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MATHEMATICAL ANALYSIS OF A NONDIMENSIONAL THREE SPECIES FOOD CHAIN MODEL WITH RATIO DEPENDENCE

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ABSTRACT. A model of three trophic level food chain with ratio dependence is considered. The existencem uniqueness and stability of its solutions are investigated.

1. INTRODUCTION

The classical prey-dependent predator-prey system often takes the general form of

$$\begin{cases} x'(t) = & xg(x) - cp(x) \\ y'(t) = & (p(x) - d)y, \end{cases} \tag{1.1}$$

where, x, y stand for prey and predator density, respectively $p(x)$ is the so-called predator functional response and c, $d > 0$ are the conversion rate and predator's death rate respectively. If

$$p(x) = \frac{mx}{a+x},\ g(x) = r\Big(1 - \frac{x}{k}\Big),$$

then (1.1)becomes the following well-known predator-prey model with Michaelis-Menten functional response [3,6].

$$\begin{cases} x'(t) = rx\Big(1 - \dfrac{x}{k}\Big) - c\dfrac{mxy}{a+x}, & x(0) > 0, \\ y'(t) = \Big(\dfrac{mx}{a+x} - d\Big)y, & y(0) > 0 \end{cases} \tag{1.2}$$

where, r, k, a, m are positive constants that stand for prey intrinsic growth rate, carrying capacity, half saturation constant, maximal predator growth rate respectively. Recently there is a growing evidences [5] that is in some situation, especially when predator have to search for food, a more suitable general predator-prey theory should be based on the

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so-called ratio-dependent theory, which can be roughly stated as that the per capita predator growth rate should be a function of the ratio of prey to predator abundance.

The system

$$
\begin{cases} x'(t) = rx\left(1 - \dfrac{x}{k}\right) - c\dfrac{mxy}{x+ay}, & x(0) > 0, \\ y'(t) = \left(\dfrac{mx}{x+ay} - d\right)y, & y(0) > 0 \end{cases} \tag{1.3}
$$

was studied by Hsu, Hwang and Kuang [7], Kuang and Beretta [2], Jost et al [1].

For the mathematical models of multiple species interaction, we studied a model of two predators competing for a single prey with ratio-dependence in [2]. Another important mathematical model of multiple species interaction is the so-called food chain model. In the paper of Freedman and Waltman [4], the authors studied the persistence a classical three species food chain model.

Mathematical models of many biological control processes naturally call for differential systems with three equations describing the growth of plant and top predator, respectively. The interaction of these three species often forms a simple food chain.

In this paper, we shall study a Michaelis-Menten (or Holling type II) functional response and its applications to biological control.

The rest of this paper is organized as follows: In section 2, we introduce the mathematical model, and we study the existence and uniqueness of solution. In section 3, we investigate the stability of the interior equilibrium E.

2. The model:

Consider the following three trophic level food chain model with ratio dependence.

$$
\begin{cases} x'(t) = rx\left(1 - \frac{x}{k}\right) - c_1\frac{xy}{a_1x+y+z} - c_2\dfrac{xz}{a_2x+y+z}, & x(0) > 0 \\ y'(t) = y\left[-d_1 + e_1\dfrac{c_1x}{a_1x+y+z}\right], & y(0) > 0 \\ z'(t) = z\left[-d_2 + e_2\dfrac{c_2x}{a_2x+y+z}\right], & z(0) > 0 \end{cases} \tag{2.1}
$$

where, x, y, z stand for the population density of prey-predator and top predator, respectively. For c_i, e_i, a_i, d_i, $i = 1, 2$ are the yield constant, maximal predator growth rates, half-saturation constants and predator's death rates respectively. r and k are the prey intrinsic growth rate and carrying capacity respectively. Observe that the simple relation of these three species: z prey on y and only on y, and y prey on x and nutrient recycling is not accounted for this simple relation produces the so-called simple food chain.

For simplicity, we non-dimensionalizes the system (2.1) with the following scaling:

$$rt \to \bar{t}, \quad \frac{x}{k} \to \bar{x}, \quad y \to \bar{y}, \quad \frac{c_i}{r} \to \bar{c}_i, \quad ka_i \to \bar{a}_i$$
$$\frac{d_i}{r} \to \bar{d}_i, \quad \frac{e_i}{k} \to \bar{e}_i.$$

Then the system (2.1) takes the form

$$(2.2) \qquad \begin{cases} x'(t) = x(1-x) - c_1 \dfrac{xy}{a_1x+y+z} - c_2 \dfrac{xz}{a_2x+y+z} \\ y'(t) = y\Big[-d_1 + c_1e_1 \dfrac{x}{a_1x+y+z}\Big] \\ z'(t) = z\Big[-d_2 + c_2e_2 \dfrac{x}{a_2x+y+z}\Big] \end{cases}$$

Rewriting system (2.2) as

$$(2.3) \qquad \begin{cases} x'(t) = F_1(x,y,z), & x(0) > 0 \\ y'(t) = F_2(x,y,z), & y(0) > 0 \\ z'(t) = F_3(x,y,z), & z(0) > 0 \end{cases}$$

The function $F_i(x,y,z)$, $i = 1,2,3$ are defined, they are continuously differentiable in the domain $\{(x,y,z) : x \geq 0, y \geq 0, z \geq 0\}$, obviously

$$\lim_{(x,y,z)\to(0,0,0)} F_i(x,y,z) = 0, \quad i = 1,2,3.$$

If we extend the domain of $F_i(x,y,z)$ to:$\{(x,y,z) : x \geq 0, y \geq 0, z \geq 0\}$, that is, if we can show that

$$\lim_{(x,y,z)\to(0,0,0)} F_i(x,y,z) = 0,$$

then $(0,0,0)$ is an equilibrium point of (2.2).

$$\lim_{(x,y,z)\to(0,0,0)} F_1(x,y,z) = \lim_{(x,y,z)\to(0,0,0)} x(1-x) - c_1 \lim_{(x,y,z)\to(0,0,0)} \frac{xy}{a_1x+y+z}$$
$$- c_2 \lim_{(x,y,z)\to(0,0,0)} \frac{xz}{a_2x+y+z}$$

let $\epsilon > 0$, we want to find $\delta > 0$ such that $\left|\frac{xy}{a_1x+y+z}\right| < \epsilon$ and $\left|\frac{xz}{a_2x+y+z}\right| < \epsilon$, whenever $0 < \sqrt{x^2+y^2+z^2} < \delta$.

$$\begin{aligned}\left|\frac{xy}{a_1x+y+z}\right| &= \frac{|x||y|}{|a_1x+y+z|} = \frac{x}{a_1x+y+z}|y|, \quad (x,y,z>0)\\ &< |y| \qquad (x < a_1x+y+z)\\ &< \sqrt{x^2+y^2+z^2}\\ \left|\frac{xz}{a_1x+y+z}\right| &< |z| < \sqrt{x^2+y^2+z^2}.\end{aligned}$$

Thus, if we choose $\delta = \epsilon$ and let $0 < \sqrt{x^2+y^2+z^2} < \delta$, then $\left|\frac{xy}{a_1x+y+z}\right| < \epsilon$, and $\left|\frac{xz}{a_2x+y+z}\right| < \epsilon$.

Hence

$$\lim_{(x,y,z)\to(0,0,0)} F_1(x,y,z) = 0.$$

Similarly

$$\lim_{(x,y,z)\to(0,0,0)} F_i(x,y,z) = 0, \qquad i = 2,3$$

Hence, we complete the $(0,0,0)$ interior equilibrium point of (2.2). Also, $(1,0,0)$ is an interior equilibrium point (2.2).

The following theorem gives conditions for the total extinction of all the three species and conditions of the extinction of both middle and top predators.

Theorem 2.1. *Assume that $e_1c_1 > d_1$ and $e_2c_2 > d_2$. If $\dfrac{c_1}{1+\delta_1} + \frac{c_2}{1+\delta_2} > 1$ and $\dfrac{x(0)}{y(0)} < \delta_1$, $\dfrac{z(0)}{y(0)} < \delta$. Then*

$$\lim_{t\to\infty}(x(t),y(t),z(t)) = (0,0,0).$$

If $c_1 + c_2 < 1$ for $d_i > 0$, $i = 1,2$. Then

$$\lim_{t\to\infty}(x(t),y(t),z(t)) = (1,0,0).$$

Proof. From the above, we have $\lim_{t\to\infty} y(t) = 0$ and $\lim_{t\to\infty} z(t) = 0$.

Assume first that $\dfrac{c_1}{1+\delta_1} + \dfrac{c_2}{1+\delta_2} > 1$ with $\dfrac{x(0)}{y(0)} < \delta_1$, $\dfrac{z(0)}{y(0)} < \delta_2$. We claim that $\dfrac{x(t)}{y(t)} < \delta_1 \ \forall t > 0$ and $\dfrac{z(t)}{y(t)} < \delta_2 \ \forall t > 0$ otherwise, there is a $t_1 > 0$ such that $\dfrac{x(t)}{y(t)} < \delta_1$,

$\frac{z(t)}{y(t)} < \delta_2$, for $t \in [0, t_1]$ and $\frac{x(t_1)}{y(t_1)} = \delta_1$, $\frac{z(t_1)}{y(t_1)} = \delta_2$. Thus for $t \in [0, t_1]$, we have

$$x'(t) < x - \frac{c_1 xy}{a_1 x + y + z} - c_2 \frac{xy}{a_2 x + y + z}$$
$$< x\left[1 - \frac{c_1}{1+\delta_1} - \frac{c_2}{1+\delta_2}\right] \quad \text{for} \quad \frac{x(0)}{y(0)} < \delta_1, \frac{z(0)}{y(0)} < \delta_2$$

and

$$y'(t) > -d_1 y, \quad z'(t) > -d_2 z,$$

which yield

$$x(t) < x(0) \exp\left[1 - \frac{c_1}{1+\delta_1} - \frac{c_2}{1+\delta_2}\right] t$$
$$y(t) > y(0) \exp[-d_1]t, \quad z(t) > z(0) \exp[-d_2]t.$$

Then

$$\frac{x(t)}{z(t)} < \frac{x(0) \exp\left[1 - \frac{c_1}{1+\delta_1} - \frac{c_2}{1+\delta_2}\right] t}{y(0) \exp[-d_1 t]} < \frac{x(0)}{y(0)} < \delta_1$$

Similarly $\frac{z(t)}{y(t)} < \delta_2$.

Then for all t, we have

$$x(t) < x(0) \exp\left[1 - \frac{c_1}{1+\delta_1} - \frac{c_2}{1+\delta_2}\right] t \to 0 \quad \text{as} \quad t \to \infty.$$

This proves that $\lim_{t\to\infty} \Big(x(t), y(t), z(t)\Big) = (0, 0, 0)$.

Also, we have

$$x'(t) > x - x^2 - c_1 x - c_2 x = x(1 - x - c_1 - c_2)$$

Simple comparison argument shows that

$$\liminf_{t\to\infty} x(t) \geq 1 - c_1 - c_2 > 0.$$

Hence for any $c_1 + c_2 > \epsilon > 0$ with $d_i > 0$, $i = 1, 2$ $y(t) \to 0$ and $z(t) \to 0$ as $t \to \infty$, we have

$$\lim_{t\to\infty} \Big(x(t), y(t), z(t)\Big) = (1, 0, 0).$$

Now, we consider the existence and uniqueness of the interior equilibrium

$$E^*(x^*, y^*, z^*), x^*, y^*, z^* > 0.$$

From equations (2.2), we have

$$(e_1 c_1 - d_1 a_1)x^* - d_1(y^* + z^*) = 0$$

and

$$(e_2c_2 - d_2a_2)x^* - d_2(y^* + z^*) = 0.$$

From the above two equations, we obtain

$$\frac{e_1c_1 - d_1a_1}{d_1} = \frac{e_2c_2 - d_2a_1}{d_2}$$

Hence

$$y^* + z^* = \frac{e_1c_1 - d_1a_1}{d_1}x^* = \frac{e_2c_2 - d_2a_2}{d_2}x^*,$$

and

$$x^*(1 + x^*) - c_1\frac{x^*y^*}{a_1x^* + y^* + z^*} - c_2\frac{x^*z^*}{a_2x^* + y^* + z^*} = 0.$$

Also,

$$\begin{aligned} x^*(1 - x^*) &= \frac{d_1}{e_1}y^* + \frac{d_2}{e_2}z^* \\ &< \frac{d_1}{e_1}(y^* + z^*) + \frac{d_2}{e_2}(y^* + z^*) \\ &= \left(\frac{d_1}{e_1} + \frac{d_2}{e_2}\right)\left(\frac{e_1c_1 - d_1a_1}{d_1}\right)x^* \end{aligned}$$

Hence

$$(1 - x^*) < \left(\frac{d_1}{e_1} + \frac{d_2}{e_2}\right)\left(\frac{e_1c_1 - d_1a_1}{d_1}\right) \tag{2.4}$$

$$x^* > 1 - \left(\frac{d_1}{e_1} + \frac{d_2}{e_2}\right)\left(\frac{e_1c_1 - d_1a_1}{d_1}\right)$$

and

$$1 > \left(\frac{d_1}{e_1} + \frac{d_2}{e_2}\right)\left(\frac{e_1c_1 - d_1a_1}{d_1}\right) \qquad (x^* > 0)$$

or

$$\frac{e_1c_1 - d_1a_1}{d_1} = \frac{e_2c_2 - d_2a_2}{d_2} < \frac{d_1}{e_1} + \frac{d_2}{e_2}.$$

□

We have the following lemma.

Lemma 2.2. *The interior equilibrium point $E^*(x^*, y^*, z^*)$ of the system (2.2) exists iff the following conditions are satisfied*

$$(2.5) \qquad \begin{cases} e_1c_1 > a_1d_1, & \text{(i)} \\ e_2c_2 > a_2d_2, & \text{(ii)} \\ \dfrac{e_1c_1 - d_1a_1}{d_1} < \dfrac{d_1}{e_1} + \frac{d_2}{e_2}. & \text{(iii)} \end{cases}$$

Also, we need the following lemma

Lemma 2.3. *The solution $x(t), y(t)$ and $z(t)$ of (2.2) are positive and bounded for all $t \geq 0$.*

Proof. Obviously the solutions $x(t), y(t), z(t)$ are positive for $t \geq 0$ and given any $0 < \epsilon < 1$, $x(t) \leq 1 + \epsilon$ for t sufficiently large.

From (2.2), it follows that

$$x' + \frac{y'}{e_1} + \frac{z'}{e_2} = x(1-x) - \frac{d_1}{e_1}y - \frac{d_2}{e_2}z.$$

Since $x - x^2 \leq x$ and let $d = \min\{d_1, d_2\}$, hence

$$\begin{aligned} x' + \frac{y'}{e_1} + \frac{z'}{e_2} &\leq x - d\left(\frac{y}{e_1} + \frac{z}{e_2}\right) \\ &= x - d\left(x + \frac{y}{e_1} + \frac{z}{e_2}\right) + xd \\ &= (1+d)x - d\left(x + \frac{y}{e_1} + \frac{z}{e_2}\right) \\ &\leq (1+d)(1+\epsilon) - d\left(x + \frac{y}{e_1} + \frac{z}{e_2}\right) \\ &= \xi - d\left(x + \frac{y}{e_1} + \frac{z}{e_2}\right), \end{aligned}$$

where

$$\xi = (1+d)(1+\epsilon).$$

But

$$\left(x + \frac{y}{e_1} + \frac{z}{e_2}\right) + d\left(x + \frac{y}{e_1} + \frac{z}{e_2}\right) = \xi.$$

Hence

$$\left(x + \frac{y}{e_1} + \frac{z}{e_2}\right) \leq \frac{\xi}{d} + \epsilon,$$

for sufficiently large t. Hence $x(y), y(t)$ and $z(t)$ are bounded. $\square$

If the death rate of top predator is no less than its maximum birth rate, we have the following lemma

Lemma 2.4. *If* $e_1c_1 \leq a_1d_1$ *and* $e_2c_2 \leq a_2d_2$*, then* $\lim_{t\to\infty} y(t) = 0$ *and* $\lim_{t\to\infty} z(t) = 0$.

Proof. From (2.2), we have

$$y' = -y\left[\frac{(a_1d_1 - e_1c_1)x + d_1(z+y)}{a_1x + y + z}\right].$$

This leads to $y' < 0$, thus $y(t)$ is decreasing and positive. Hence $\lim_{t\to\infty} y(t)$ exists and nonnegative, we claim $\lim_{t\to\infty} y(t) = 0$. Otherwise, there is a positive constant η, such that $\lim_{t\to\infty} y(t) = \eta$. Given that $\eta > \epsilon > 0$, there exist $t_0 > 0$, such that

$$|y(t) - \eta| \leq \epsilon \quad \text{for} \quad t > t_0$$

Since

$$\frac{x+y}{a_1x + y + z} < 1.$$

Then

$$\frac{y'}{y} = \frac{-a_1d_1x + e_1c_1x - d_1(y+z)}{a_1x + y + z} = \frac{-d_1(y+z)}{a_1x + y + z} < -d_1.$$

Then

$$y(t) < y(t_0)\exp[-d(t - t_0)].$$

As $t \to \infty$, we have $y(t) < 0$, which is a contradiction.
Hence

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

Similarly, we can prove

$$\lim_{t\to\infty} z(t) = 0.$$

□

3. Stability of E^*:

In this section, we assume that E^* exist and we shall study its local stability. The variational matrix of (2.2) at E^* is given by

$$M|_{E^*} = \begin{bmatrix} m_{11} & m_{12} & m_{13} \\ m_{21} & m_{22} & m_{23} \\ m_{31} & m_{32} & m_{33} \end{bmatrix}$$

where

$$m_{11} = -x^* + \frac{d_1^2}{e_1^2}\frac{a_1}{c_1}\frac{y^*}{c^*} + \frac{d_2^2}{e_2^2}\frac{a_2}{c_2}\frac{z^*}{c^*}$$

$$m_{12} = -\frac{d_1}{e_1} + \frac{d_1^2}{e_1^2}\frac{y^*}{c_1 x^*} + \frac{d_2^2}{e_2^2}\frac{z^*}{c_2 x^*}$$

$$m_{13} = \frac{d_1^2}{c_1^2}\frac{y^*}{c_1 x^*} - \frac{d_2}{e_2} + \frac{d_2^2}{e_2^2}\frac{z^*}{c_2 x^*}$$

$$m_{21} = d_1\frac{y^*}{x^*} - \frac{d_1^2}{e_1}\frac{a_1}{c_1}\frac{y^*}{x^*} = \frac{d_1 y^*}{c^*}\left(1 - \frac{d_1 a_1}{e_1 c_1}\right), \quad (m_{21} > 0)$$

$$m_{22} = m_{23} = -\frac{d_1^2}{e_1}\frac{y^*}{c_1 x^*} \qquad (m_{22}, m_{23} < 0)$$

$$m_{31} = d_2\frac{z^*}{x^*} - \frac{d_2^2}{e_2}\frac{a_2}{c_2}\frac{z^*}{x^*} = \frac{d_2 z^*}{x^*}\left(1 - \frac{d_2 a_2}{e_2 c_2}\right), \quad (m_{31} > 0)$$

$$m_{32} = m_{33} = -\frac{d_2^2}{e_2}\frac{z^*}{c_2 x^*}$$

The characteristic equation of M is

$$\begin{aligned} f(\lambda) &= \det(M - \lambda I) = 0 \\ &= -\lambda^3 + \lambda^2(m_{11} + m_{22} + m_{33}) \\ &\quad + \lambda(-m_{11}m_{22} - m_{11}m_{33} - m_{22}m_{33} + m_{32}m_{23} + m_{21}m_{12} + m_{31}m_{13}) \\ &\quad + (m_{11}m_{22}m_{33} - m_{11}m_{32}m_{23} - -m_{12}m_{21}m_{33} + m_{12}m_{23}m_{31} \\ &\qquad\qquad + m_{13}m_{21}m_{32} - m_{31}m_{22}m_{13}) \end{aligned}$$

Then the roots λ of $f(\lambda) = 0$ satisfy

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0 \tag{3.1}$$

where

$$\begin{aligned} A_1 &= -(m_{11} + m_{22} + m_{33}) \\ A_2 &= m_{11}m_{22} + m_{11}m_{33} - m_{21}m_{12} - m_{31}m_{13} \\ A_3 &= (m_{33}m_{21} + m_{22}m_{31})(m_{12} - m_{13}) \end{aligned}$$

By the Routh-Huruitz criterion, a set of necessary and sufficient conditions for all the roots of (3.1) to have negative real pats is

$$A_1 > 0, \quad A_3 > 0 \quad \text{and} \quad A_1A_2 > A_3. \tag{3.2}$$

In the folowing Theorem, a sufficient condition is given for the local stability of E^*.

Theorem 3.1. *If $m_{11} < 0, m_{12} < 0, m_{13} < 0$ and $m_{12} < m_{13}$. Then E^* is locally asymptotically stable.*

Proof. It is easy to verify $A_i > 0$, $i = 1, 2, 3$, if $m_{11} < 0, m_{12} < 0, m_{13} < 0, m_{12} < m_{13}$ and calculate $A_1 A_2 - A_3$, then

$$\begin{aligned} A_1 A_2 - A_3 = & -m_{11}^2 m_{22} - m_{11}^2 m_{33} + m_{11} m_{21} m_{12} + m_{11} m_{31} m_{13} - m_{11} m_{21}^2 \\ & - m_{11} m_{22} m_{33} + m_{22} m_{21} m_{13} + m_{22} m_{31} m_{13} - m_{11} m_{33} m_{22} \\ & - m_{11} m_{33}^2 + m_{33} m_{13} m_{31} - (m_{33} m_{21} + m_{22} m_{31})(m_{12} - m_{13}) \\ & - m_{22} m_{31} m_{12} + m_{33} m_{21} m_{13} + m_{22} m_{31} m_{13} \\ & + m_{22} m_{31}(2m_{13} - m_{12} > 0. \end{aligned}$$

Hence E^* is local asymptotically stable. □

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