Dynamics of a stoichiometric discrete producer-grazer model

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Dedicated to Jim Cushing on the occasion of his 62nd birthday

In the last decade, several theoretical models based on stoichiometric principles as well as field and laboratory experiments have shown that nutritional quality of the prey can have dramatic and counterintuitive impact. For example, the predator can become extinct while having plentiful prey in a completely deterministic system. The explanation lies in the bad nutritional quality of the prey that precludes the predator from efficiently converting the consumed food into its own biomass. Another effect is the halt of oscillations that are ubiquitous to predator-prey systems, which happens when bad prey quality drives the system through a saddle-node bifurcation. We note that all the existing models exhibiting these effects are continuous in time. However, in experiments, data are collected on discrete time intervals and many producers in nature have non-overlapping generations. Such scenarios call for discrete equation models. Hence we ask: (1) to what degree stoichiometric effects are just artifacts of continuous time models? (2) Can novel stoichiometric effects arise in discrete systems? Here, by comparing a continuous stoichiometric model to its discrete analog, we show that stoichiometric impacts of prey quality persist in discrete system. Moreover, not only bad prey quality can pull the system out of oscillations but also it can halt chaotic dynamics that surfaces in the discrete system. Stoichiometric mechanisms become increasingly important in our understanding of food web dynamics and our results suggest the robustness of these mechanisms to the discretization of time.

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1. Introduction

Predator-prey interactions are one of the major forces shaping food webs. Starting with the work of Lotka [1] and Volterra [2], modeling these interactions has been one of central themes in mathematical ecology. A basic assumption in Lotka's and Volterra's models, and in virtually all their subsequent modifications, is that higher prey abundance cannot hurt predator growth rate. Indeed, the most widely used predator functional responses

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(Holling Type I, II, and III) are all non-decreasing (monotonic) functions of prey abundance. This seemingly sound assumption, however, can fail for several reasons. For example, at a higher density, prey might exhibit “group defense” by being able to better deter predator attacks in large groups, better disguise itself in large numbers, or, in case of filamentous algae, jam filtering apparatus of its predator *Daphnia* (e.g. [3,4] and references therein). Note that in all these cases, predators reduce their growth, because they are simply forced to consume less prey. In other words, both the consumption of prey and the predator growth are non-monotone functions of prey density.

Another reason for non-monotone predator growth stems from the consideration of prey quality. This case has an interesting twist to it, because at the higher prey densities, the predator consumes more prey, but its poor quality reduces the conversion of the prey biomass into predator biomass. In other words, the consumption of the prey is a monotone function of its density, but the predator growth is still non-monotone. To better understand the underlying biology, we briefly describe a few of the experiments that clearly demonstrated this effect.

Urabe and Sterner [5] grew algae at different light intensities in phosphorus (P) limited batch cultures. As light input was increased, algal density increased as well, but the concentration of P in algae decreased. This happened because higher light intensity directly stimulated photosynthetic fixation of carbon—the bulk of the dry weight of algae—but it did not directly affect the uptake of P. Phosphorus is an essential element for all life and the predator in these experiments, zooplankton *Daphnia*, has relatively high requirements for P. At high light intensity, the predator faced high prey density but of low P content, which hurt its growth. Moreover, at the very high light intensity, due to extremely low P content in algae, the zooplankton went to extinction despite having a superabundance of food! Urabe *et al.* [6] grew algae at different carbon dioxide (CO_2) concentrations and also in P limited conditions. Elevated CO_2 concentrations boosted photosynthesis and, similarly to the experiments with varying light intensity, resulted in higher food abundance but poor food quality, which again negatively affected predator’s growth. Nelson *et al.* [7] also found profound effects of prey quality on the dynamics of zooplankton-algal system. The system exhibited two distinct dynamic possibilities: either an equilibrium with high predator biomass and low prey biomass of good quality, or an equilibrium with low predator biomass and high prey biomass of bad quality.

The effects of prey quality on predator-prey dynamics are not limited to aquatic systems. Terrestrial plants grown under elevated CO_2 concentrations generally grow better, but usually have lower nitrogen (N) concentration [8] and, in addition, can have lower concentration of vital micronutrients [9]. Newman *et al.* [10] showed that aphids *Rhopalosiphum padi* feeding on fescue grown under elevated CO_2 had more than 82% lower density. Gypsy moth caterpillars that fed on plants grown under twice-ambient CO_2 levels grew slower and had higher mortality rates [11]. The increase in atmospheric CO_2 concentrations is one of the most uniform impacts of humankind on the biosphere and, hence, can alter the quality of the base of natural and man-managed food webs—plants and alga—across the globe. Hence, understating the interplay between prey quality and prey quantity on predator-prey dynamics becomes of not only academic but also of high practical importance.

Several mathematical models have addressed this issue and despite (or, may be, due to) their simplicity have captured the essence of the above experiments. Andersen [12],

Loladze *et al.* [13] and Muller *et al.* [14], showed that variable chemical composition (i.e. stoichiometry) of prey can significantly affect predator-prey dynamics. In particular, they showed that high prey density coupled with very poor quality can drive the predator to the deterministic extinction. In addition, Loladze *et al.* [13] showed the existence of the two equilibria that were later observed in the above described [7] experiments. Biodiversity implications of a two-predator one-prey stoichiometry model is discussed in [15]. A mechanistic derivation of a stoichiometric plant-herbivore model and its interpretation is provided by Kuang *et al.* [16]. All these models also showed that an increase in prey quantity accompanied by decrease in its quality can halt oscillations in predator-prey system. These effects are due to the decreased energy flow from the prey to the predator. In other words, though the predator consumes more prey, it effectively converts less of it into its own biomass.

All these stoichiometric models are continuous in time. This raises the question about the sensitivity of the results to the discretization of time. After all, almost all data collected are discrete in time. Moreover, models of Loladze *et al.* [13] and Muller *et al.* [14], are two dimensional autonomous ODEs, which mathematically preclude any possibility of chaos. Because even one dimensional discrete systems can potentially exhibit chaos, a natural question is if the interplay between prey quality and simple predator-prey dynamics can lead to chaos.

Motivated by these questions we compare the dynamics of one of the continuous models [13] with its discrete analog. In particular, we ask whether the following most important features observed in the experiments and exhibited in the continuous model “survive” the discretization: (1) deterministic extinction of the predator when it faces abundant food but of very low quality (2) the existence of an equilibrium with high predator:prey ratio when prey quality is high and the existence of the other equilibrium with low predator:prey ratio when prey quality is low. (3) the halt of oscillatory dynamics caused by low prey quality. In addition we ask whether chaotic dynamics can arise under a biologically plausible parameter set and if it does, whether low prey quality can halt chaos.

2. The model

Our discrete stoichiometric producer-grazer model will be based on the following continuous time producer-grazer system due to Loladze *et al.* [13]

$$\begin{aligned}\frac{dx}{dt} &= bx \left[1 - \frac{x}{\min(K, (P - \theta y)/q)} \right] - f(x)y, \\ \frac{dy}{dt} &= c \min\left(1, \frac{P - \theta y}{\theta x}\right) f(x)y - dy.\end{aligned}\tag{2.1}$$

where x is the density of producer (in milligrams of carbon per liter, mg C/l), y is the density of grazer (mg C/l), b is the intrinsic growth rate of producer (day^{-1}), d is the specific loss rate of grazer that includes metabolic losses (respiration) and death (day^{-1}), c is a constant production efficiency (yield constant), K is the producer's constant carrying capacity that depends on some external factors such as light intensity and $f(x)$ is the grazer's ingestion rate, which may be a Holling type II functional response.

To facilitate our discrete model formulation and its comparison with model (2.1), it is convenient to recall here its main model assumptions. They are

A1. The total mass of phosphorus P in the entire system is fixed, i.e. the system is closed for phosphorus with total of P (mg P/l).

A2. Phosphorus to carbon ratio ($P:C$) in the producer varies, but it never falls below a minimum q (mg P/mg C); the grazer maintains a constant $P:C$ ratio, denoted by θ (mg P/mg C).

A3. All phosphorus in the system is divided into two pools: phosphorus in the grazer and phosphorus in the producer.

Assumption (A1) assumes the system is closed for P . This is approximately true for a short period of time in natural systems where species' birth and death processes are confined in closed settings, like large lakes, or big farmland. Assumption (A3) essentially assumes that free phosphorus is immediately taken by the plant. One of the unusual features of this model is that the carrying capacity of the producer depends on the density of the grazer. In the absence of the grazer, the carrying capacity of the producer reads

$$k = \min(K, P/q)$$

which depends only on light and phosphorus availability.

There are several ways of deriving discrete time versions of dynamical systems corresponding to continuous time formulations. One of the ways of deriving difference equations modeling the dynamics of populations with non-overlapping generations is based on appropriate modifications of models with overlapping generations. In this approach, differential equations with piecewise constant arguments are useful. For literature on differential equations with piecewise constant arguments, we refer to Weiner [17].

We assume that the per capita growth rates in equation (2.1) change only at the time of each measurement. Incorporating this aspect in equation (2.1) yields the following modified system

$$\begin{aligned} \frac{1}{x(t)} \frac{dx(t)}{dt} &= b \left[1 - \frac{x([t])}{\min(K, (P - \theta y([t]))/q)} \right] - \frac{f(x([t]))y([t])}{x([t])}, \\ \frac{1}{y(t)} \frac{dy(t)}{dt} &= c \min \left(1, \frac{P - \theta y([t])}{\theta x([t])} \right) f(x([t])) - d, \quad t \neq 0, 1, 2, \dots \end{aligned} \quad (2.2)$$

Here $[t]$ denotes the integer part of $t \in (0, +\infty)$. Equations of the type (2.2) are known as differential equations with piecewise constant arguments and these equations occupy a position midway between differential equations and difference equations.

By a solution of equation (2.2), we mean a function $(x, y)^T$, which is defined for $t \in [0, +\infty)$, and possesses the following properties:

1. x, y is continuous on $[0, \infty)$;
2. the derivative $dx(t)/dt, dy(t)/dt$ exist at each point $t \in [0, \infty)$ with the possible exception of the points $t \in \{0, 1, 2, \dots\}$, where left-sided derivatives exist;
3. the equations in (2.2) are satisfied on each interval $[n, n+1)$ with $n = 0, 1, 2, \dots$

On any interval of the form $[n, n+1)$, $k = 0, 1, 2, \dots$, we can integrate equation (2.2) and obtain for $n \leq t < n+1$, $n = 0, 1, 2, \dots$

$$\begin{aligned} x(t) &= x(n) \exp \left\{ \left[b - \frac{bx(n)}{\min(K, (P - \theta y(n))/q)} - \frac{f(x(n))y(n)}{x(n)} \right] (t - n) \right\} \\ y(t) &= y(n) \exp \left\{ \left[c \min \left(1, \frac{P - \theta y(n)}{\theta x(n)} \right) f(x(n)) - d \right] (t - n) \right\}, \end{aligned} \quad (2.3)$$

Letting $t \rightarrow n+1$, we obtain from equation (2.3) that

$$\begin{aligned} x(n+1) &= x(n) \exp \left\{ b - \frac{bx(n)}{\min(K, (P - \theta y(n))/q)} - \frac{f(x(n))y(n)}{x(n)} \right\}, \\ y(n+1) &= y(n) \exp \left\{ c \min \left(1, \frac{P - \theta y(n)}{\theta x(n)} \right) f(x(n)) - d \right\}, \end{aligned} \quad (2.4)$$

which is a discrete time analogue of system (2.1). In the following sections, we will focus our attention on system (2.4). Throughout the rest of this paper, we consider only biologically meaningful initial values. We thus assume that $x(0) > 0$ and $P/\theta > y(0) > 0$.

3. Boundedness of solutions

In Loladze *et al.* [13], it is assumed that the function $f(x)$ in system (2.1) is a bounded smooth function satisfying

$$f(0) = 0, f'(x) > 0, f'(0) < \infty \quad \text{and} \quad f''(x) < 0 \quad \text{for} \quad x > 0.$$

In this paper, for convenience we assume that $f(x) = xp(x)$. It has been proved in [13] that

$$\lim_{x \rightarrow 0} p(x) = f'(0) < \infty, \quad p'(x) < 0, \quad x > 0.$$

It is easy to see that the both components of the solution of equation (2.4) stay positive when exist. Notice that the function $F(x) = x \exp b(1 - x/K)$ achieves its maximum at $x = K/b$, we have

$$x(n+1) < x(n) \exp \left\{ b - \frac{bx(n)}{K} \right\} \leq \frac{K}{b} e^{b(1-1/b)} \equiv u.$$

Hence, for all nonnegative integers n , we have

$$x(n) \leq \max \{x(0), u\} \equiv U.$$

If $cf(U) \leq d$, then it is clear that for all $n > 0$, we have $y(n) \leq y(0)$. We thus assume below that $cf(U) > d$. Let v be large enough so that

$$cf(Ue^{b-p(U)v}) < d.$$

We claim that for all nonnegative integers n , we have

$$y(n) \leq \max \{y(0), v\} e^{2cf(U)-2d} \equiv V.$$

This is obviously true for $n = 1, 2$.

Assume the above claim is false. Assume first the case that

(I): $y(0) \leq v$. Then for some $n_1 > 2$, $v < y(n_1 - 2) \leq V$, $v < y(n_1 - 1) \leq V$, and $y(n_1) > V$. In this case, we have (using the property of $p'(x) < 0$)

$$x(n_1 - 1) \leq x(n_1 - 2)e^{b-p(x(n_1-2))y(n_1-2)} < Ue^{b-p(U)v}.$$

This implies that

$$y(n_1) < y(n_1 - 1) \exp \{cf(Ue^{b-p(U)v}) - d\} < y(n_1 - 1) \leq V,$$

a contradiction, indicating the claim is true for this case.

(II): Assume now the case of $y(0) > v$. In this case, we have

$$x(1) < Ue^{b-p(U)v},$$

which implies that

$$y(2) < y(1).$$

In other words, as long as $y(n) > v$, then $y(n+2) < y(n+1)$. Hence there are two possibilities, either (i) for some $y(n^*) \leq v$ for some $n^* > 0$; or (ii) $y(n) > v$ for all $n > 0$. In case of (ii), we have $y(n)$ strictly decreasing for $n > 1$ and the claim is obviously true. In case of (i), from the proof of case (I), we see that for $y(n) < V$ for $n > n^*$ and hence the claim is also true.

Summarizing the above arguments, we arrive at the following boundedness result for model (2.4).

THEOREM 3.1 For equation (2.4), we have for all $n > 0$,

$$x(n) \leq \max \left\{ x(0), \frac{K}{b} e^{b(1-1/b)} \right\} \equiv U \quad \text{and} \quad y(n) \leq \max \{y(0), v\} e^{2cf(U)-2d},$$

where v is any number satisfying $cf(Ue^{b-p(U)v}) < d$.

A straightforward consequence of the above theorem is that

$$\Delta = \left\{ (x, y) : 0 < x < \frac{K}{b} e^{b(1-1/b)}, 0 < y < v \right\}$$

is positively invariant. Indeed, we have

THEOREM 3.2 For (2.4), Δ is globally attractive with respect to initial values $x(0), y(0)$ such that $x(0) > 0$ and $P/\theta > y(0) > 0$.

Proof It is easy to see from the model equations and the proof of the above theorem that for large values of n , $x(n) \in (0, (K/b)e^{b(1-1/b)})$. Notice that if $y(n) > v$ for all $n > 0$, then $y(n)$ must have a limit $y^* \geq v$. Hence for large values of n , we have

$$y(n) < y(n-1) \exp \{cf(Ue^{b-p(U)v}) - d\}.$$

Letting $n \rightarrow \infty$ yields

$$y^* \leq y^* \exp \{cf(Ue^{b-p(U)v}) - d\} < y^*.$$

This contradicts $y^* > v > 0$, proving the theorem. $\square$

Observe that the function $g(b) = (K/b)e^{b(1-1/b)}$ achieves its minimum value K at $b = 1$ for positive values of b . In other words, the perceived carrying capacity for equation (2.4) can be exceeded if $b \neq 1$. This is a stark contrast to the continuous model (2.1). Indeed, if the model is more carefully (mechanistically) derived, then the perceived carrying capacity in continuous models may not even be approached [16].

4. Equilibria

To facilitate the equilibria analysis in the following discussion, we rewrite equation (2.4) as

$$\begin{aligned} x(n+1) &= x(n) \exp \{F(x(n), y(n))\} \\ y(n+1) &= y(n) \exp \{G(x(n), y(n))\} \end{aligned} \quad (4.1)$$

where

$$\begin{aligned} F(x, y) &= b - \frac{bx}{\min(K, (P - \theta y)/q)} - yp'(x), \\ G(x, y) &= c \min \left(x, \frac{P - \theta y}{\theta} \right) p(x) - d. \end{aligned}$$

The nullclines of equation (2.4) are given by (see figure 1 for a sample set of nullclines)

$$\text{Producer nullclines : } x[1 - \exp \{F(x, y)\}] = 0, \quad \text{i.e., } x = 0 \quad \text{or} \quad F(x, y) = 0,$$

$$\text{Grazer nullclines : } y[1 - \exp \{G(x, y)\}] = 0, \quad \text{i.e., } y = 0 \quad \text{or} \quad G(x, y) = 0$$

The variational matrix of equation (2.4), after some straightforward algebraic calculations, reads

$$J(x, y) = \begin{pmatrix} \exp \{F(x, y)\} + x \exp \{F(x, y)\} F_x(x, y) & x \exp \{F(x, y)\} F_y(x, y) \\ y \exp \{G(x, y)\} G_x(x, y) & \exp \{G(x, y)\} + y \exp \{G(x, y)\} G_y(x, y) \end{pmatrix}$$

where

$$\begin{aligned} F_x(x, y) &= \frac{\partial F(x, y)}{\partial x} = -\frac{b}{\min(K, (P - \theta y)/q)} - yp'(x) \\ F_y(x, y) &= \frac{\partial F(x, y)}{\partial y} = \begin{cases} -p(x) < 0, & y < \frac{P}{\theta} - \frac{Kq}{\theta} \\ -\frac{qb\theta x}{(P - \theta y)^2} - p(x) < 0, & y > \frac{P}{\theta} - \frac{Kq}{\theta} \end{cases} \\ G_x(x, y) &= \frac{\partial G(x, y)}{\partial x} = \begin{cases} c[p(x) + xp'(x)] > 0, & y < P/\theta - x \\ c(P - \theta y)\theta^{-1}p'(x) < 0, & y > P/\theta - x \end{cases} \\ G_y(x, y) &= \frac{\partial G(x, y)}{\partial y} = \begin{cases} 0, & y < P/\theta - x \\ -cp(x) < 0, & y > P/\theta - x \end{cases} \end{aligned} \quad (4.2)$$

A very important feature of equation (2.4) is that $G_x(x, y)$ change its sign along line $y = P/\theta - x$. Hence $\exp \{G(x, y)\}$, which measure the effect of producer density on grazer

Figure 1. A sample set of nullclines for (2.4).

growth rate, decreases with respect to x . Conventional ecological theory, consider this effect as positive or null and thus traditionally classifies grazer-producer and indeed all other predator-prey interaction as $(+, -)$ relation. In this model the line $y = P/\theta - x$, divides the phase plane into two biologically meaningful regions: $I = \{(x, y) : 0 < x < P/\theta, 0 < y < P/\theta - x\}$ and $II = \{(x, y) : 0 < x < P/\theta, y > P/\theta - x\}$. In region I , the grazer-producer interaction maintains the traditional $(+, -)$ relation, but changes to $(-, -)$ relation in region II where both are competing for the limited resource P .

4.1 Boundary equilibria

In order to study the stability of equilibria, we introduce the following standard lemma (see p57 of Edelstein-Keshet [18]).

LEMMA 4.1 (Jury Test) *Let A be a 2×2 constant matrix. Both characteristic roots of A have magnitude less than 1 if and only if*

$$2 > 1 + \text{Det}(A) > |\text{Tr}(A)|. \quad (4.3)$$

The possible equilibria or steady states of equation (2.4) solve the system of algebraic equations

$$x[1 - \exp\{F(x, y)\}] = 0, \quad y[1 - \exp\{G(x, y)\}] = 0.$$

It is easy to observe that the equilibria of equation (2.4) are exactly the same as those of equation (2.1).

The only boundary equilibria are $E_0 = (0, 0)$ and $E_1 = (k, 0)$.

At E_0 , the Jacobian takes the form

$$J(E_0) = \begin{pmatrix} e^b & 0 \\ 0 & e^{-d} \end{pmatrix}.$$

It is clear that one characteristic root e^{-d} has magnitude less than 1 while the other has magnitude e^b larger than 1. Consequently, the origin E_0 is always unstable.

At E_1 , the Jacobian is

$$J(E_1) = \begin{pmatrix} 1 - b & kF_y(k, 0) \\ 0 & \exp\{G(k, 0)\} \end{pmatrix}$$

where

$$G(k, 0) = c \min\left(k, \frac{P}{\theta}\right)p(k) - d.$$

By Lemma 4.1, we reach the following conclusion.

THEOREM 4.1 *For equation (2.4), the origin E_0 is always unstable. The only other boundary equilibrium is E_1 . It is locally asymptotically stable if*

$$0 < b < 2 \quad \text{and} \quad c \min\left(k, \frac{P}{\theta}\right)p(k) < d;$$

it is unstable if

$$b > 2 \quad \text{or} \quad c \min\left(k, \frac{P}{\theta}\right)p(k) > d.$$

Proof If we let λ_1 and λ_2 be the characteristic roots of $J(E_1)$, then, the condition

$$0 < b < 2 \quad \text{and} \quad c \min\left(k, \frac{P}{\theta}\right)p(k) < d$$

ensures that $|\lambda_i| < 1$, $i = 1, 2$. While condition

$$b > 2 \quad \text{or} \quad c \min\left(k, \frac{P}{\theta}\right)p(k) > d$$

implies $|\lambda_1| > 1$ or $|\lambda_2| > 1$ □

Remark 4.1 From [13], we know that $G(x, 0) = 0$ has a unique solution $x_1 \in (0, P/\theta)$ and a unique solution $x_2 \in (P/\theta, \infty)$, $G(k, 0) > 0$ for $x_1 < k < x_2$ and $G(k, 0) < 0$ for $k \notin [x_1, x_2]$. For equation (2.1), if $x_1 < k < x_2$ then E_1 is unstable; if $k \notin [x_1, x_2]$ then E_1 is stable. But for equation (2.4), the situation is quite different since E_1 can be possibly stable or possibly unstable when $x_1 < k < x_2$ or $k \notin [x_1, x_2]$.

If $p(x) = r/(a+x)$, then one can easily derive sufficient conditions for the stability of E_0 and E_1 in equation (2.4).

4.2 Internal equilibria

Since both equations (2.4) and (2.1) have the same equilibria, from Loladze *et al.* [13], we claim that equation (2.4) possibly has multiple positive equilibria. In the following, we assume that $E^* = (x^*, y^*)$ is such an equilibrium and discuss its local stability. We will also compare our findings to that of Loladze *et al.* [13] for equation (2.1).

The Jacobian at the positive equilibria (x^*, y^*) reads

$$J(E^*) = J(x^*, y^*) = \begin{pmatrix} 1 + x^* F_x & x^* F_y \\ y^* G_x & 1 + y^* G_y \end{pmatrix}$$

where

$$F_x = F_x(x^*, y^*), \quad F_y = F_y(x^*, y^*), \quad G_x = G_x(x^*, y^*), \quad G_y = G_y(x^*, y^*).$$

Its trace and determinant are

$$\begin{aligned} \text{Tr}(J(E^*)) &= 2 + x^* F_x + y^* G_y, \\ \text{Det}(J(E^*)) &= 1 + x^* F_x + y^* G_y + x^* y^* [F_x G_y - F_y G_x] \\ &= \text{Tr}(J(E^*)) - 1 + x^* y^* [F_x G_y - F_y G_x]. \end{aligned}$$

respectively. We have the following theorem on the local asymptotical stability of the internal equilibrium E^* .

THEOREM 4.2 *In Region I (i.e., $y^* < P/\theta - x^*$), the following are true.*

- If the producer's nullcline is increasing at E^* (i.e., $F_x > 0$), then E^* is unstable.
- If the producer's nullcline is decreasing at E^* (i.e., $F_x < 0$) and

$$\frac{1}{2} x^* y^* F_y G_x - 2 < x^* F_x < x^* y^* F_y G_x, \quad (4.4)$$

then E^* is locally asymptotically stable.

- If the producer's nullcline is decreasing at E^* (i.e., $F_x < 0$) and

$$F_x > y^* F_y G_x \quad \text{or} \quad x^* F_x < \frac{1}{2} x^* y^* F_y G_x - 2 \quad (4.5)$$

then E^* is unstable.

In Region II (i.e., $y^ > P/\theta - x^*$), the following are true.*

- If the slope of the producer's nullcline at E^* is greater than the grazer's (i.e., $-G_x/G_y < -F_x/F_y$), then E^* is unstable.
- If the slope of the grazer's nullcline at E^* is greater than the producer's (i.e., $-G_x/G_y > -F_x/F_y$) and

$$\frac{1}{2} x^* y^* [F_y G_x - F_x G_y] - 2 < x^* F_x + y^* G_y < x^* y^* [F_y G_x - F_x G_y] \quad (4.6)$$

then E^* is locally asymptotically stable.

- If the slope of the grazer's nullcline at E^* is greater than the producer's (i.e., $-G_x/G_y > -F_x/F_y$) and

$$\begin{aligned} x^*F_x + y^*G_y &< \frac{1}{2}x^*y^*[F_yG_x - F_xG_y] - 2, \quad \text{or} \\ x^*F_x + y^*G_y &> x^*y^*[F_yG_x - F_xG_y] \end{aligned} \quad (4.7)$$

then E^* is unstable.

Proof We split the analysis into two cases depending on whether E^* is in Region *I* or *II*.

Case 1 Suppose E^* is in Region *I*. Then equation (4.2) implies that at E^* , $F_y < 0$, $G_x > 0$, $G_y = 0$. Note that,

$$\text{Tr}(J(E^*)) = 2 + x^*F_x = 2 + x^*\left(-\frac{F_x}{F_y}\right)(-F_y)$$

and $-(F_x/F_y)$ is the slope of the producer's nullcline, it follows that

$$\text{Tr}(J(E^*)) > 2$$

if the producer's nullcline is increasing at E^* . Therefore, E^* is unstable if $F_x > 0$. Assume that the producer's nullcline is decreasing at E^* , i.e., $F_x < 0$. If equation (4.4) holds, then one can easily prove that equation (4.3) holds. Consequently, E^* is stable. If equation (4.5) holds, then equation (4.3) is not valid. So E^* is unstable.

Case 2 Suppose E^* lies in Region *II*. Then system (4.2) yields that at E^* , $F_y < 0$, $G_x < 0$, $G_y < 0$.

Note that

$$\text{Det}(J(E^*)) = 1 + x^*F_x + y^*G_y + x^*y^*F_yG_y \left[\left(-\frac{G_x}{G_y}\right) - \left(-\frac{F_x}{F_y}\right) \right].$$

If the slope of the producer's nullcline at E^* is greater than the grazers's, i.e., $-G_x/G_y < -F_x/F_y$, then $1 + \text{Det}(J(E^*)) < \text{Tr}(J(E^*))$, which implies that equation (4.3) does not hold. Hence, E^* is unstable. If the slope of the grazer's nullcline at E^* is greater than the producer's, then

$$-\frac{F_x}{F_y} < -\frac{G_x}{G_y} < 0.$$

If equation (4.6) holds, then one can easily show that system (4.3) holds. Consequently, E^* is stable. If equation (4.7) is valid, then E^* is unstable since equation (4.3) is not valid. $\square$

Remark 4.2 For equation (2.1), it has been shown by [13] that, in Region *I*, E^* is locally asymptotically stable if the producer's nullcline at E^* is decreasing; if the producer's nullcline at it is increasing, then E^* is unstable. In Region *II*, if the producer's nullcline at it declines more steeply than the grazer's, then E^* is locally asymptotically stable; otherwise, E^* is unstable. Compare this conclusion with Theorem 4.2, we see that the discretization of equation (2.1) can destabilize the internal equilibria.

5. Numerical simulations

In this section, we carry out systematic numerical simulations to support and complement our analytical findings and compare with those of the corresponding continuous system. In particular, we will discuss the impact of discretization on the modelling of the dynamical interaction between producers and the grazers.

In the following, we assume that $p(x) = r/(a + x)$. We will study numerically the following producer-grazer systems with Holling type II functional response

$$\begin{aligned} x(n+1) &= x(n) \exp \left\{ b - \frac{bx(n)}{\min(K, (P - \theta y(n))/q)} - \frac{cy(n)}{a + x(n)} \right\} \\ y(n+1) &= y(n) \exp \left\{ e \min \left(1, \frac{P - \theta y(n)}{\theta x(n)} \right) \frac{cx(n)}{a + x(n)} - d \right\}, \end{aligned} \quad (5.1)$$

and

$$\begin{aligned} \frac{dx}{dt} &= bx \left[1 - \frac{x}{\min(K, (P - \theta y)/q)} \right] - \frac{cxy}{a + x} \\ \frac{dy}{dt} &= e \min \left(1, \frac{P - \theta y}{\theta x} \right) \frac{cxy}{a + x} - dy \end{aligned} \quad (5.2)$$

We carry out numerical simulation for equations (5.1) and (5.2) with parameters used in [13], which are listed in table 1. Parameters in table 1 are adapted from Andersen [12] and Urabe and Sterner [5]. These parameters are biologically realistic.

In figure 2, we compare the solutions of the two systems with varying carbon carrying capacity K . It is clear that the dynamics of equation (5.1) is almost exactly the same as those of equation (5.2) when $K = 0.25, 0.75, 1.0$ and 2.0 . In $(d_1)-(d_2)$ and $(c_1)-(c_2)$, we observe the classic Rosenzweig's paradox of enrichment: an increase in K destabilizes one of the positive equilibria. However, a further increase in K stabilize the system to another positive equilibrium (see $(d_3)-(c_3)$). For very large values of K , we see $(d_4)-(c_4)$ the deterministic extinction of the grazers.

The bifurcation diagrams in figure 3 illustrate how the dynamics of the grazer in equations (5.1) and (5.2) varies with K . For small K , the grazer can not persist due to starvation. When K increases further, the grazer persists at an stable equilibrium and its density at stable equilibrium increases with K . Then, the stable equilibrium loses its stability to a limit cycle, the amplitude of which increases with K . The system exhibits the Rosenzweig's paradox enrichment. This trend stops when the limit cycle go through an saddle-node bifurcation and the grazer's density tends to a newly emerged stable equilibrium and the grazer's density at stable equilibrium decreases due to the worsening food quality. Finally, the grazer dies out due to low food quality. There is some subtle but important differences between the dynamics of equations (5.1) and (5.2): (1) the internal equilibrium of equation (5.1) lose its stability earlier than the corresponding one of (5.2); (2) the amplitude of the oscillation in discrete model is larger than that of continuous model.

In fact, the discretization can cause much greater impact on the dynamics of system (2.1). For example, from the bifurcation diagram in figure 5, one can easily observe that the dynamics of equation (5.1) is very different from the corresponding continuous time version for K close to and larger than 3. For the continuous producer-grazer system with parameter

Figure 2. The parameters are defined in table 1 and the initial conditions are $x = 0.5$ (mg C l^{-1}) and $y = 0.25$ (mg C l^{-1}). (d_i) and (c_i) denote the dynamics of (5.1) and (5.2) with different K , respectively.

values described in figure 4, the global attractor is either the boundary equilibrium $(k, 0)$ or the internal equilibrium E^* (see figure 4(b)). There is no limit cycle attractor. While for the corresponding discrete time producer-grazer system, the situation is quite complicated and different (see figure 4(a)). The global attractor can be a boundary equilibrium, an internal equilibrium, or a “limit cycle” attractor, or even a stranger attractor. As K increases through a series of bifurcation values, the solution $y(k)$ exhibits a series of bifurcations. When $K = 1.2, 1.4, 1.45$, equation (5.1) admits 2-, 4-, 8-cycle periodic solution, respectively. The distance between bifurcations in K -space becomes smaller and smaller. There is thus a hierarchy of solutions of period 2^n for every n , and each is associated with a parameter interval in which it is stable. When $K = 1.6$, equation (5.1) exhibits chaotic behavior. In other words, equation (5.1) exhibits a typical kind of behavior of nonlinear difference equation models: they go through the periodic doubling route to chaos.

Figure 5 exhibits another interesting limiting dynamics of equation (5.1). Figure 5(a) shows the familiar periodic doubling route to chaos for the producer’s density. However, the grazer’s density crashes and quickly reach zero shortly after the producer entering the chaos zone. This clearly suggests that chaotic producer densities provides an important factor for the extinction of grazer populations. This interesting and important biological insight is totally lost in the continuous model (2.1) (see figure 5(c) and (d)).

Figure 3. A bifurcation diagram of the grazer density against K . All other parameters are as in table (1) except K , which varies from 0 to 2. (a) depicts the bifurcation for the discrete system (5.1) and (b) depicts the bifurcation diagram for the continuous system (5.2).

6. Discussion

The analysis of our discrete models (2.4) and (5.1) shows that they retain most of the important dynamical features exhibited by its continuous analogs (2.1) and (5.2) Loladze *et al.* [13] and other stoichiometrically explicit continuous models [12,14].

In particular, very low prey quality can drive the predator to the deterministic extinction. This happens because the prey with very low P:C, despite being a good source of calories, does not provide enough P to support the predator's growth. Moreover, any further increase in prey quantity further deteriorates its quality by diluting limited amount of P in the system with additional C.

On the other hand if prey quality is good, then systems (2.1) and (2.4) behave like traditional energy based predator-prey model, i.e. the dynamics is completely governed by the amount of biomass, but not its quality. In this case, it is possible to have an equilibrium with high predator biomass supported by low prey biomass (figure 2 (d_1), (c_1)), in which case most of the productivity of the prey is transferred to the predator. Any increase in the prey productivity, modeled via increases in carrying capacity K , leads to further increase in the predator biomass without changing prey biomass at the equilibrium. This is "the paradox of enrichment" (Rosenzweig [19]) as the prey seems to have no benefit of the enrichment.

Figure 4. All parameters are as in table (1) except that $b = 2.9$ and K varying from 0 to 2. (a) A bifurcation diagram of the grazer density against K for (5.1); (b) A bifurcation of the grazer density against K for (5.2); (c), (d) and (e) exhibit 2-, 4-, and 8-cycle periodic solutions of (5.1), where $K = 1.2$, 1.42 and 1.45, respectively; (f) chaotic behavior of (5.1) with $K = 1.6$: there is population explosion, crashback and slow recovery.

Further enrichment leads to the destabilization of the equilibrium via Hopf bifurcations. The amplitude of the resulting limit cycle increases with the further enrichment. This trend would continue indefinitely in traditional predator-prey models. However, in the stoichiometrically explicit models, both the continuous (5.2) and the discrete (5.1), show that an ever increasing amplitude of the limit cycle is not the only possible scenario. If the enrichment fuels into the system only one of the elements of which prey is made, in our case C, then the resulting low quality of the prey can halt oscillations and stabilize the system at the equilibrium. At this newly emerged node, high prey biomass supports low predator biomass (figure 2 (d_3), (c_3)). Here, any further enrichment actually benefits the prey but further hurts the predator. Thus, no enrichment paradox happens when the prey's quality is low (i.e. when P:C of the prey is lower than P:C of the predator). The existence (not simultaneous) of two equilibria with strikingly different ratios of prey to predator has been experimentally demonstrated by Nelson *et al.* [7].

The continuous and the discrete stoichiometric models exhibit same qualitative phenomena. This suggests the robustness of underlying effects of prey quality on predator-prey dynamics. Moreover, the discrete model shows that chaos can arise in stoichiometric system due to variation in food quality. Andersen [12] was the first to discuss such possibility and provided some analysis in his continuous model, but the simpler

Figure 5. Bifurcation diagrams of the grazer density plotted against b . The parameters are defined in table 1 except $K = 1.6$ and b varies from 0 to 3. (a, b) Bifurcation curves for (5.1); (c, d) Bifurcation curves for (5.2).

predator-prey models of Loladze *et al.* and Muller *et al.* [13,14] could not exhibit chaos as two-dimensional autonomous ODE systems. Yes, the simple discrete model (5.1) clearly shows period-doubling route to chaos (figure 4), which happens within biologically plausible parameter range. This supports Andersen's [12] argument on the possibility of chaos in stoichiometric systems.

In our model (2.4), as in the other stoichiometric models, predator's growth is not a monotone function of prey density. Predator-prey systems with non-monotonic functional

Table 1. Parameters in (5.1) (From Loladze *et al.* [13]).

Parameter	Value	Unit
P Total phosphorus	0.025	mg P l^{-1}
e Maximum production efficiency in carbon terms	0.8	
b Maximal growth rate of the producer	1.2	day^{-1}
d Grazer loss rate (includes respiration)	0.25	day^{-1}
θ Grazer constant P/C	0.03	$(\text{mg P})/(\text{mg C})$
q Producer minimal P/C	0.0038	$(\text{mg P})/(\text{mg C})$
c Maximum ingestion rate of the grazer	0.81	day^{-1}
a Half-saturation of ingestion response	0.25	mg C l^{-1}
K Producer carrying capacity limited by light	0.25–2.0	mg C l^{-1}

responses were considered before (e.g. [3,4]). However, there is an important difference. In non-stoichiometric models, the predator consumes less prey at higher density because catching prey at higher density is more difficult for some reasons (e.g. the ability of prey individuals to better defend or disguise themselves in large groups). Thus, higher prey density reduces predator attacks. The most dramatic phenomena that comes from this effect is the deterministic extinction of the predator. Note that in such cases, predator functional response is strongly correlated (often taken as proportional) to the predator numerical response. In the stoichiometric models, predator's consumption (functional response) is a *monotone* function of prey density. However, lower prey quality that arises at higher prey density makes predator's growth (numerical 'response') a *non-monotone* function of prey density. Thus, higher prey density does not reduce predator attacks, but hurts predator via reduced assimilation efficiency. This effect can be so strong that it may drive the predator to deterministic extinction.

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