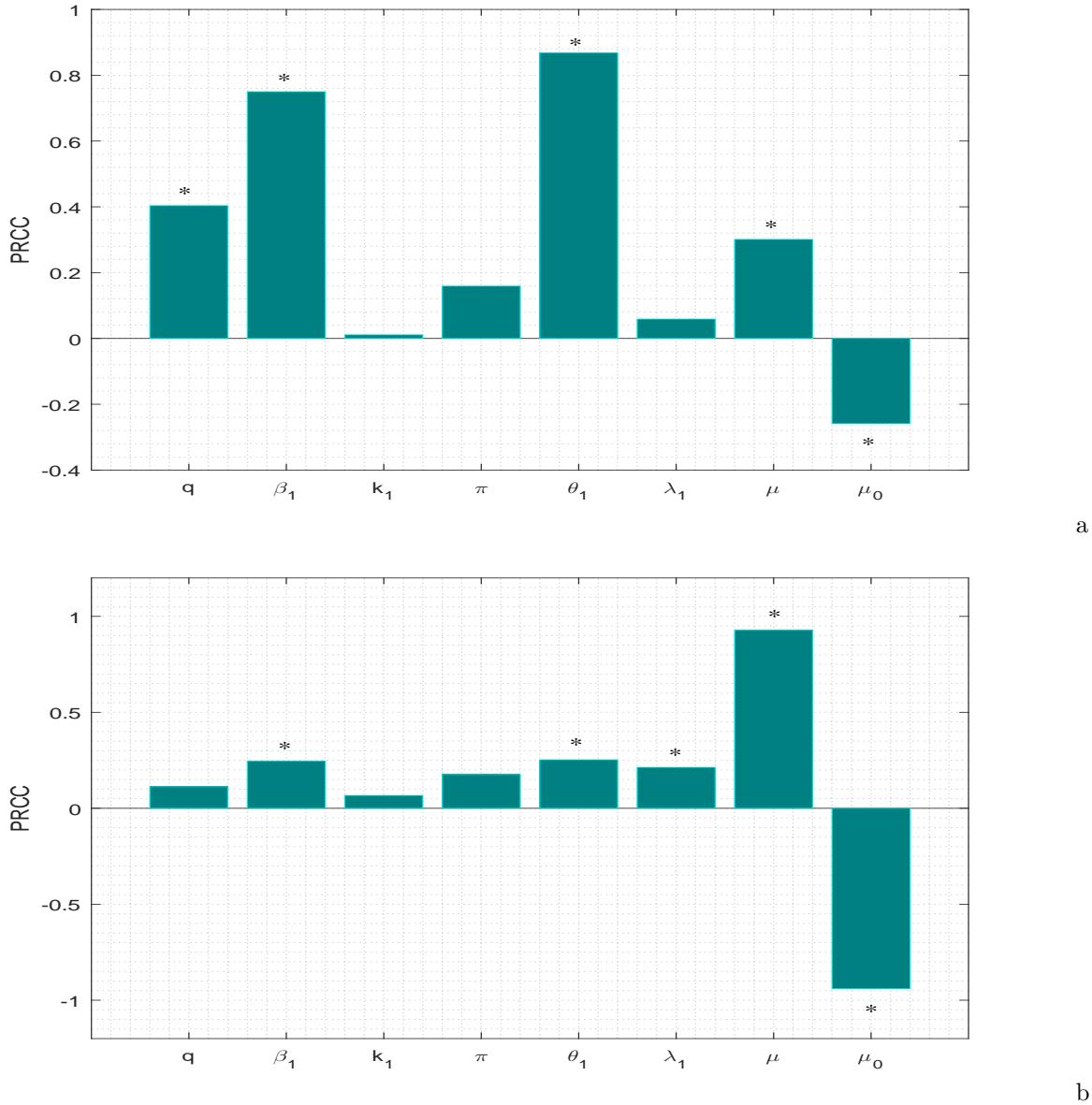


Figure 13: Effect of uncertainty of the model (2.1) on (a) algae and (b) bacteria. Significant parameters are marked by *. Initial conditions are chosen as $(0.12, 1.15, 0.1, 0.06)$. The mean values of parameters are chosen as in Table 1.