Global Dynamics in a Stoichiometric Food Chain Model with Two Limiting Nutrients

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Abstract

Ecological stoichiometry studies the balance of energy and multiple chemical elements in ecological interactions to establish how the nutrient content affect food-web dynamics and nutrient cycling in ecosystems. In this study, we formulate a food chain with two limiting nutrients in the form of a stoichiometric population model. A comprehensive global analysis of the rich dynamics of the targeted model is explored both analytically and numerically. Chaotic dynamic is observed in this simple stoichiometric food chain model and is compared with traditional model without stoichiometry. The detailed comparison reveals that stoichiometry can reduce the parameter space for chaotic dynamics. Our findings also show that decreasing producer production efficiency may have only a small effect on the consumer growth but a more profound impact on the top predator growth.

Keywords: stoichiometry; predator-prey system; food quality; C:P ratio

1. Introduction

Ecological stoichiometry is the study of the balance of energy (usually represented by carbon) and multiple chemical elements (such as phosphorus, nitrogen) in ecological interactions [1]. Most ecological studies have until recently overlooked the sources and consequences of this chemical heterogeneity. The stoichiometric ratios of elements, such as carbon and phosphorus, have complex dynamics as they vary within and across trophic levels. Since all organisms are structurally composed of multiple chemical elements combined in certain proportions, it is natural to incorporate the effects of food quality, as well as quantity into ecological modeling.

A wide variety of stoichiometric population models have been proposed and analyzed in recent years describing the intriguing effects of variable prey quantity and quality on the predator growth [2, 3, 4, 5]. Many of these models are related to or based on the so-called LKE model, a concise and elegant two-dimensional Lotka-Volterra type model that incorporates chemical heterogeneity of the first two trophic levels of a food chain by Loladze, Kuang and Elser [6]. The model was named as LKE model by an abbreviation for the three authors Loladze, Kuang, and Elser to distinguish from other similar models [7]. Compared with the traditional Lotka-Volterra type model, the production efficiency in LKE model is described by a minimum function due to the limitations of energy and nutrient conversion. Mathematically, the presence of minimum functions in LKE type models embodies richer dynamics and presents many challenges for the study of the global dynamics of stoichiometric models.

In ecology, competition contributes much to the structure and function of communities and is also well studied in the context of ecological stoichiometry as predation. Stoichiometry

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has been widely investigated in the competition model. For example, Loladze et al. [8] and Miller et al. [9] proposed some stoichiometric models to analyze the competition between two predators exploiting one autotrophic prey and two-patch consumer-resource systems. Competition models incorporating stoichiometry via the effects of low nutrient food content can be meaningful in explaining biodiversity and providing a mechanism for deterministic extinction.

Chaotic dynamics often appear in high-dimensional models incorporating competition interaction. For example, Huisman and Weissing [10] used a high dimensional model incorporating multiple resources and species to show that the resource competition model can generate oscillations and chaos when species compete for three or more resources. The stoichiometric competition model of two predators and one prey in Deng and Loladze [11] and Wang et al. [12] exhibited chaotic coexistence of the competing species. Yamamichi et al. [13] studied a quantitative genetic model and found that the rapid evolution of the consumer stoichiometric trait can lead to chaotic dynamics.

Peace [14] presents a natural extension of the LKE model to three trophic levels and investigates thoroughly the effects of light and nutrient availability on ecological transfer efficiencies. The LKE type simple food chain model studied in [14] not only confirms that food chain efficiency is lower in tritrophic food chains than ditrophic food chains and consumer efficiency is lower in the presence of predation constraints, but also reveals that in fixed low nutrient environments, food chain efficiency is highest in light level conditions such that the primary producer and consumer have similar stoichiometric compositions, while in fixed high nutrient environments, food chain efficiency is highest for intermediately low light levels such that the phosphorus:carbon ratio of the primary producer is higher than the phosphorus:carbon ratio of the consumer.

Even though food quality plays an important role in determining consumer productivity, most existing food chain models neglect stoichiometric constraints. Hastings and Powell studied chaos in a three-species food chain model without stoichiometry [15]. In this paper, we would like to compare and contrast in greater details the dynamics between the model with stoichiometry proposed in [14] and the traditional non-stoichiometric food chain models proposed in [15]. We also try to explore the parameter space systematically. Moreover, the effect of stoichiometry on the chaotic behavior in food chain model is unclear and deserves more attention. Motivated by these considerations, the principal aim of this study is to better elucidate the complex dynamics of the food chain model that takes into account the effect of stoichiometry, the food quality on the population growth, and the flow of energy across multiple trophic levels.

The remainder of this paper is organized as follows. In Section 2, we provide justifications for the formulation of the simple LKE type food chain model studied in [14]. In Section 3, we present a preliminary mathematical analysis of the model. In Section 4, we conduct a systematic numerical simulations about the internal equilibria and bifurcation analysis of this model. We end this paper with a discussion section containing some biological implications of our mathematical findings and computational observations.

2. The model

In this study, we model a closed ecological system consisting of three trophic levels: producer, consumer, and a top predator. We can think of the producer as phytoplankton, the consumer as zooplankton, and predator as fish. All are placed in a well-mixed system open only to light

and air. In the model construction, we follow a course outlined in [6], which deals with one consumer-one prey interactions.

Let us start with a conventional model of MacArthur-Rosenzweig type, which describes a system of three trophic levels of a food chain, which is similar with model in [15]

$$\begin{aligned}\frac{dx}{dt} &= bx \left(1 - \frac{x}{K}\right) - f(x)y, \\ \frac{dy}{dt} &= e_y f(x)y - g(y)z - d_y y, \\ \frac{dz}{dt} &= e_z g(y)z - d_z z.\end{aligned}\tag{2.1}$$

Here $x(t)$, $y(t)$ and $z(t)$ represent the biomass of the producer, consumer, and predator, respectively, measured in terms of C (carbon). b is the maximum growth rate of the producer. d_y and d_z are the loss rate of consumer and predator respectively. The consumer's ingestion rate, $f(x)$ is taken to be a monotonic increasing and bounded differentiable function, $f'(x) > 0$ and $f''(0) < 0$ with $\lim_{x \rightarrow \infty} f(x) = \hat{f}$, where $\hat{f}$ is a constant. $g(y)$ represents the predator's ingestion rate, which we assume to be similar to Holling type II functional response (Monod or Michaelis-Menten type functions), which has the same properties as $f(x)$. e_y and e_z are the maximum production efficiencies of the consumer and predator. The second law of thermodynamics requires that $e_y < 1$ and $e_z < 1$. K is the producer carrying capacity in terms of C and represents the light intensity. Suppose that we fix light intensity at a certain value and let the producer grow without the consumer and with ample nutrients. Then producer density will increase until self-shading ultimately stabilizes it at some value, K . Thus, every K value corresponds to a specific limiting light intensity and we might model the influence of higher light intensity as having the effect of raising K [6].

For simplicity, in addition to C, we consider only one more chemical element: P (phosphorus). The choice of C is clear, because this element comprises the bulk of the dry weight of the most organisms. Instead of P, however, one can choose any other element as long as it is essential to all species in the system (e.g. nitrogen, sulfur, or calcium) [8]. Using only two elements is a gross simplification of reality, but it is a qualitative step forward from conventional 'chemically homogeneous' models like model (2.1). Most importantly, the inclusion of just two elements allows us to explicitly model producer quality by applying the mass balance law.

We express the above considerations in the following assumptions:

ASSUMPTION 1. The total mass of phosphorus in the entire system is fixed, i.e., the system is closed for phosphorus with a total of P_T (mgPL⁻¹).

The following important stoichiometric principles lead to the next assumption. Every organism requires at least a certain, species-specific, fraction of phosphorus in their biomass. We say 'at least', because in producers P : C can vary significantly within a species. For example, the green algae *Scenedesmus acutus* can have cellular P : C ratios (by mass) that range from 1.6×10^{-3} to 13×10^{-3} . In animals, P : C varies much less within a species. For example, *Daphnia*'s somatic elemental composition appears to be homeostatically regulated within narrow bounds (P : C around 31×10^{-3} by mass), even when food P : C diverges strongly [16].

ASSUMPTION 2. Producer's P : C varies, but never falls below a minimum q (mgP/mgC); consumer and predator maintain a constant P : C, θ_y and θ_z (mgP/mgC), respectively.

ASSUMPTION 3. All phosphorus in the system is divided into three pools: phosphorus in the consumer and predator and the rest as P potentially available for producer.

From these two assumptions it follows that P available for the producer at any given time is $P_T - \theta_y y - \theta_z z$ (mgP)/L. Recalling that P : C in the producer should be at least q (mgP/mgC), one obtains that the producer density cannot exceed $(P_T - \theta_y y - \theta_z z)/q$ (mgC)/L. In the spirit of Liebig's Law of the Minimum, the combination of light and P limits the carrying capacity of the producer to

$$\min \left(K, \frac{P_T - \theta_y y - \theta_z z}{q} \right). \quad (2.2)$$

Next, we show how stoichiometry brings 'food quality' into the model and affects production efficiency of the consumer and predator.

While producer stoichiometry varies, by Assumption 2 consumer and predator must maintain a specific P : C, θ_y and θ_z , respectively. Following [17], we say that the producer is optimal food for the consumer if its P : C is equal to or greater than θ_y . 'Optimal' here means that the grazer is able to maximally utilize the energy (carbon) content of consumed food, 'wasting' any excess of phosphorus it ingests. Thus, we replace the constant production efficiency e_y and e_z in model (2.1) by the following parameter: $\hat{e}_y$ and $\hat{e}_z$. These are the maximal production efficiency which are achieved if the consumer and predator uptake food of optimal quality. Due to thermodynamic limitations, $\hat{e}_y < 1$ and $\hat{e}_z < 1$.

The producer P content varies as $(P_T - \theta_y y - \theta_z z)/x$. If the producer's P : C $> \theta_y$, then the consumer converts consumed producer with the maximal (in C terms) efficiency $\hat{e}_y$ and egests any excess of ingested P. If the producer's P : C $< \theta_y$, then the consumer will be unable to fully utilize all the C ingested. This reduces the growth efficiency in C terms. Hence, production efficiency is not a constant, but depends on both energetic and nutrient limitations. The following minimum function provides the simplest way to capture such effects of variable producer quality on consumers' growth efficiency

$$\hat{e}_y \min \left(1, \frac{(P_T - \theta_y y - \theta_z z)/x}{\theta_y} \right). \quad (2.3)$$

Similar to the consumer's growth efficiency, we also obtain a minimum function describing the effect of consumer quality on predator's growth efficiency as follows,

$$\hat{e}_z \min \left(1, \frac{\theta_y}{\theta_z} \right). \quad (2.4)$$

Notice that (2.4) is simpler than (2.3). This is because the production efficiency of the predator is constant due to the assumption that both the consumer and the predator species maintain a specific value of P : C. If $\theta_y > \theta_z$, then the consumer's quality does not reduce the production efficiency. If $\theta_y < \theta_z$, then the predator will not be able to fully utilize the consumed C and grow at the reduced rate $\hat{e}_z \frac{\theta_y}{\theta_z}$.

Finally, we incorporate the variable carrying capacity (2.2) and the modified production

Table 1: Parameters of model (2.5) with default values

Parameter	Description	Values	Unit
P_T	Total phosphorus	0.12	mgPL ⁻¹
$\hat{e}_y$	Maximal production efficiency in carbon terms for consumer	0.8	
$\hat{e}_z$	Maximal production efficiency in carbon terms for predator	0.75	
b	Maximal growth rate of the producer	1.2	day ⁻¹
d_y	Consumer loss rate (include respiration)	0.25	day ⁻¹
d_z	Predator loss rate (include respiration and predation)	0.003	day ⁻¹
θ_y	Consumer constant P : C	0.03	mgP/mgC
θ_z	Predator constant P : C	0.013	mgP/mgC
q	Producer minimal P : C	0.0038	mgP/mgC
c_1	Maximum ingestion rate of the consumer	0.81	day ⁻¹
a_1	Half-saturating of consumer	0.25	mgCL ⁻¹
c_2	Maximum ingestion rate of the predator	0.03	day ⁻¹
a_2	Half-saturating of predator	0.75	mgCL ⁻¹
K	Producer carrying capacity limited by light	0 – 10	mgCL ⁻¹

Notes: The parameters correlated with producer (e.g. phytoplankton) and consumer (e.g. zooplankton) were selected from [18] and [19]. The parameters correlated with predator (e.g. fish) are chosen from [20] and [21].

efficiency (2.3) and (2.4) into model (2.1), resulting in:

$$\begin{aligned}
\frac{dx}{dt} &= bx \left(1 - \frac{x}{\min(K, (P_T - \theta_y y - \theta_z z)/q)} \right) - f(x)y, \\
\frac{dy}{dt} &= \hat{e}_y \min \left(1, \frac{(P_T - \theta_y y - \theta_z z)/x}{\theta_y} \right) f(x)y - g(y)z - d_y y, \\
\frac{dz}{dt} &= \hat{e}_z \min \left(1, \frac{\theta_y}{\theta_z} \right) g(y)z - d_z z.
\end{aligned} \tag{2.5}$$

This is the LKE type simple food chain model studied in [14]. When $z = 0$, model (2.5) becomes the LKE model [6]. The parameter values are listed in Table 1.

In the following sections, we investigate the consequences of the assumptions made in order to gain biological insights.

3. Qualitative analysis

3.1. Preliminaries

The boundedness and positive invariance of the solutions of (2.5) are assured by the following theorem, which demonstrates that (2.5) is biologically well defined.

Theorem 3.1. *Solutions with initial conditions in the closed triangular truncated cone (or triangular pyramid if $K \geq P/q$) (Fig. 1)*

$$\Delta = \{(x, y, z) : 0 \leq x \leq k, 0 \leq y \leq P_T/\theta_y, 0 \leq z \leq P/\theta_z, qx + \theta_y y + \theta_z z \leq P_T\}$$

Figure 1: Positively invariant set Δ of (2.5). (a) $K \geq P_T/q$ and Δ is a triangular pyramid. (b) $K < P_T/q$ and Δ is a triangular truncated cone. Here the plane, $\theta_y x + \theta_y y + \theta_z z = P_T$, divides Δ into two regions.

1 remain there for all forward time, where $k = \min(K, P_T/q)$.

2 *Proof.* Let $S(t) = (x(t), y(t), z(t))$ be a solution of (2.5) with $S(0) \in \Delta$. Assume that there
 3 exists a time $t_1 > 0$ such that $S(t_1)$ touches or crosses a boundary of Δ for the first time. The
 4 following cases prove the theorem by contradiction.

5 Case 1. $x(t_1) = 0$.

6
 7 Let $f'(0) = \lim_{x \rightarrow 0} \frac{f(x)}{x}$ and $\bar{y} = \max_{t \in [0, t_1]} y(t) < P_T/\theta_y$. Then, for every $t \in [0, t_1]$, one has

$$\begin{aligned} \frac{dx}{dt} &= bx \left(1 - \frac{x}{\min(K, (P_T - \theta_y y - \theta_z z)/q)} \right) - f(x)y \\ &\geq -f(x)y \geq -\max_{t \in [0, t_1]} \frac{f(x)}{x} \bar{y} x \equiv \alpha x. \end{aligned}$$

11 This implies that $x(t_1) \geq x(0)e^{\alpha t_1} > 0$, where α is a constant. This contradicts $x(t_1) = 0$ and
 12 proves that $S(t_1)$ does not reach this boundary.

13 Case 2. $y(t_1) = 0$.

14 Let $g'(0) = \lim_{y \rightarrow 0} g(y)/y$ and $\bar{z} = \max_{t \in [0, t_1]} z(t) < P_T/\theta_z$. Then, for every $t \in [0, t_1]$, we have

$$\begin{aligned} \frac{dy}{dt} &= \hat{e}_y \min \left(1, \frac{(P_T - \theta_y y - \theta_z z)/x}{\theta_y} \right) f(x)y - g(y)z - d_y y \\ &\geq -g(y)z - d_y y \geq - \left(\max_{t \in [0, t_1]} \frac{g(y)}{y} \bar{z} + d_y \right) y \equiv \beta y. \end{aligned}$$

18 This implies that $y(t_1) \geq y(0)e^{\beta t_1} > 0$, where β is a constant. This contradicts $y(t_1) = 0$ and
 19 proves that $S(t_1)$ does not reach this boundary.

20 Case 3. $z(t_1) = 0$.

21 For every $t \in [0, t_1]$, one has

$$\frac{dz}{dt} = \hat{e}_z \min \left(1, \frac{\theta_y}{\theta_z} \right) g(y)z - d_z z \geq -d_z z.$$

This implies that $z(t_1) \geq z(0)e^{-d_z t_1} > 0$. This contradicts $z(t_1) = 0$ and proves that $S(t_1)$ does not reach this boundary.

Case 4. $qx(t_1) + \theta_y y(t_1) + \theta_z z(t_1) = P_T$.

From the fact that

$$bx \left(1 - \frac{x(t_1)}{\min(K, (P_T - \theta_y y(t_1) - \theta_z z(t_1))/q)} \right) \leq bx \left(1 - \frac{x(t_1)}{(P_T - \theta_y y(t_1) - \theta_z z(t_1))/q} \right) = 0,$$

$0 < \hat{e}_y, \hat{e}_z < 1$, and $\min(\theta_y, q) \leq q$, it follows that

$$\begin{aligned} \frac{d(qx + \theta_y y + \theta_z z)}{dt} \Big|_{t=t_1} &= qx'(t_1) + \theta_y y'(t_1) + \theta_z z'(t_1) \\ &\leq y(t_1)[(\hat{e}_y \min(\theta_y, q) - q)f(x(t_1)) - \theta_y d_y] \\ &\quad + z(t_1)[(\hat{e}_z \min(\theta_y, \theta_z) - \theta_y)g(y(t_1)) - \theta_z d_z] \leq 0. \end{aligned}$$

Thus, $S(t_1)$ can not cross this boundary.

Case 5. $x(t_1) = k$.

For every $t \in [0, t_1]$, we have

$$\begin{aligned} \frac{dx}{dt} &= bx \left(1 - \frac{x}{\min(K, (P_T - \theta_y y - \theta_z z)/q)} \right) - f(x)y \\ &\leq bx \left(1 - \frac{x}{\min(K, (P_T - \theta_y y - \theta_z z)/q)} \right) \\ &\leq bx \left(1 - \frac{x}{\min(K, P_T/q)} \right) \\ &= bx \left(1 - \frac{x}{k} \right). \end{aligned}$$

Then $x(t_1) \leq k$ by a standard comparison argument, thus $S(t_1)$ can not cross this boundary.

To conclude, the set Δ is positively invariant with respect to (2.5). $\square$

To simplify the following analysis, we rewrite (2.5) in the following form,

$$\frac{dx}{dt} = xF(x, y, z), \quad \frac{dy}{dt} = yG(x, y, z), \quad \frac{dz}{dt} = zH(x, y, z), \quad (3.1)$$

where

$$\begin{aligned} F(x, y, z) &= b \left(1 - \frac{x}{\min(K, (P_T - \theta_y y - \theta_z z)/q)} \right) - \frac{f(x)}{x}y, \\ G(x, y, z) &= \hat{e}_y \min \left(1, \frac{(P_T - \theta_y y - \theta_z z)/x}{\theta_y} \right) f(x) - \frac{g(y)}{y}z - d_y, \\ H(x, y, z) &= \hat{e}_z \min \left(1, \frac{\theta_y}{\theta_z} \right) g(y) - d_z. \end{aligned}$$

Partial derivatives of $F(x, y, z)$, $G(x, y, z)$ and $H(x, y, z)$ are listed as follows,

$$\begin{aligned}
F_x &= \frac{\partial F}{\partial x} = -\frac{b}{\min(K, (P_T - \theta_y y - \theta_z z)/q)} - \left(\frac{f(x)}{x}\right)' y, \\
F_y &= \frac{\partial F}{\partial y} = \begin{cases} -\frac{f(x)}{x} < 0, & qK + \theta_y y + \theta_z z < P_T, \\ -\frac{bq\theta_y x}{(P_T - \theta_y y - \theta_z z)^2} - \frac{f(x)}{x} < 0, & qK + \theta_y y + \theta_z z > P_T, \end{cases} \\
F_z &= \frac{\partial F}{\partial z} = \begin{cases} 0, & qK + \theta_y y + \theta_z z < P_T, \\ -\frac{bq\theta_z x}{(P_T - \theta_y y - \theta_z z)^2} < 0, & qK + \theta_y y + \theta_z z > P_T, \end{cases} \\
G_x &= \frac{\partial G}{\partial x} = \begin{cases} \hat{e}_y f'(x) > 0, & \theta_y x + \theta_y y + \theta_z z < P_T, \\ \hat{e}_y \frac{P_T - \theta_y y - \theta_z z}{\theta_y} \left(\frac{f(x)}{x}\right)' < 0, & \theta_y x + \theta_y y + \theta_z z > P_T, \end{cases} \\
G_y &= \frac{\partial G}{\partial y} = \begin{cases} -\left(\frac{g(y)}{y}\right)' z > 0, & \theta_y x + \theta_y y + \theta_z z < P_T, \\ -\hat{e}_y \frac{f(x)}{x} - \left(\frac{g(y)}{y}\right)' z, & \theta_y x + \theta_y y + \theta_z z > P_T, \end{cases} \\
G_z &= \frac{\partial G}{\partial z} = \begin{cases} -\frac{g(y)}{y} < 0, & \theta_y x + \theta_y y + \theta_z z < P_T, \\ -\hat{e}_y \frac{\theta_z f(x)}{\theta_y x} - \frac{g(y)}{y} < 0, & \theta_y x + \theta_y y + \theta_z z > P_T, \end{cases} \\
H_x &= \frac{\partial H}{\partial x} = 0, \\
H_y &= \frac{\partial H}{\partial y} = \hat{e}_y \min\left(1, \frac{\theta_y}{\theta_z}\right) g'(y) > 0, \\
H_z &= \frac{\partial H}{\partial z} = 0.
\end{aligned}$$

To determine the local stability of these equilibria, we consider the Jacobian of (3.1)

$$J(x, y, z) = \begin{pmatrix} F + xF_x(x, y, z) & xF_y(x, y, z) & xF_z(x, y, z) \\ yG_x(x, y, z) & G + yG_y(x, y, z) & yG_z(x, y, z) \\ zH_x(x, y, z) & zH_y(x, y, z) & H + zH_z(x, y, z) \end{pmatrix}.$$

3.2. Equilibria on the boundary

To find equilibria, we solve

$$xF(x, y, z) = 0, \quad yG(x, y, z) = 0, \quad zH(x, y, z) = 0. \quad (3.2)$$

The boundary equilibria are $E_0(0, 0, 0)$, $E_1(k, 0, 0)$, and $E_2(\bar{x}, \bar{y}, 0)$.

At the origin, the Jacobian matrix takes the form

$$J(E_0) = \begin{pmatrix} b & 0 & 0 \\ 0 & -d_y & 0 \\ 0 & 0 & -d_z \end{pmatrix}.$$

It is easy to see the eigenvalues have different signs. Thus, E_0 is always unstable. This implies that a complete collapse of (2.5) is impossible.

At E_1 , the Jacobian matrix is

$$J(E_1) = \begin{pmatrix} -b & kF_y(k, 0, 0) & kF_z(k, 0, 0) \\ 0 & \hat{e}_y \min\left(1, \frac{P_T}{k\theta_y}\right) f(k) - d_y & 0 \\ 0 & 0 & -d_z \end{pmatrix}.$$

If $G(k, 0, 0) = \hat{e}_y \min(1, \frac{P_T}{k\theta_y})f(k) - d_y > 0$, then E_1 is unstable. If $G(k, 0, 0) < 0$, i.e., $d_y > \hat{e}_y \min(1, \frac{P_T}{k\theta_y})f(k)$, then E_1 is locally asymptotically stable; Biologically, it implies that, when the consumer's death rate is larger than its growth rate, the consumer dies out, and the predator goes extinct, and finally the producer tends to its minimum carrying capacity k (considering the combining effect of light and nutrient).

Figure 2: Stoichiometry confined feasible region of (2.5) in phase space: the truncated triangular pyramid case. In Region I, the consumer's growth is limited by the food quantity just as that in the classical Lotka-Volterra. In Region II, the consumer's growth is constrained by the food quality (producer's $P : C$). In particular, $E_2(\bar{x}, \bar{y}, 0)$ can be studied in the $x-y$ phase plane. Competition for P between the consumer and the producer alters their interactions from $(+, -)$ in Region I to $(-, -)$ in Region II. This bends the consumer nullcline in Region II. This shape of the consumer nullcline, with two x -intercepts, creates the potential for multiple positive steady states. A solid circle denotes a stable equilibrium and a clear circles represents an unstable equilibrium.

The boundary equilibrium $E_2(\bar{x}, \bar{y}, 0)$ indicates the extinction of the predator. Thus E_2 can be viewed as the internal equilibrium of the degenerating simpler two-dimensional system only with one consumer on one producer. $E_2(\bar{x}, \bar{y}, 0)$ can be studied in the $x-y$ phase plane. As we see in Fig. 2, the producer nullcline is hump shaped, a usual feature of many predator-prey models. The consumer nullcline, however, has an unusual shape of a right triangle (in conventional consumer-resource models, it is a vertical line or an increasing curve). Here, multiple equilibria are possible because two nullclines with such shapes can intersect more than once. It is not difficult to find that the intersections are all below the peak of the

consumer nullcline. Simple computation produces

$$\bar{y} \leq \bar{y}_{max} = \frac{P_T}{\theta_y} - f^{-1}\left(\frac{d_y}{\hat{e}_y}\right).$$

Then the following two inequalities provide sufficient criteria for the existence of E_2 :

$$G(k, 0, 0) = \hat{e}_y \min\left(1, \frac{P}{k\theta_y}\right) f(k) - d_y > 0 \quad (3.3)$$

and

$$H(\bar{x}, \bar{y}_{max}, 0) = \hat{e}_z \min\left(1, \frac{\theta_y}{\theta_z}\right) g(\bar{y}_{max}) - d_z < 0. \quad (3.4)$$

In fact, (3.3) indicates that the consumer's growth rate is larger than its death rate, which ensures the survival of the consumer. (3.4) reveals that, even with a sufficiently large biomass of the consumer, the predator's death rate is greater than its growth rate and hence the predator can not survive. These two conditions together ensure the existence of E_2 . When (3.3) and (3.4) are satisfied, the stability of E_2 can be analyzed by using the method of nullclines in [6]. The stability type of an equilibrium can sometimes be determined by the way nullclines intersect. In Region I, the internal equilibrium is locally asymptotically stable if the producer nullcline crossing it is decreasing; if the producer nullcline crossing it is increasing, then the equilibrium is a repeller. In Region II, any internal equilibrium is locally asymptotically stable if the producer nullcline crossing it declines steeper than the grazer's; otherwise, the equilibrium is a saddle.

3.3. Internal equilibria

If system (2.5) has an internal equilibrium $E^*(x^*, y^*, z^*)$, then it satisfies $F(x^*, y^*, z^*) = 0$, $G(x^*, y^*, z^*) = 0$ and $H(x^*, y^*, z^*) = 0$. To determine the type of species interactions occurring at this equilibrium, it is convenient to examine the Jacobian matrix at E^* which takes the following form,

$$J(x^*, y^*, z^*) = \begin{pmatrix} x^* & 0 & 0 \\ 0 & y^* & 0 \\ 0 & 0 & z^* \end{pmatrix} A(x^*, y^*, z^*).$$

where

$$A(x^*, y^*, z^*) = \begin{pmatrix} F_x & F_y & F_z \\ G_x & G_y & G_z \\ H_x & H_y & H_z \end{pmatrix}$$

is the ecosystem matrix of our system. Due to the complexity of the system (2.5), we can not study the stability of positive equilibrium routinely by Routh-Hurwitz criteria but only via qualitative analysis by ecosystem matrix. In this matrix, the ij -th term measures the effect of the j -th species on the i -th species's per capita growth rate.

If the producer quality is good for consumer, i.e. $(P_T - \theta_y y^* - \theta_z z^*)/x^* > \theta_y$, then the ecosystem matrix at E^* takes the following form

$$\begin{pmatrix} +/- & - & - \\ + & +/- & - \\ 0 & + & 0 \end{pmatrix},$$

which means that the interaction between the consumer and the producer is of conventional $(+, -)$ type.

If the producer quality is bad for the consumer, i.e. $(P_T - \theta_y y^* - \theta_z z^*)/x^* < \theta_y$, then the ecosystem matrix takes the form

$$\begin{pmatrix} +/ - & - & - \\ - & +/ - & - \\ 0 & + & 0 \end{pmatrix},$$

which implies that the interaction between the consumer and the producer is changed from the traditional $(+, -)$ to $(-, -)$, that is, the producer and the consumer compete with each other and the competition lies in two species not only internally but also interspecifically for the limited P content. The increase of the producer with bad quality will not promote the consumer's growth.

An unusual and important property of (2.5) is that the sign of $\partial G / \partial x$ changes from positive to negative as soon as the producer's P : C is less than that of the consumer's. This negative derivative means that, higher producer density reduces the growth rate of consumer. If the quality of producer is bad, then any further increase in the producer's density deteriorates the quality of producer, which offsets the benefit provided by the higher producer density to the consumer that has already been limited by P. This effect is in sharp contrast to many conventional population dynamics models.

4. Numerical simulation

In order to numerically well illustrate the interactions among three trophic levels and to deepen the analysis of (2.5), we choose the functional response as a Monod (Michaelis-Menten or Holling type II functional response) type function, i.e.,

$$f(x) = \frac{c_1 x}{a_1 + x}, \quad g(y) = \frac{c_2 y}{a_2 + y}.$$

The parameter values are listed in Table 1. These values were mainly selected from [18] and [19] and have been applied by [6] and [22] for guidance in setting parameters at biologically realistic values. The parameters correlated with the predator (e.g. fish) are chosen from [20] and [21]. We use the same initial value with $x(0) = 0.5 \text{ mgCL}^{-1}$, $y(0) = 0.5 \text{ mgCL}^{-1}$ and $z(0) = 0.5 \text{ mgCL}^{-1}$ for all the numerical simulations with MATLAB R2010a.

4.1. Numerical analysis of internal equilibria

Here we provide a numerical analysis on the interior equilibria for varying values of carrying capacity K . We fix all other parameters with values listed in Table 1.

If the system (2.5) has an internal equilibrium $E^*(x^*, y^*, z^*)$, from $H(x^*, y^*, z^*) = 0$, it follows that

$$y^* = g^{-1} \left(\frac{d_z}{\hat{e}_z \min(1, \frac{\theta_y}{\theta_z})} \right).$$

Then the internal equilibria can be studied by degenerating the system onto the 2-dimensional $x - z$ plane by setting $y = y^*$. The internal equilibrium can be found at the interaction of the two curves $F(x, y^*, z) = 0$ (we denote it as $F_0(x, z) = 0$) and $G(x, y^*, z) = 0$ (we denote it as $G_0(x, z) = 0$) in the $x - z$ plane (Fig. 3 (a)). It is easy to find that there is only one

Figure 3: (a) Stoichiometry confined feasible region of (2.5) in phase space: the truncated triangular pyramid case. The shaded surface is defined by $y = y^*$. (b) Location of the internal equilibria in the $x - z$ plane (i.e., the scenario of $y = y^*$ in (a)). The peak-shaped curve is defined by $G_0(x, z) = 0$, which will never change its shape as K varies. The red curves are defined by $F_0(x, z) = 0$ with different K values. A solid circle denotes a stable equilibrium while a clear circle represents an unstable equilibrium.

internal equilibrium if it exists (Fig. 3 (b)). As K increases, the internal equilibrium moves on the curve of $G_0(x, z)$ from left to right. When the light intensity is very low ($0 < K < 0.5$) or very high ($K > 6.5$), the internal equilibrium is stable (Fig. 4 (a and d)). When the light intensity is at intermediate level ($0.5 < K < 6.5$), the internal equilibrium is unstable. There will be a periodic orbit (Fig. 4 (b)) or singular orbit (Fig. 4 (c)) circling around it.

4.2. Numerical bifurcation analysis

The parameter K , indirectly represents the light intensity or energy input into the system. The light intensity can change the producer's quality [19], and as the analytical analyses in the previous section suggest that the change of producer's $P : C$ can profoundly affect the food web and predation between different trophic levels. Bifurcation diagram provides a clear and visual way to understand how the behavior of a dynamical system depends on a parameter. Here we analyze the dynamics of (2.5) by choosing K as the bifurcation parameter (i.e. light intensity). The bifurcation diagram and spectrum of the maximum Lyapunov exponent diagram (Fig. 5) provide further insight on how system (2.5) responds to the light enrichment as K increases from 0 to 10.0 mgCL⁻¹. We will also present some simulation of time series along the gradient of light intensity K from 0 to 10 mgCL⁻¹ in eight numerical runs (Fig. 6) as assistant intuitive analysis.

When the light intensity is low (e.g., $0 < K < 0.7$ in Fig. 5 (a)), the producer's quality is quite good and the dynamics of (2.5) are very similar to that of the conventional model. In particular, when the light intensity is low enough (e.g. $0 < K < 0.15$ in Fig. 5 (a)), both the consumer and the predator can not survive due to starvation and now the boundary equilibrium $(K, 0, 0)$ is stable. Too low light intensity can only support the survival of the producer with a very low population size, and Fig. 6 (a) shows such a typical case with $K = 0.1$. As the light intensity K increases (e.g., $0.15 < K < 0.2$ in Fig. 5 (a)), the consumer starts to survive and $(\bar{x}, \bar{y}, 0)$ is the attractor; the light intensity at such level can support the producer and the consumer, but not the predator (e.g., Fig. 6 (b) with $K = 0.18$). As K increases further (e.g., from 0.2 to 0.5 in Fig. 5 (a)), all the populations survive and coexist at a stable internal equilibrium (x^*, y^*, z^*) (e.g., Fig. 6 (c) with $K = 0.4$). The equilibrium density

Figure 4: Attractor of (2.5) in phase space with different K . (a) $K = 0.4$ and E^* is the attractor. (b) $K = 0.6$ and the periodic orbit around E^* is the attractor (a limit cycle). The phase trajectory tends to a limit circle and E^* is unstable. (c) $K = 1$ and the trajectory when $z > 4$ is the attractor (a chaos). The phase trajectory spirally climbs up and then tends to a singular orbit and E^* is unstable. (d) $K = 6$ and E^* is the attractor. Here, the initial value is $x(0) = 0.5 \text{ mgCL}^{-1}$, $y(0) = 0.5 \text{ mgCL}^{-1}$, and $z(0) = 0.5 \text{ mgCL}^{-1}$; the red clear circle denotes E^* being unstable (in (b) and (c)) while the red solid circle represents E^* being asymptotically stable (in (a) and (d)).

of producer increases with the increasing of K while the consumer's equilibrium density keeps constant at 0.1, and, in this case, the light intensity is sufficient to support the survival of the whole system. As K is increased through a threshold value (e.g., $K = 0.5$ in Fig. 5 (a)), the internal equilibrium E^* loses its stability and (2.5) undergoes a supercritical Hopf bifurcation at this threshold value. As a result, a limit cycle is born. This limit cycle starts with zero amplitude and will grow as K is further increased in a reasonable interval (e.g., $0.5 < K < 0.7$ Fig. 5 (a)). The system (2.5) exhibits Rosenzweig's paradox of enrichment [23]. Fig. 6 (d) shows periodic oscillating dynamics when $K = 0.6$. In this case, the population densities do not saturate at any certain values any more. All the three populations oscillate around an unstable internal equilibrium.

When K further increases (e.g., from $K = 0.7$ in Fig. 5 (a)), the dynamics of (2.5) are significantly different from that of the LKE model due to addition of the secondary predator. When the light intensity increases to some intermediate level (e.g., $0.7 < K < 1.1$ in Fig. 5 (a)), (2.5) admits chaotic dynamics. The simulation of the spectra of maximum Lyapunov exponent (MLE) of (2.5) against K in Fig. 5 (b) effectively supports this claim since the maximum Lyapunov exponent $\lambda > 0$ when the light intensity is intermediate (e.g., $0.7 < K < 1.1$ in

Figure 5: Dynamic behaviors for system (2.5) with respect to light intensity (K) varying from 0 to 10 mgCL^{-1} . (a) Bifurcation diagram of the equilibrium densities of producer (in red), consumer (in blue), and predator (in black) plotted against K . (b) Spectrum of the maximum Lyapunov exponent (MLE, λ) of (2.5) against K . The MLE is positive for $0.7 < K < 1.1$, which shows the existence of chaotic dynamics. (c) Bifurcation diagram of the production efficiency for consumer defined in (2.3) plotted against K . The horizontal dashed line represents the maximum production efficiency for consumer ($\hat{e}_y$). The values of parameters are listed in Table 1.

Fig. 5 (b)). As a typical example, for $K = 1$, the trajectory in phase space (Fig. 4 (c)) and the solution curve (Fig. 6 (e)) show all populations oscillate irregularly and admit chaotic dynamics.

When the light intensity increases through an intermediate threshold value (e.g., $K = 1.1$ in Fig. 5 (a)), the dynamics of (2.5) change abruptly, the chaotic behavior disappears via a ‘saddle-node’ bifurcation, and then (2.5) again achieves equilibrium at the stable internal equilibrium for a small interval (e.g., $1.1 < K < 1.12$ in Fig. 5 (a)). At a threshold value (e.g., $K = 1.12$ in Fig. 5 (a)), (2.5) admits supercritical Hopf bifurcation once again and, when K increases from 1.12 to 6.5, all populations oscillate periodically (e.g., Fig. 6 (f) with $K = 4$). As K increases from intermediate levels to high levels (e.g., $1.12 < K < 6.5$ in Fig. 5 (a)), the mean values of the oscillatory density of the producer have a tendency to rise while that of the predators catches an opposite trend due to the bad quality of the producer. The amplitude of the limit cycle solution gradually increases from zero, and then decreases to zero again. When through a threshold value (e.g., $K = 6.5$ in Fig. 5 (a)), a Hopf bifurcation occurs to (2.5) and the limit cycle turns into stable internal equilibrium E^* when K is large enough (e.g., $6.5 < K < 9.8$ in Fig. 5 (a)). Fig. 6 (g) shows a case study with $K = 8$. Extremely high light intensity leads to a catastrophic crash of both predator and consumer. The predator tends to perish first (e.g., Fig. 5 (a) with $K = 9.8$) and then the consumer goes extinct (e.g., Fig. 5 (a) with $K = 10$). Fig. 6 (h) is a case study with $K = 10$ that both predator and consumer tend to perish. Due to the extinction of higher trophic levels, the primary level of the food chain (i.e., producer) can possibly be in some bloom state. Higher level of abundance of producer is associated with lower level of abundance of consumer and predator, as in the [24] experiments.

Fig. 5 (c) shows the relationship between the production efficiency in carbon terms for consumer (2.3) and the producer carrying capacity. From Fig. 5 (a), (c) and Fig. 6, one finds the following trends. When the light intensity is low (e.g., $0 < K < 1.1$ in Fig. 5 (c)), the production efficiency for consumer can reach its maximum rate. Higher light intensity leads to greater production by the producer species. The consumer and the predator species exhibit similar growth dynamics when K is small (e.g., $0 < K < 1.1$ in Fig. 5 (a)). However, the mean production efficiency of the consumer species decreases when the light intensity continues to rise at high levels (e.g., $K > 1.1$ in Fig. 5 (c)), which often means that the producer’s P:C ratio is lower than that of consumer. In such cases, the population densities of the top two trophic levels decline as K increases at high levels (e.g., $K > 1.1$ in Fig. 5 (a)).

5. Conclusion and discussion

Ecological stoichiometry stresses the importance of incorporating the effects of food quality into food web models. Instead of focusing on the study of ecological transfer efficiencies of stoichiometric models of two and three trophic levels as in [14], we study on the effect of stoichiometry on chaotic solution behavior in food chain model with three trophic levels. We also explore the model dynamics and its relationship to the parameter space systematically. Contrast to conventional models, this stoichiometric food chain model does not assume a constant (+,-) relationship between consumer and producer. It reflects the fact that all species share common essential chemical elements in different proportions. Compared with the well established two dimensional stoichiometric producer-grazer LKE model [6], model (2.5) exhibits richer and more complicated dynamics. The attractor of the LKE model is either a boundary equilibrium or an internal equilibrium or a limit cycle, while the attractors of (2.5) can possibly be a boundary equilibrium, an internal equilibrium, a limit cycle, or even

Figure 6: Typical time series of (2.5) with K varying from 0 to 10. (a) $K = 0.1$ and E_1 is asymptotically stable. (b) $K = 0.18$ and E_2 is asymptotically stable. (c) $K = 0.4$ and E^* is asymptotically stable. (d) $K = 0.6$ and (2.5) admits periodic oscillating dynamics. (e) $K = 1$ and (2.5) shows chaotic dynamics. (f) $K = 4$ and all populations in (2.5) oscillate periodically. (g) $K = 8$ and E^* is asymptotically stable. (h) $K = 10$ and E_1 is asymptotically stable. Here, the values of parameters except K are listed in Table 1, and the initial conditions are $x(0) = 0.5 \text{ mgCL}^{-1}$, $y(0) = 0.5 \text{ mgCL}^{-1}$, and $z(0) = 0.5 \text{ mgCL}^{-1}$.

1 a strange attractor (chaos) (see Fig. 4 and 6). Chaotic dynamics and a strange attractor can
2 emerge in (2.5) with biologically plausible parameter values. Below we summarize a few of
3 our computational observations and their biological implications.

Figure 7: Bifurcation diagram of the mean densities of producer, consumer and predator plotted against producer's quality for (2.5). The red dotted line, the blue solid line and the black dashed line represent the mean density of producer, consumer and predator with respect to producer's quality ($P : C$), respectively. The three vertical dashed lines represent the producer minimal $P : C$, consumer constant $P : C$, predator constant $P : C$, respectively. Arrows represent the directions as K increases.

4 Nutrient recycling rates play an important role to alter ecosystem level nutrient availabil-
5 ity. Fig. 7 shows the mean densities of producer, consumer and predator with respect to
6 producer' quality ($P : C$). We are interested in the case when the producer' quality is lower
7 than consumer's quality, i.e. producer's quality varies in (q, θ_y) . Consumer will waste some
8 carbon ingested to maintain its fixed $P:C$ ratio due to the low food quality. Intuitively, the
9 density of consumer shall decrease along with the decreasing production efficiency. However,
10 Fig. 7 together with Fig. 5 show that predator's mean density decreases obviously, while
11 the consumer's mean density maintains at an approximate constant value when producer's
12 quality decreases in the interval (q, θ_y) . Mathematically, when K varies at high level (e.g.
13 $1.1 < K < 9.8$ in Fig. 5), consumer's density at the positive equilibrium does not change
14 much, while producer's and predator's densities vary more noticeably. Biologically, consumer
15 as the intermediate trophic level fixes its $P : C$, which intensifies the competition of phos-
16 phorus between producer and predator. As K increases at high level (e.g. $1.1 < K < 9.8$
17 in Fig. 5), the producer will control more nutrient resources and significantly reduce the
18 top predator population level. Our study suggests that decreasing producer's quality may
19 have smaller detrimental effect on the density of consumer compare to its indirect but more
20 profound detrimental impact on the top predator's density.

21 Fig. 8 (a) represents the bifurcation diagram of (2.1), which elucidates the dynamic
22 evolution of (2.1) corresponding to the light energy enrichment as K increases from 0 to
23 10.0 mgCL^{-1} . All the values of parameters are the same as those in (2.5). Observe that
24 (2.1) shows strong oscillatory dynamics and the equilibrium cyclic densities increase with the
25 increase of the light intensity, while the stoichiometric model (2.5) shows something quite dif-
26 ferent. When the light intensity is very high, the population densities tend to a stable steady
27 state instead of oscillatory solution. Predator density shows an obvious decreasing trend when

Figure 8: Dynamic behaviors for system (2.1) with respect to light intensity (K) varying from 0 to 10 mgCL^{-1} . (a) Bifurcation diagram of the equilibrium densities of producer (in red), consumer (in blue), and predator (in black) plotted against K . (b) Spectrum of the maximum Lyapunov exponent (MLE, λ) of (2.1) against K . The MLE is positive for $1.2 < K < 1.5$ and $2.9 < K < 10$, which shows the existence of chaotic dynamics. The values of parameters are listed in Table 1.

light intensity increases at high levels. Predator and consumer species may perish when the light intensity is extremely high. The deterministic extinction of consumer species was already shown in the LKE model. An interesting finding of this paper is the producer quality induced deterministic extinction of predator species when consumer species persists.

Fig. 8 (a) also suggests that the traditional three trophic levels model (2.1) of MacArthur-Rosenweig type admits paradox of enrichment and also chaotic dynamics, which shows the similar result with [15]. Fig. 8 (b) represents the spectrum of maximum Lyapunov exponent of (2.1) against K , which proves that (2.1) admits chaotic dynamics when the light intensity varies in high level (e.g., $1.2 < K < 1.5$ and $2.9 < K < 10$ in Fig. 8 (b)). While, model (2.5) admits chaotic dynamics only at intermediate level (e.g., $0.7 < K < 1.1$ in Fig. 5 (b)). Compared with the traditional model (2.1) with MacArthur-Rosenweig type, the biologically plausible parameter ranges for having chaotic dynamics of model (2.5) with stoichiometry changes and is smaller than that of the traditional food chain model.

In summary, our analytical and numerical analysis suggest the following implications:

- Since nutrients flow across multiple trophic levels, decreasing producer's quality may have only a small effect on the consumer growth but a more profound impact on the top

predator growth indirectly.

- The stoichiometric food chain model maintains similar dynamics to that of the traditional one when the food quality of producer is good. However, when the food quality of producer is poor, the stoichiometric food chain model provides more reasonable mechanisms for the deterministic extinction of predator, which may differ from that of the traditional one. We also find that predator tends to perish earlier than consumer when light intensity (K) increases at extremely high light levels.
- Stoichiometry changes the parameter ranges for the existence of chaotic dynamics of food chain model with three trophic levels. When the traditional food chain model admits chaotic behavior, the stoichiometry mechanism shrinks the parameter ranges for the existence of chaotic dynamics. Biologically, chaotic dynamic provides a plausible explanation for the complex coexistence observed in natural ecosystems.

Figure 9: Each point represents the efficiency for an individual mesocosm, obtained by using production rates averaged over the experiment for each trophic level. Horizontal lines represent treatment means, and letters indicate treatments that are significantly different from each other (adapted from [25]).

The model (2.5) may be applied to model some aquatic ecosystems. Consider the scenario that a system consists of one phytoplankton species (x), one zooplankton species (y) and one fish species (z) in our model. The effect of abiotic factors on the phytoplankton growth is one of the most intriguing issues in aquatic ecosystem due to the frequent outbreaks of phytoplankton blooms. The increasing of carrying capacity K (light intensity) can have a significant effect on the aquatic ecosystem. When the light intensity is low, the population size increases with the increasing of light intensity. When the light is medium, the ecosystem becomes complicated and population quantity can not be easily predicted due to the possible chaotic dynamics. Additional gain of light intensity may generate more rapid growth of phytoplankton. But the lower food chain efficiency caused by stronger light intensity may lead to lower production of higher trophic levels when light intensity is strong. Dickman et al. [25] used experiments to study the effect of light, nutrient, and food-chain length on the planktonic energy transfer efficiency across multiple trophic levels. Fig. 9 shows that no matter whether the system is

1 in high or low light conditions, nutrient transfer efficiency is higher in the low light condition
2 than that in high light condition. When the light is extremely high, phytoplankton blooms
3 while the zooplankton and the fish may go extinct.

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