4. SUB-LETHAL EFFECTS OF HAB TOXIN ON REEF-FISH POPULATION

4.1 Introduction

Algal blooms occur worldwide and in some areas it is a common seasonal occurrence. Certain algal species undergo a rapid increase and form visible patches on the water surface and are often associated with harmful or toxic effects, referred to as harmful algal blooms (HAB) [47]. As observed by Brusle [48], these blooms may be noxious for aquatic species and especially marine and freshwater fish by producing specific toxins that affect the reproduction of aquatic organisms either by decreasing the amount or quality of gametes or by affecting embryonic development. Researchers [49] contend that adults of some species may be insensitive to toxins but early stages are more prone to intoxication because they lack effective enzymatic systems to detoxify the toxins and are more exposed to the toxins due to a higher metabolic growth rate. Such impact on early life stages of the species contributes to significant population change depending on the severity of the bloom in terms of density and duration [50, 51].

The dinoflagellates are a major marine phytoplankton group found in aquatic biosystems and are also the symbiont of corals. HAB is formed by toxic species, mostly dinoflagellates containing toxins that result in paralytic, diarrhetic, neurotoxic, amnesic shellfish poisoning (PSP, DSP, NSP, and ASP) and ciguatera fish poisoning (CFP) [52]. Studies by Berry et al. [53] and Brinson and Ramsdell [54] have shown that fish may be exposed to harmful dinoflagellate blooms during the different stages of their reproduction process — as adults during sexual maturation, as eggs and as larvae. Toxin exposure during early development of some fishes is of

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particular concern because the embryos and larvae of the fish species are vulnerable
to the dissolved toxins released by algae into the water column during HAB [55].
Several dinoflagellate species produce chemical compounds that reduces the growth
and reproduction of fishes [56]. One of these *Gambierdiscus toxicus*, appears to be
most significant in ciguatera ecology. This unicellular microalgae is generally found
attached to macrophytes that grow on dead coral substrates. *Gambierdiscus toxicus*
is the source of ciguatoxins (CTXs). The adverse effects of CTX on fish embryos by
microinjecting CTX into the egg yolk of medaka *Oryzias latipes* embryos are studied
by Edmunds et al. [57]. While the embryos are microinjected with low levels of
CTX, the embryos exhibit significantly reduced hatching success. This sensitivity
of embryonic fish to CTX may represent an unrecognized threat to the reproductive
success of reef fish. As observed by Dickey and Plakas [58], CTX impairs embryonic
and larval stages of development in *Oryzias latipes*, decrease larval survivability,
and expedites toxin transfer from *Gambierdiscus toxicus* to higher trophic levels
through bio-accumulation.

A mathematical model of a food chain is presented where there is a constant supply
of dissolved limiting nutrient. CTX producing *Gambierdiscus toxicus* are present at
the first trophic level and the CTX sensitive herbivorous fish *Oryzias latipes* at the
second trophic level. *Gambierdiscus toxicus* take the dissolved limiting nutrient for
its growth. *Oryzias latipes* carries out its feeding from *Gambierdiscus toxicus* only.
The growth rate of the fish is inhibited by the sub-lethal effect of CTX produced by
the dinoflagellates. We will examine the effects of CTX produced by *Gambierdiscus
有毒* on *Oryzias latipes*.

### 4.2 The basic model

We have considered a model where there is a constant supply of input nutrient,
whose concentration at time $t$ is $S(t)$. CTX producing *Gambierdiscus toxicus* are
introduced in the system at first trophic level whose concentration at time $t$ is $x(t)$.
The CTX-sensitive fishes *Oryzias latipes* are introduced in the second trophic level
with concentration $y(t)$ at time $t$ whose growth rate is inhibited by the toxin CTX. It
is assumed that $y(t)$ takes the nutrient from $x(t)$ only. The concentration of CTX
at time $t$ is denoted by $p(t)$. We assume that the uptake rate of *Gambierdiscus toxicus* follows hyperbolic Holling type II functional response and the uptake rate of *Oryzias latipes* follows sigmoid Holling type III functional response.

The basic equations with all the parameters are:

\[
\begin{align*}
\frac{dS}{dt} &= (S^0 - S)D_1 - \frac{m_1 S x}{a_1 + S} \\
\frac{dx}{dt} &= x \left[ (1 - K) \frac{\alpha_1 m_1 S}{a_1 + S} - D_2 - \frac{m_2 x y e^{-\mu p}}{a_2^2 + x^2} \right] \\
\frac{dy}{dt} &= y \left( \frac{\alpha_2 m_2 x^2 e^{-\mu p}}{a_2^2 + x^2} - D_3 \right) \\
\frac{dp}{dt} &= K x \frac{\alpha_1 m_1 S}{a_1 + S} - pD_4
\end{align*}
\]  

(4.1)

where $S(0) \geq 0, x(0) \geq 0, y(0) \geq 0, p(0) \geq 0$.

Here $S^0$ is the input nutrient concentration, $D_1$ and $D_4$ are the washout rates of the input nutrient and CTX respectively whereas $D_2, D_3$ are the death rates of *Gambierdiscus toxicus* and *Oryzias latipes* respectively. Also, $m_i$'s are the maximal growth (‘birth’) rates, $a_i$'s are the Michaelis-Menten or ‘half saturation’ constants, which are the nutrient concentrations at which the functional response of the species is half maximal and $\alpha_i$'s are growth efficiency of the organisms so that $0 < \alpha_i < 1$ ($i = 1, 2$), $e^{-\mu p}$ is the degree of sensitivity (i.e.) the degree of inhibition of $p$ on the growth rate of $y$; all of these are positive quantities \[45\]. The parameter $K$ represents the fraction of the consumption of $x(t)$ devoted to produce the inhibitor. Since the dinoflagellate is toxin-producing, we have $K > 0$. If $K = 1$, then the resource used by dinoflagellates are fully devoted for CTX production leading to the extinction of the dinoflagellates. So, $K \in (0, 1)$.

### 4.3 Non-dimensionalization of the problem

Let us change the variables of the system (4.1) to non dimensional ones \[44\] by substituting $\bar{S} = \frac{S}{S^0}, \bar{x} = \frac{x}{\alpha_1 S^0}, \bar{y} = \frac{y}{\alpha_1 \alpha_2 S^0}, \bar{t} = D_1 t, \tilde{a}_1 = \frac{a_1}{S^0}, \tilde{a}_2 = \frac{a_2}{\alpha_1 S^0}, \bar{D}_2 = \frac{D_2}{D_1}, \bar{D}_3 = \frac{D_3}{D_1}, \bar{D}_4 = \frac{D_4}{D_1}, \bar{m}_1 = \frac{m_1}{D_1}, \bar{m}_2 = \frac{m_2}{D_1}, \bar{p} = \frac{p}{\alpha_1 S^0}, \bar{u} = \mu \alpha_1 S^0$

Under these substitutions by dropping the bar’s the system (4.1) reduces to

\[
\frac{dX}{dt} = f(X)
\]  

(4.2)
where $X = \begin{pmatrix} S & x & y & p \end{pmatrix}^T$ and $f(X) = \begin{pmatrix} F & G & H & I \end{pmatrix}^T$ with

\[
F \equiv 1 - S - \frac{m_1Sx}{a_1+S},
\]

\[
G \equiv x \left[ (1 - K) \frac{m_1S}{a_1+S} - D_2 - \frac{m_2xye^{-\rho x}}{a_2^2 + x^2} \right],
\]

\[
H \equiv y \left( \frac{m_2xe^{-\rho x}}{a_2^2 + x^2} - D_3 \right),
\]

\[
I \equiv K \frac{m_1Sx}{a_1+S} - pD_4.
\]

$S(0) \geq 0, x(0) \geq 0, y(0) \geq 0, p(0) \geq 0.$

### 4.4 Boundedness of the System

**Theorem 4.4.1.** For all $\epsilon > 0$, there exists $t_\epsilon > 0$ such that all the solutions of (4.2) enter into the set $B = \{(S, x, y, p) \in \mathbb{R}^4 : S(t) + x(t) + y(t) + p(t) \leq \frac{1}{D} + \epsilon\}$ whenever $t \geq t_\epsilon$, where $D = \min\{1, D_2, D_3, D_4\}$.

**Proof:** Let $\Sigma(t) = S(t) + x(t) + y(t) + p(t)$.

Then $\frac{d}{dt}(\Sigma(t)) + (\Sigma(t))D \leq 1$, where $D = \min\{1, D_2, D_3, D_4\}$.

Let $u(t)$ be the solution of $\frac{du(t)}{dt} + Du(t) = 1$, satisfying $u(0) = \Sigma(0)$.

Then $u(t) = \frac{1}{D} + (\Sigma(0) - \frac{1}{D}) e^{-tD} \to \frac{1}{D}$ as $t \to \infty$.

By comparison, it follows that $\lim_{t \to \infty} \sup [S(t) + x(t) + y(t) + p(t)] \leq \frac{1}{D}$. \hfill $\Box$

Let us define $\lambda_1 = \frac{a_1D_2}{m_1(1 - K) - D_2}$ and $\lambda_2 = a_2 \sqrt{\frac{D_1}{m_2 - D_3}}$ where $m_1 > \frac{D_2}{1 - K}$ and $m_2 > D_3$.

Then $\lambda_1$ is the break-even concentration of $x(t)$, representing the concentration of the nutrient when the derivative of $x(t)$ is zero, in absence of the predator $y(t)$ and $\lambda_2$ represents the break-even concentration of $y(t)$ in absence of the internal inhibitor.

The following theorem states the condition under which the species cannot survive even, in the absence of predation:

**Theorem 4.4.2.**

(i) If $m_1 \leq \frac{D_2}{1 - K}$, then $x(t) \to 0$ and $y(t) \to 0$ as $t \to \infty$.

(ii) If $m_2 \leq D_3$, then $y(t) \to 0$ as $t \to \infty$.

(iii) If $m_1 > \frac{D_2}{1 - K}$ and $\lambda_1 > 1$, then $x(t) \to 0$ and $y(t) \to 0$ as $t \to \infty$.

(iv) If $m_2 > D_3$ and $\lambda_2 > \frac{1}{D}$, then $y(t) \to 0$ as $t \to \infty$.

**Proof:** (i) Since $\frac{ds}{dt} \leq 1 - S$, it follows that for all $\epsilon > 0$, there exists $t_\epsilon > 0$ such that $S(t) \leq 1 + \epsilon$, for all $t \geq t_\epsilon$. 
If \( m_1 \leq \frac{D_2}{1-K} \), then \( \frac{dx}{dt} \leq -xD_2 \left( \frac{a_1}{a_1 + S} \right) < 0. \)

Thus we get, \( \int_{x(t_e)} x(t) \frac{dt}{dt} \leq -D_2 \left( \frac{a_1}{a_1 + \epsilon} \right) (t-t_e) \) which gives \( x(t) \leq x(t_e)e^{-\frac{a_1D_2(t-t_e)}{1+a_1+\epsilon}} \)

Therefore, \( \lim_{t \to \infty} x(t) = 0 \) and consequently \( \lim_{t \to \infty} y(t) = 0. \)

(ii) Since \( \lim_{t \to \infty} \sup\{S(t) + x(t) + y(t) + p(t)\} \leq \frac{1}{B} \), it follows that for all \( \epsilon > 0 \), there exists \( t_\epsilon > 0 \) such that \( x(t) \leq \frac{1}{B} + \epsilon \), for all \( t \geq t_\epsilon \).

If \( m_2 \leq D_3 \), then \( \frac{dy}{dt} \leq -yD_3 \left( \frac{a_2^2}{a_2^2 + (\frac{1}{B} + \epsilon)^2} \right) < 0. \)

Thus we get, \( \int_{y(t_\epsilon)} y(t) \frac{dt}{dt} \leq -D_3 \left( \frac{a_2^2}{a_2^2 + (\frac{1}{B} + \epsilon)^2} \right) (t-t_\epsilon) \) which gives \( y(t) \leq y(t_\epsilon)e^{-\frac{a_2^2D_3(t-t_\epsilon)}{1+a_2^2+\epsilon}} \)

Therefore, \( \lim_{t \to \infty} y(t) = 0. \)

(iii) For all \( \epsilon > 0 \), there exists \( t_\epsilon > 0 \) such that \( 0 \leq S(t) \leq 1 + \epsilon \), for all \( t \geq t_\epsilon \).

Thus, if \( \lambda_1 > 1 + \epsilon \) for all \( t \geq t_\epsilon \) holds, then
\[
\frac{dx}{dt} \leq x \left( \frac{1}{(1-K)m_1-D_2}(S-S_\lambda) \right) \leq x \left( \frac{(1-K)m_1-D_2}{1} \right) < 0.
\]

This implies if \( \lambda_1 > 1 \) and \( m_1 > \frac{D_2}{1-K} \), then \( x(t) \to 0 \) as \( t \to \infty \) and consequently \( y(t) \to 0 \) as \( t \to \infty \).

(iv) For all \( \epsilon > 0 \), there exists \( t_\epsilon > 0 \) such that \( 0 \leq x(t) \leq \frac{1}{B} + \epsilon \), for all \( t \geq t_\epsilon \).

Thus, \( \frac{dy}{dt} \leq y \left( \frac{m_2-D_3}{a_2^2+x^2} \right) \leq y \left( \frac{m_2-D_3}{\frac{a_2^2}{a_2^2+x^2}} \right) < 0 \), if \( \lambda_2 > \frac{1}{B} + \epsilon \) for all \( t \geq t_\epsilon \).

Therefore, if \( \lambda_2 > \frac{1}{B} \) and \( m_2 > D_3 \) hold, then \( y(t) \to 0 \).

Under the hypothesis of theorem (4.4.2), it follows that

(i) if the maximal growth rate of \( Gambierdiscus toxicus \) is less than or equal to \( \frac{D_2}{1-K} \), then none of the species in first and second trophic levels will survive.

(ii) If the maximal growth rate of \( Oryzias latipes \) is less than or equal to its washout rate then \( Oryzias latipes \) cannot survive.

(iii) If the maximum growth rate of \( Gambierdiscus toxicus \) is greater than \( \frac{D_2}{1-K} \) and the break-even concentration \( \lambda_1 > 1 \), then none of the species in first and second trophic levels will survive.

(iv) If the maximal growth rate of \( Oryzias latipes \) is greater than its washout rate and the break-even concentration \( \lambda_2 > \frac{1}{B} \), then \( Oryzias latipes \) becomes extinct.
4.5 Permanence of the System

The system will be permanent if there exists \( u_i, M_i \in (0, \infty) \) such that \( u_i \leq \lim_{t \to \infty} u_i(t) \leq M_i \), for each organism \( u_i(t) \) in the system. From biological point of view, permanence of a system ensures coexistence of the organisms in the long run.

Since \( S(t) + x(t) + y(t) + p(t) < \frac{1}{D} \) as \( t \to \infty \) it follows that there exists positive numbers \( M_1, M_2 \) with \( M_1 + M_2 < \frac{1}{D} \) such that \( x(t) \leq M_1, y(t) \leq M_2 \) for large \( t \).

We assume that \( m_1 > \frac{D_2}{1-K} \) and \( m_2 > D_3 \).

**Theorem 4.5.1.** If there exists positive numbers \( s_1, x_1 \) with \( \lambda_1 < s_1 < \lambda_1 + \frac{m_1 m_2 M_1 M_2 \lambda_1 (1-K)}{D_2 a_2^2 ((1-K) m_1 - D_2) - m_2 M_1 M_2}, a_2 > \sqrt{\frac{m_2 M_1 M_2 \lambda_1}{a_1 D_2}}, \) and \( x_1 \geq \sqrt{\frac{a_2 D_3}{m_2 e^{-p}(1-K) - D_3}} > \lambda_2 \), then for large values of \( t \) there exists positive numbers \( y_1, p_1, P_1 \) such that each solution of the system (4.2) with positive initial values enters in the compact set \( \{(S, x, y, p) : s_1 \leq s(t) \leq 1, x_1 \leq x(t) \leq M_1, y_1 \leq y(t) \leq M_2, p_1 \leq p(t) \leq P_1 \} \) and remains in it finally.

**Proof:** Since \( \lim_{t \to \infty} \sup [S(t) + x(t) + y(t) + p(t)] \leq \frac{1}{D} \), it follows that

\[
\lim_{t \to \infty} \sup [x(t) + y(t)] < \frac{1}{D}.
\]

Therefore, there exists \( T_1 > 0 \) such that \( x(t) \leq M_1 \) and \( y(t) \leq M_2 \), for all \( t \geq T_1 \) where \( M_1, M_2 \) are finite positive constants with \( M_1 + M_2 < \frac{1}{D} \).

If possible, let \( \lim_{t \to \infty} S(t) = 0 \).

Therefore, for all \( \epsilon > 0 \), there exists \( t_\epsilon > 0 \) such that \( S(t) \leq \epsilon \), for all \( t \geq t_\epsilon \).

Therefore, for all \( t \geq t_\epsilon \), \( S(t) + \frac{m_1 x(t) S(t)}{a_1 + S(t)} \leq \epsilon + \frac{m_1 M_1 \epsilon}{a_1 + \epsilon} < 1 \) which implies \( \frac{ds}{dt} < 0 \) for all \( t \geq t_\epsilon \), contradicting to our assumption.

Therefore, there exists \( s_1 > 0 \) such that for \( T_2 > 0 \) we have \( S(t) \geq s_1, \forall t > T_2 \).

Again, \( \frac{ds}{dt} \leq 1 - S \) implies for all \( \epsilon_1 > 0 \), there exists \( T_3 > 0 \) such that \( S(t) \leq 1 + \epsilon_1 \), for all \( t \geq T_3 \). Thus, for all \( t \geq \max\{T_2, T_3\} \), we have \( s_1 \leq S(t) \leq 1 \).

For \( t > \max\{T_1, T_2, T_3\} \) we have \( \frac{dx}{dt} \geq x \left((1-K) \frac{m_1 s_1}{a_1} - D_2 - \frac{m_2 M_1 M_2}{a_1^2 + x^2}\right) \). This implies \( \frac{dx}{dt} \mid_{x=x_1} \geq 0 \) for \( t > \max\{T_1, T_2, T_3\} \) where \( x_1 = \sqrt{\frac{m_2 M_1 M_2 (s_1 - 1)}{(1-K) m_1 - D_2}} - a_2^2 \).

Also, for \( x_1 > 0 \) we must have \( m_1 > \frac{D_2}{1-K}, a_2 > \frac{m_2 M_1 M_2 \lambda_1}{a_1 D_2} \) and \( \lambda_1 < s_1 < \lambda_1 + \frac{m_1 m_2 M_1 M_2 \lambda_1 (1-K)}{D_2 a_2^2 ((1-K) m_1 - D_2) - m_2 M_1 M_2} \).

This implies that there exists \( T_4 > 0 \) such that \( x_1 \leq x(t) \leq M_1 \) for all \( t > T_4 \).

Also, \( \frac{dp}{dt} \mid_{p=p_1} \leq 0 \), where \( P_1 = \frac{m_1 M_1 K}{D_4 (a_1 + 1)} \).

Therefore, \( \exists T_5 > 0 \) such that \( p(t) \leq P_1, \forall t > T_4 \).
For $t > T_4$ we have $\frac{dp}{dt} \mid_{p=p_1} \geq 0$, where $p_1 = \frac{Km_1x_1s_1}{D_4(a_1+s_1)}$.

This implies that $\exists T_6 > 0$ such that $p(t) \geq p_1, \forall t > T_6$.

Again for $t > \max\{T_5, T_6\}$ we have

$$\frac{dy}{dt} \geq y \left( \frac{m_2x_2^2}{a_2^2y_1^2}e^{-μt} - D_3 \right) \geq 0$$

for $x_1 \geq \sqrt{\frac{a_2^2D_3}{m_2e^{-μt} - D_3}} > \lambda_2$.

Therefore, for $x_1 \geq \sqrt{\frac{a_2^2D_3}{m_2e^{-μt} - D_3}} > \lambda_2$ there exists $T_7 > 0$ and $y_1 > 0$ such that $y(t) \geq y_1$, for all $t > T_7$.

Let $T = \max\{T_1, T_2, \ldots, T_7\}$. Then for $t > T$, there exists finite positive real numbers $s_1, x_1, y_1, p_1, P_1$ with $λ_1 < s_1 < λ_1 + \frac{m_1m_2M_1M_2λ_1(1-K)}{D_2[a_2^2((1-K)m_1-D_2)-m_2M_1M_2]}, x_1 \geq \sqrt{\frac{a_2^2D_3}{m_2e^{-μt} - D_3}} > λ_2$ and $a_2^2 > \frac{m_2M_1M_2λ_1}{a_1D_2}$ such that $s_1 \leq s(t) \leq 1, x_1 \leq x(t) \leq M_1, y_1 \leq y(t) \leq M_2, p_1 \leq p(t) \leq P_1$.

**Corollary 4.1.** If $\lim_{t \to \infty} y(t) = 0$, then there exists finite positive real numbers $s_1, x_1, p_1, P_1, M_1$ with $M_1 < 1, λ_1 < s_1 \leq 1$ such that for large values of $t$, $s_1 \leq s(t) \leq 1, x_1 \leq x(t) \leq M_1, p_1 \leq p(t) \leq P_1$.

### 4.6 Equilibria and their Stability

The system (4.2) possesses the following equilibria:

(i) *Gambierdiscus toxicus* and *Oryzias latipes* free equilibrium $E_0 = (1, 0, 0, 0)$;

(ii) *Oryzias latipes* free equilibrium $E_1 = \left( λ_1, \frac{(1-λ_1)(1-K)}{D_2}, 0, \frac{K(1-λ_1)}{D_4} \right)$;

(iii) the equilibrium of coexistence $E^* = (S^*, x^*, y^*, p^*)$, where $p^*$ is a positive root of the equation

$$D_4p - K \left( 1 - \frac{f(p)+\sqrt{f^2(p)+4a_1}}{2}, x^* = a_2\sqrt{\frac{D_3}{m_2e^{-μp^*} - D_3}} \right) = 0,$$

and $y^* = \frac{\sqrt{D_3}}{D_3} \left\{ (1-K) \frac{m_1s^*}{a_1+s^*} - D_2 \right\}$.

**Criterion for existence of $E_1$**

The rest point $E_1$ exists if $λ_1 < 1$.

**Criterion for existence of $E^*$**

$E^*$ exists if $0 < p^* < \frac{1}{μ} \ln \left( \frac{m_2}{D_3} \right)$ and $D_2 > \frac{m_1s^*(1-K)}{a_1+s^*}$.

We analyze the local stability of system (4.2) by using eigenvalue analysis of the Jacobian matrix evaluated at the appropriate equilibrium.

**Lemma 4.6.1.**

The critical point $E_0$ of the system (4.2) is locally asymptotically stable if $λ_1 > 1$. 
Proof: At $E_0$ the variational matrix is

$$
\begin{bmatrix}
-1 - \frac{m_1}{a_1+1} & 0 & 0 \\
0 & \frac{(1-K)m_1}{a_1+1} - D_2 & 0 \\
0 & 0 & -D_3 \\
0 & \frac{m_1K}{a_1+1} & 0 - D_4
\end{bmatrix}
$$

Therefore, the system (4.2) is stable at $E_0$ if $\frac{(1-K)m_1}{a_1+1} - D_2$ (i.e.) if $\lambda_1 > 1$. □

Lemma 4.6.2.

The critical point $E_1 = \left( \lambda_1, \frac{(1-\lambda_1)(1-K)}{D_2}, 0, \frac{K(1-\lambda_1)}{D_4} \right)$ of the system (4.2) is locally asymptotically stable if any one of the following two conditions hold:

(i) $\lambda_1(1-K) + \lambda_2D_2 \geq 1 - K$;

(ii) $\lambda_1(1-K) + \lambda_2D_2 < 1 - K$ and $D_4 < \frac{\mu K(1-\lambda_1)}{c}$, where $c = \ln \left[ \frac{m_2(1-\lambda_1)^2(1-K)^2}{\mu D_3\{a_2D_2^2+(1-\lambda_1)^2(1-K)^2\}} \right]$.

Proof: At $E_1$ the variational matrix is

$$
\begin{bmatrix}
-1 - \frac{a_1D_2(1-\lambda_1)}{m_1\lambda_1^2(1-K)} & 0 & 0 & -\frac{\mu K(1-\lambda_1)}{D_4} \\
\frac{a_1D_2(1-\lambda_1)}{m_1\lambda_1^2(1-K)} & 0 & -\frac{m_2(1-K)^2(1-\lambda_1)^2}{a_2D_2^2+(1-\lambda_1)^2(1-K)^2} & 0 \\
\frac{K\lambda_1(1-\lambda_1)D_2}{m_1\lambda_1^2(1-K)} & KD_2(1-K) & 0 & -D_3 \\
\frac{K\lambda_1(1-\lambda_1)D_2}{m_1\lambda_1^2(1-K)} & KD_2(1-K) & 0 & -D_4
\end{bmatrix}
$$

(4.3)

The two eigenvalues are $\mu_{11} = -D_4 < 0$, $\mu_{12} = -D_3 + \frac{m_2(1-K)^2(1-\lambda_1)^2}{a_2D_2^2+(1-\lambda_1)^2(1-K)^2}$ and the two other eigenvalues are given by $u^2 + u \left\{ 1 + \frac{a_1D_2(1-\lambda_1)}{m_1\lambda_1^2(1-K)} \right\} + \frac{a_1D_2(1-\lambda_1)}{m_1\lambda_1^2(1-K)} = 0$.

Since $\lambda_1 < 1$, the roots of this quadratic equation have negative real parts.

Now, $\mu_{12} < 0$ if $e^{-\frac{\mu K(1-\lambda_1)}{D_4}} < \frac{\mu K(1-\lambda_1)}{D_4} \frac{m_2(1-K)^2(1-\lambda_1)^2}{a_2D_2^2+(1-\lambda_1)^2(1-K)^2}$.

If $\frac{D_3[a_2D_2^2+(1-\lambda_1)^2(1-K)^2]}{m_2(1-\lambda_1)^2(1-K)^2} \geq 1$ (i.e.) if $\lambda_1(1-K) + \lambda_2D_2 \geq 1 - K$, then $\mu_{12} < 0$ and so $E_1$ is stable.

If $\lambda_1(1-K) + \lambda_2D_2 < 1 - K$, then $E_1$ is stable for $D_4 < \ln \left[ \frac{m_2(1-\lambda_1)^2(1-K)^2}{\mu D_3\{a_2D_2^2+(1-\lambda_1)^2(1-K)^2\}} \right]$. □

Lemma 4.6.3.

The system (4.2) has no periodic solution around the positive equilibrium if $m_1 < a_1L$ where $L$ is the minimum of the following:

(a) $1 + D_2 + \frac{m_1a_1x^*}{(a_1+S)^2} + \frac{2a_2^2D_3y^*}{x^*(a_2^2+x^*)} - D_3(1+y^*\mu)$,

(b) $1 + \frac{ma_1x^*}{(a_1+S)^2} - D_3y^*\mu - \frac{2a_2^2D_3y^*}{x^*(a_2^2+x^*)}$,

(c) $\frac{1}{2} \left( 1 + D_4 + \frac{ma_1x^*}{(a_1+S)^2} \right)$,
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Now, \(\frac{1}{2} (D_2 + \frac{2a_1^2 D_4 y^*}{x^2(a_2^2 + x^2)} - 2D_3 y^* \mu),\)
\((e) \frac{1}{3} (D_2 - D_3 + D_4 + \frac{2a_1^2 D_4 y^*}{x^2(a_2^2 + x^2)}),\)
\((f) D_4 - \frac{2a_1^2 D_4 y^*}{x^2(a_1^2 + x^2)};\)

**Proof:** Second additive compound matrix \(J^{(2)}\) of the Jacobian of (4.2) at \(E^*\) is

\[
\begin{bmatrix}
F_S|_{E^*} + G_x|_{E^*} & G_y|_{E^*} & G_p|_{E^*} & 0 & 0 & 0 \\
H_x|_{E^*} & F_S|_{E^*} & H_p|_{E^*} & F_x|_{E^*} & 0 & 0 \\
I_x|_{E^*} & 0 & F_S|_{E^*} + I_p|_{E^*} & 0 & F_x|_{E^*} & 0 \\
0 & G_S|_{E^*} & 0 & G_x|_{E^*} & H_p|_{E^*} & -G_p|_{E^*} \\
-I_S|_{E^*} & 0 & G_S|_{E^*} & 0 & G_x|_{E^*} + I_p|_{E^*} & G_y|_{E^*} \\
0 & 0 & 0 & -I_x|_{E^*} & H_x|_{E^*} & I_p|_{E^*}
\end{bmatrix}
\]

where \(F_S|_{E^*} = -1 - \frac{m_1 a_1 x^*}{(a_1+S)^2}, F_x|_{E^*} = -\frac{m_1 S^*}{a_1+S^*}, G_S|_{E^*} = \frac{m_1 a_1 x^*(1-K)}{(a_1+S)^2},\)
\(G_x|_{E^*} = \frac{1-Km_1 S^*}{a_1+S^*} - D_2 \frac{2a_1^2 D_4 y^*}{x^2(a_1^2 + x^2)}, G_y|_{E^*} = -D_3, G_p|_{E^*} = \mu y^* D_3,\)
\(H_x|_{E^*} = \frac{2a_1^2 D_4 y^*}{x^2(a_1^2 + x^2)}, H_p|_{E^*} = -\mu y^* D_3, I_S|_{E^*} = \frac{Km_1 a_1 x^*}{(a_1+S)^2}, I_x|_{E^*} = \frac{Km_1 a_2 x^*}{(a_1+S)^2}, I_p|_{E^*} = -D_4.\)

Logarithmic norm \(\mu_{\infty}\) endowed by the norm \(|X|_\infty\) of \(J^{(2)}, |X|_\infty = \sup_i |X_i|,\) is \(\mu_{\infty}(J^{(2)})\) is the supremum of the following:

\((i) F_S|_{E^*} + G_x|_{E^*} + D_3(1 + \mu y^*),\)
\((ii) F_S|_{E^*} + \mu y^* D_3 + H_x|_{E^*} + |F_x|_{E^*},\)
\((iii) F_S|_{E^*} + I_p|_{E^*} + F_x|_{E^*} + |I_x|_{E^*},\)
\((iv) G_x|_{E^*} + 2\mu y^* D_3 + |G_S|_{E^*},\)
\((v) G_x|_{E^*} + I_p|_{E^*} + D_3 + |I_S| + |G_S|_{E^*},\)
\((vi) I_p|_{E^*} + |I_x|_{E^*} + |H_x|_{E^*}.\)

Now, \(F_S|_{E^*} + G_x|_{E^*} + D_3(1 + \mu y^*) < 0\) if
\(m_1 a_1 < 1 + D_2 + \frac{m_1 a_1 x^*}{(a_1+S)^2} + \frac{2a_1^2 D_4 y^*}{x^2(a_2^2 + x^2)} - D_3(1 + y^* \mu),\)
\(F_S|_{E^*} + \mu y^* D_3 + |H_x|_{E^*} + |F_x|_{E^*} < 0\) if
\(m_1 a_1 < 1 + \frac{m_1 a_1 x^*}{(a_1+S)^2} - D_3 y^* \mu - \frac{2a_1^2 D_4 y^*}{x^2(a_2^2 + x^2)},\)
\(F_S|_{E^*} + I_p|_{E^*} + |F_x|_{E^*} + |I_x|_{E^*} < 0\) if
\(m_1 a_1 < \frac{1}{2} \left(1 + D_4 + \frac{m_1 a_1 x^*}{(a_1+S)^2}\right),\)
\(G_x|_{E^*} + 2\mu y^* D_3 + |G_S|_{E^*} < 0\) if
\(m_1 a_1 < \frac{1}{2} \left(D_2 + \frac{2a_1^2 D_4 y^*}{x^2(a_1^2 + x^2)} - 2D_3 y^* \mu\right),\)
\(G_x|_{E^*} + I_p|_{E^*} + D_3 + |I_S| + |G_S|_{E^*} < 0\) if
\(m_1 a_1 < \frac{1}{3} \left(D_2 - D_3 + D_4 + \frac{2a_1^2 D_4 y^*}{x^2(a_2^2 + x^2)}\right).\)
If the conditions stated in Lemma (4.6.3) hold, then the interior equilibrium point $E^*$ of the system (4.2) is locally asymptotically stable.

\[ I_{p|E^*} + |I_x|E^*| + |H_x|E^*| < 0 \text{ if} \]
\[ m_1 \frac{a_1}{a_1} < D_4 - \frac{2a_2D_3y^*}{x^*(a_2^2 + x^*2)}. \]

Let $L$ be the min. of the six quantities:
\[ 1 + D_2 + \frac{m_1 a_1 x^*}{(a_1 + S)^2} + \frac{2a_2D_3y^*}{x^*(a_2^2 + x^*2)} - D_3(1 + y^* \mu), \]
\[ 1 + \frac{m_1 a_1 x^*}{(a_1 + S)^2} - D_3 y^* \mu - \frac{2a_2D_3y^*}{x^*(a_2^2 + x^*2)}, \]
\[ \frac{1}{3} \left(1 + D_4 + \frac{m_1 a_1 x^*}{(a_1 + S)^2}\right), \]
\[ \frac{1}{3} \left(D_2 + \frac{2a_2D_3y^*}{x^*(a_2^2 + x^*2)} - 2D_3 y^* \mu\right), \]
\[ \frac{1}{3} \left(D_2 - D_3 + D_4 + \frac{2a_2D_3y^*}{x^*(a_2^2 + x^*2)}\right) \text{ and} \]
\[ D_4 - \frac{2a_2D_3y^*}{x^*(a_2^2 + x^*2)}. \]

Therefore, if $m_1 < a_1 L$ then $\mu_\infty(J^{(2)}) < 0$.

A direct application of Li-Muldowney’s method [34] we can say that under the aforesaid conditions the system (4.2) has no periodic solution around $E^*$. □

All the organisms in the system will persist [35] if $u(t) > 0$ as $t \to \infty$, for each organism $u(t)$. The condition given in the following lemma rules out the possibility of extinction of any organism in the system.

**Lemma 4.6.4.** The system (4.2) is persistent if $\lambda_1 < 1, \lambda_1(1 - K) + \lambda_2 D_2 < 1 - K$ and $D_4 \geq \frac{\mu K(1 - \lambda_1)}{c}$, where $c = \ln \left[\frac{m_2(1 - \lambda_1)^2(1 - K)^2}{D_3(a_2^2 D_2^2 + (1 - \lambda_1)^2(1 - K)^2)}\right]$.

**Proof:** In order to prove the persistence of the system (4.2) we shall show that all the boundary equilibria of the system (4.2) are repellers.

The system is unstable at $E_0$ if $\lambda_1 \leq 1$.

If $\lambda_1(1 - K) + \lambda_2 D_2 < 1 - K$ and $D_4 \geq \ln \left[\frac{\mu K(1 - \lambda_1)}{m_2(1 - \lambda_1)^2(1 - K)^2} D_3(a_2^2 D_2^2 + (1 - \lambda_1)^2(1 - K)^2)}\right]$ then $E_1$ is unstable.

Thus, the boundary equilibria of the system (4.2) are unstable if $\lambda_1 < 1, \lambda_1(1 - K) + \lambda_2 D_2 < 1 - K$ and $D_4 \geq \ln \left[\frac{\mu K(1 - \lambda_1)}{m_2(1 - \lambda_1)^2(1 - K)^2} D_3(a_2^2 D_2^2 + (1 - \lambda_1)^2(1 - K)^2)}\right]$.

Also, the system (4.2) is bounded.

Therefore, the system (4.2) is persistent under the aforesaid conditions. □

If the conditions stated in Lemma (4.6.3) and Lemma (4.6.4) hold, then the interior equilibrium point $E^*$ of the system (4.2) is locally asymptotically stable.
4.7 Numerical simulations

In this section we present numerical simulations as demonstrated in [37, 38, 59] by using MATLAB. We investigate the effect of the various parameters on the qualitative behavior of the system (4.2) using parameter values as given in Table 4.1.

<table>
<thead>
<tr>
<th>Original Parameters</th>
<th>Description of Parameters</th>
<th>Default value</th>
<th>Dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s^0$</td>
<td>Constant input nutrient concentration</td>
<td>0.7</td>
<td>mass/volume</td>
</tr>
<tr>
<td>$a_1$</td>
<td>Half saturation constant for uptake of $S$ by $x$</td>
<td>0.3</td>
<td>mass/ volume</td>
</tr>
<tr>
<td>$a_2$</td>
<td>Half saturation constant for uptake of $x$ by $y$</td>
<td>0.2</td>
<td>mass/ volume</td>
</tr>
<tr>
<td>$K$</td>
<td>Fraction of the consumption of $x$ devoted for producing $p$</td>
<td>0.3</td>
<td>-</td>
</tr>
<tr>
<td>$m_1$</td>
<td>Maximal growth rate of $x$ on $S$</td>
<td>3</td>
<td>1/time</td>
</tr>
<tr>
<td>$m_2$</td>
<td>Maximal growth rate of $y$ on $x$</td>
<td>4</td>
<td>1/time</td>
</tr>
<tr>
<td>$D_1$</td>
<td>Washout rate of input nutrient</td>
<td>0.5</td>
<td>1/time</td>
</tr>
<tr>
<td>$D_2$</td>
<td>Death rate of Gambierdiscus</td>
<td>0.3</td>
<td>1/time</td>
</tr>
<tr>
<td>$D_3$</td>
<td>Death rate of Oryzias latipes</td>
<td>0.2</td>
<td>1/time</td>
</tr>
<tr>
<td>$D_4$</td>
<td>Washout rate of CTX</td>
<td>0.5</td>
<td>1/time</td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>Growth efficiency of $x$ on $S$</td>
<td>0.6</td>
<td>-</td>
</tr>
<tr>
<td>$\alpha_2$</td>
<td>Growth efficiency of $y$ on $x$</td>
<td>0.5</td>
<td>-</td>
</tr>
<tr>
<td>$\mu$</td>
<td>Parameter associated with degree of sensitivity ($e^{-\mu p}$)</td>
<td>10</td>
<td>volume/mass</td>
</tr>
</tbody>
</table>

Tab. 4.1: Default set of parameter values.

Firstly, we will verify the feasibility of the criterion of stability as given in section (4.6) by means of the following numerical examples:

**Example: 4.1**

Under the set of parameter values as given in Table 4.1, it is observed that the system (4.2) approaches to the equilibrium at $E^* = (0.5542, 0.2196, 0.4508, 0.1337)$ in the form of a stable focus with eigenvalues $-1, -1.1745, -0.3547 \pm i0.5832$ (cf. Fig.4.1). Since $0.1337 = p^* < \frac{1}{\mu} \ln \left( \frac{m_2}{D_3} \right) = 0.5482$, the condition for existence of $E^*$ is satisfied. Again, we obtain $0.189 = \lambda_1 (1 - K) + \lambda_2 D_2 < 1 - K = 0.7$ and $D_4 \geq \frac{\mu K (1 - \lambda_1)}{c} = 0.5191$, satisfying the condition for persistence in lemma (5.6.4).
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Fig. 4.1: Time series analysis of the system for the parameters as given in Table 4.1. The system (4.2) has a stable focus at $E^*$. 

Fig. 4.2: Time series analysis of the system for $S^0 = 1.6$ and other parameters as given in Table 4.1. The system (4.2) has a stable node at $E_1$.

Example: 4.2

For $S^0 = 0.15$, other parameters as in Table 4.1, the system (4.2) is locally asymptotically stable at $E_1 = (0.625, 0.4375, 0, 0.1125)$ with eigenvalues $-1, -1.2351, -0.2221, -0.2651$. Since $\lambda_1 = 0.625 < 1$, the criterion for existence of $E_1$ is satisfied. Also, $0.8819 = \lambda_1 (1 - K) + \lambda_2 D_2 > 1 - K = 0.7$, satisfying lemma 4.6.2(i).
Example: 4.3
For $S^0 = 1.6$, leaving all other parameters unaltered, the system (4.2) approaches to a stable node at $E_1 = (0.0625, 1.0938, 0, 0.2813)$ with eigenvalues $-1, -0.5787, -11.8499, -0.0944$ (cf. Fig.4.2). In this case we obtain $\lambda_1 = 0.0625 < 1$, satisfying the criterion for existence of $E_1$. Also, $0.0882 = \lambda_1 (1 - K) + \lambda_2 D_2 < 1 - K = 0.7$ and $D_4 < \frac{\mu K (1 - \lambda_1)}{c} = 1.19$. Thus, lemma 5.6.2(ii) is satisfied.

Example: 4.4
For $S^0 = 0.05$, leaving all other parameters unaltered, the system (4.2) approaches to a stable node at $E_0 = (1, 0, 0, 0)$ with eigenvalues $-1, -1, -0.24, -0.4$ (cf. Fig.4.3). In this case we obtain $\lambda_1 = 1.875$, satisfying lemma (4.6.1).

![Graphs](image)

**Fig. 4.3:** Time series analysis of the system for $S^0 = 0.05$ and other parameters as given in Table 4.1. The system (4.2) has a stable node at $E_0$.

**Effect of $K$:**
For $K = 0.3$ and other parameter values as given in Table 4.1, the system (4.2) is locally asymptotically stable at $E^*$. If the value of $K$ is increased to 0.6, the system (4.2) becomes stable at $E_1$. Further, increasing $K$ (viz. $K = 0.8$) the system (4.2) stabilizes at $E_0$ (cf. Fig.4.4). Therefore, with high allocation of the consumption of *Gambierdiscus toxicus* on producing CTX, the concentration of CTX gradually increases as long as the growth of *Gambierdiscus toxicus* is not hampered. If this allocation exceeds beyond a certain extent, all the species in the system (4.2) be-
Fig. 4.4: Phase plane diagram of the system for $K = 0.3$ and other parameter values as given in Table 4.1, the system is locally asymptotically stable at $E^*$ (in blue). If the value of $K$ is increased to 0.6, the system becomes stable at $E_1$ (in black). Further, increasing $K$ (viz. $K = 0.8$) the system (4.2) stabilizes at $E_0$ (in red).

Combined effect of $\mu$ and $S^0$:
If the value of $\mu$ is increased to $\mu = 20$, leaving all other parameters unaltered, the system (4.2) approaches to $E_1$ (cf. Fig.4.5). In this case by lowering the value of $S^0$, the system (4.2) becomes stable at $E^*$.

Combined effect of $S^0$ and $D_i$ ($i = 1, 2, 3$):
For $S^0 = 1.6$ and all other parameters as in Table 4.1, the system (4.2) is stable at $E_1$. Increasing $D_2$ (viz. $D_2 = 0.75$) the system (4.2) becomes stable at $E^*$.

For $S^0 = 2$ and all other parameters as given in Table 4.1, the system (4.2) is locally asymptotically stable at $E_1$. The following changes of the values of $D_1$ and $D_3$ stabilizes the system (4.2) at $E^*$:

(a) Decreasing the washout rate $D_1$ of the nutrient to $D_1 = 0.32$ the system (4.2) becomes oscillatory around $E^*$ (cf. Fig.4.6). Further decreasing the value of $D_1$ (viz. $D_1 = 0.25$) the system (4.2) stabilizes at $E^*$.

(b) If the death rate of $Oryzias latipes$ is lowered (viz. $D_3 = 0.1$) the system (4.2) becomes stable at $E^*$.
Fig. 4.5: Phase plane diagram of the system for $\mu = 20$ and other parameter values as given in Table 4.1, the system (4.2) is locally asymptotically stable at $E_1$ (in black). In this case by lowering the value of $S_0$, the system (4.2) becomes stable at $E^*$ (in blue).

Fig. 4.6: Time series analysis of the system for $S^0 = 2$ and other parameters as given in Table 4.1. The system (4.2) has a stable node at $E_1$ (dotted curves). For $S^0 = 2, D_1 = 0.32$, and other parameter values as given in Table 4.1, the system (4.2) is oscillatory around $E^*$ (solid curves).
The qualitative behavior of the system (4.2) is given in Table 4.2, obtained by sequentially altering the value of a particular parameter of the system while leaving all other parameters unchanged.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Range</th>
<th>Conclusions about the stability at $E_{0}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s^0$</td>
<td>$0 \leq s^0 \leq 0.09$</td>
<td>With very low concentration of the limiting nutrient, all the organisms in the system become extinct.</td>
</tr>
<tr>
<td>$K$</td>
<td>$0.75 \leq K &lt; 1$</td>
<td>Very high allocation of the consumption of Gambierdiscus toxicus on producing CTX leads to the extinction of Gambierdiscus toxicus. Consequently, Oryzias latipes become extinct.</td>
</tr>
<tr>
<td>$m_1$</td>
<td>$0 &lt; m_1 \leq 1.02$</td>
<td>Very low uptake rate of limiting nutrient by Gambierdiscus toxicus leads to the extinction of all the species in the system.</td>
</tr>
<tr>
<td>$D_3$</td>
<td>$D_3 \geq 0.88$</td>
<td>High death rate of Gambierdiscus toxicus leads to the extinction of all the species.</td>
</tr>
<tr>
<td>$a_1$</td>
<td>$0 &lt; a_1 \leq 0.2$</td>
<td>Low growth efficiency of Gambierdiscus toxicus on limiting nutrient leads to the extinction of all the species.</td>
</tr>
</tbody>
</table>

Conclusions about the stability at $E_{1}$

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Range</th>
<th>Conclusions about the stability at $E_{1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s^0$</td>
<td>$[0.09] \cup (1.56, \infty)$</td>
<td>Oryzias latipes become extinct for low input nutrient concentration. Also, with enrichment of nutrient, the concentration of Gambierdiscus toxicus increases. This leads to the increase of CTX and consequently, extinction of Oryzias latipes.</td>
</tr>
<tr>
<td>$K$</td>
<td>$0.56 \leq K \leq 0.75$</td>
<td>High allocation of the consumption of Gambierdiscus toxicus on producing CTX gradually increases the concentration of CTX resulting in the extinction of Oryzias latipes.</td>
</tr>
<tr>
<td>$m_1$</td>
<td>$1.02 &lt; m_1 \leq 1.07$</td>
<td>Low uptake rate of limiting nutrient by Gambierdiscus toxicus leads to the extinction of Oryzias latipes.</td>
</tr>
<tr>
<td>$m_2$</td>
<td>$0 &lt; m_2 \leq 1.45$</td>
<td>Low uptake rate of Gambierdiscus toxicus by Oryzias latipes leads to the extinction of Oryzias latipes.</td>
</tr>
<tr>
<td>$D_1$</td>
<td>$D_1 &gt; 0.86$</td>
<td>High dilution rate of limiting nutrient leads to low absorption of limiting nutrient by Gambierdiscus toxicus. This leads to the extinction of Oryzias latipes.</td>
</tr>
<tr>
<td>$D_2$</td>
<td>$0.71 &lt; D_2 &lt; 0.88$</td>
<td>Oryzias latipes become extinct from the system for high death rate of Gambierdiscus toxicus.</td>
</tr>
<tr>
<td>$a_1$</td>
<td>$a_1 &gt; 1.5$</td>
<td>High growth efficiency of Gambierdiscus toxicus on limiting nutrient leads to increase in concentration of CTX. This leads to the extinction of Oryzias latipes.</td>
</tr>
<tr>
<td>$a_3$</td>
<td>$0 &lt; a_3 \leq 0.18$</td>
<td>Low growth efficiency of Oryzias latipes on Gambierdiscus toxicus leads the extinction of Oryzias latipes.</td>
</tr>
<tr>
<td>$\mu$</td>
<td>$\mu &gt; 19.4$</td>
<td>High CTX sensitivity of Oryzias latipes leads the extinction of Oryzias latipes.</td>
</tr>
</tbody>
</table>

Conclusions about the stability at $E'$

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Range</th>
<th>Conclusions about the stability at $E'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s^0$</td>
<td>$0.2 &lt; s^0 \leq 1.56$</td>
<td>Concentration of limiting nutrient within this threshold leads to coexistence.</td>
</tr>
<tr>
<td>$K$</td>
<td>$0 &lt; K &lt; 0.56$</td>
<td>Allocation of the consumption of Gambierdiscus toxicus on producing CTX within this threshold generates coexistence of all the species.</td>
</tr>
<tr>
<td>$m_1$</td>
<td>$m_1 &gt; 1.07$</td>
<td>High uptake rate of limiting nutrient by Gambierdiscus toxicus leads to coexistence of all the species.</td>
</tr>
<tr>
<td>$m_2$</td>
<td>$m_2 &gt; 1.45$</td>
<td>High uptake rate of Gambierdiscus toxicus by Oryzias latipes leads to coexistence of all the species.</td>
</tr>
<tr>
<td>$D_1$</td>
<td>$0 &lt; D_1 \leq 2.25$</td>
<td>Dilution rate of limiting nutrient within this threshold leads to coexistence of all the species.</td>
</tr>
<tr>
<td>$D_3$</td>
<td>$0 &lt; D_3 \leq 0.71$</td>
<td>Death rate of Gambierdiscus toxicus within this threshold leads to coexistence of all the species.</td>
</tr>
<tr>
<td>$D_4$</td>
<td>$D_4 &lt; 0.55$</td>
<td>Death rate of Oryzias latipes within this threshold leads to coexistence of all the species.</td>
</tr>
<tr>
<td>$a_1$</td>
<td>$0.2 \leq a_1 \leq 1.15$</td>
<td>High growth efficiency of Gambierdiscus toxicus on limiting nutrient leads to increase in concentration of CTX. This leads to the extinction of Oryzias latipes.</td>
</tr>
<tr>
<td>$\mu$</td>
<td>$0 &lt; \mu \leq 19.4$</td>
<td>Low CTX sensitivity of Oryzias latipes leads to coexistence of all the species.</td>
</tr>
</tbody>
</table>

**Tab. 4.2**: Range of parameter values for stability.
4.8 Discussion

We have considered a food chain with two trophic levels in presence of a constant supply of a limiting nutrient on which the CTX producing organism *Gambierdiscus toxicus* is growing at the first trophic level, inhibiting the growth of toxin sensitive organism *Oryzias latipes*. The model is firstly studied analytically and different thresholds in terms of the model parameters are obtained which are acting as conditions under which the species associated with the system cannot thrive even in absence of competition. We obtain the threshold values for the existence and stability of various steady states of the system. We have also provided numerical simulations to substantiate our analytic results. Further numerical analysis demonstrates the following conclusions:

(i) Lowering the concentration of the limiting nutrient leads to the extinction of all the organisms. Also, with high concentration of input nutrient, *Gambierdiscus toxicus* population increases leading to the increase of concentration of toxic CTX in the system. This leads to the extinction of *Oryzias latipes* from the system.

(ii) With high nutrient concentration stable coexistence of all the species is obtained by decreasing the dilution rate of input nutrient. Also, with high nutrient concentration, stable coexistence of all the organisms can be attained for low death rate of *Oryzias latipes* or higher mortality of *Gambierdiscus toxicus*.

(iii) If *Oryzias latipes* is highly sensitive to CTX, then it becomes extinct. In such a case, decreasing the concentration of input nutrient restores the stability of the system at the equilibrium of coexistence.

(iv) Higher allocation of the consumption of *Gambierdiscus toxicus* on producing CTX gradually increases the concentration of CTX as long as the growth of *Gambierdiscus toxicus* is not hampered. Increasing the amount of this allocation beyond a certain extent leads to the extinction of all the species in the system. Since the concentration of CTX in the system determines the amount of bio-accumulated CTX in *Oryzias latipes*, it follows that the level of CTX-fish poisoning is dependent on this allocation parameter.