

A Producer-Consumer Model with Stoichiometric Elimination Mechanisms

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Abstract

Producer-consumer (predator-prey) systems have been studied for many years in terms of energy flow or mass balance of the system. In recent years related models have been adjusted to take into account not only food quantity, but also food quality. In other words, the nutrient content, or equivalently, the stoichiometric ratio of nutrient to biomass, as well as the biomass, is of interest. In this paper we start from a version of the Rosenzweig-MacArthur [11] model of a producer-consumer system and modify it by introducing stoichiometry. The model considered here includes a sediment class in addition to the producer and consumer classes. The model is open for both carbon and the nutrient. It sets “target” structural ratios for both the producer and consumer, who eliminate carbon or nutrient, whichever appears in excess. This introduction of stoichiometry allows for different bifurcation sequences and corresponding dynamics than those that appear in the Rosenzweig-MacArthur model. The stoichiometric mechanisms we use are also in contrast to those presented in the Loladze, Kuang, Elser model [9] which has become a standard starting point for stoichiometric models. Especially notable is a parameter range where we observe the coexistence of an attracting equilibrium and an attracting periodic limit cycle.

Keywords: Population model, bifurcation, producer-consumer, predator-prey, Stoichiometry

1 Introduction

Population interactions in a food chain have been studied extensively for many years. A specific interaction is the behavior of a producer which is consumed by a consumer. Such “predator-prey” systems have usually focused only on the flow of a single currency, such as energy stored in carbon compounds or biomass. This point of view is analogous to considering only food quantity, but not food quality, as affecting the growth of a consumer. One measure of food quality is the nutrient to carbon ratio of the species which is being consumed: if this ratio differs from that of the consumer, then either carbon or nutrient will be deficient relative to the consumer’s needs. The nutrient to carbon ratio, however, is typically lower in producers than it is in consumers (Sterner and Elser 2002 [12]), meaning that carbon may be in excess and nutrients may be deficient in food relative to the consumer’s needs. Because of this mismatch, researchers have recently been including stoichiometry – the ratio of nutrients to carbon – in their models [1, 4, 6, 7, 8, 9, 10, 12, 14, 15]. Many of these models exhibit the following “paradox”: increasing the food quantity available for a consumer does not necessarily benefit the consumer. Especially in nutrient-limited systems, the consumer can even be driven to extinction by a concomitant decrease in food quality.

The Loladze, Kuang, and Elser model [9] (hereafter referred to as the LKE model) has, in particular, become a standard reference model for population systems with stoichiometry. It starts with the version of the Rosenzweig-MacArthur [11] (hereafter referred to as the R-M model) predator-prey system as given in eq. (1), but adds effects on the growth of both producer and consumer due to a single limiting nutrient for which the system is closed. The nutrient limitation is assumed to reduce both the natural carrying capacity of the producer, and the efficiency of the consumer’s conversion of producer biomass to its own biomass.

The elimination model we develop and investigate in this paper is also a generalization of the R-M model. Like the LKE model, we consider the effects of a single nutrient which is coupled to carbon in species-specific ratios. We keep track of both carbon as a surrogate for energy or biomass, and the nutrient. The mechanisms used here to introduce the stoichiometry, however, are different from the LKE mechanisms in three significant ways. First, primarily for nutrient cycling, we include a sediment class along with the consumer and producer classes. (See also [4, 8, 14, 15] for models including a free nutrient class, but in pelagic systems, and with different stoichiometric mechanisms.) This leads to a six-dimensional model: carbon and nutrient in each of the consumer, producer, and sediment. Second, we assume that the

system is open to nutrient flow, whereas the LKE model assumes a closed nutrient system. Third, the assumed stoichiometric mechanisms are different: instead of fixing the nutrient to carbon ratio of the consumer, a target ratio is set, and either carbon or nutrient is eliminated, whichever appears in excess. We do the same for the producer.

We compare our model to the R-M and LKE models with a numerical bifurcation analysis of all three using matching parameter values. We compare one-parameter cuts obtained by varying the birth rate of the producer. The behavior of all three models is the same for low birth rates: as the birth rate increases, a stable “no-life” equilibrium gives way to a producer monoculture, which gives way to a stable coexistence equilibrium. This coexistence equilibrium then destabilizes in a Hopf bifurcation, spawning a stable coexistence limit cycle. Behavior of the three models differs beyond this. The limit cycle in the R-M model grows in amplitude, but undergoes no further qualitative changes [13]. For the choice of parameter values in both [9] and this paper, the limit cycle in the LKE model grows until a saddle-node bifurcation on the limit cycle destroys the cycle. The attracting coexistence equilibrium born in this bifurcation persists, but its consumer value decreases as the producer birth rate increases, finally driving the consumer extinct in a transcritical bifurcation.

In the elimination model we present in this paper, numerical continuation experiments using AUTO [3] suggest that, for our choice of auxiliary parameters, beyond the first Hopf bifurcation, there is a second Hopf bifurcation, this time restabilizing the coexistence equilibrium and spawning an unstable limit cycle. This new limit cycle (and its stable manifold) appears to separate the basin of attraction of the attracting limit cycle from the basin of the restabilized equilibrium. Later (with increasing producer birth parameter) the two limit cycles coalesce and disappear in a saddle-node bifurcation of limit cycles, apparently leaving the coexistence equilibrium as a global attractor. No further bifurcations appear to exist for further increase of the birth rate b . We explain in more detail in the rest of the paper.

This paper is organized as follows. In Section 2, we begin by reviewing the Rosenzweig-MacArthur predator-prey model (eq. (1)). We summarize the model’s dynamical behavior and related bifurcations. Next we briefly review the LKE model (eq. (2)). In Section 3 we develop our six-dimensional stoichiometric elimination model (eq. (3)). We discuss the corresponding dynamics and bifurcations in Section 4. We discuss general stoichiometric issues which have come up in the process of writing this paper, including those for experimental design, in Section 5, and summarize in Section 6.

Portions of the work presented in this paper overlap with the Master’s project of the first author [16], under the supervision of the other three

authors.

2 Background

2.1 Consumer-Producer without Stoichiometry

Rosenzweig and MacArthur [11] performed a conceptual study of predator-prey interactions. One realization of their geometric model is

$$\begin{aligned}\frac{dP}{dt} &= bP - lP^2 - d_P P - f(P)C \\ \frac{dC}{dt} &= ef(P)C - d_C C\end{aligned}\tag{1}$$

where P is producer density and C is consumer density. The system parameters are

- b = per capita birth rate of the producer without self limitation
- l = coefficient of self limitation of the producer
- d_P = per capita death rate of the producer
- e = consumption efficiency; $0 \leq e < 1$
- d_C = per capita death rate of the consumer

The predation function f is assumed to be monotonic and non-decreasing. We further assume the specific form to be a saturating Michaelis-Menten (or Hollis type II) function: $f(P) = \frac{r_{max}P}{1+hP}$. We illustrate the general behavior of the system with the choice of parameter values $l = 0.2$, $d_P = 0.1$, $r_{max} = 1$, $h = 2$, $e = 0.8$, and $d_C = 0.2$, and various b . These parameter values were chosen to match corresponding parameter values in the other two models of the paper: the LKE model of eq. (2) and the elimination model of eq. (3), introduced in Sec. 3.

Analysis. This system can be analyzed explicitly for equilibria and their stability in terms the system parameters. There are three possible equilibria: $(P, C) = (0, 0)$ where neither the producer nor the consumer exist, $(P, C) = (\frac{(b-d_P)}{l}, 0)$ where there is a producer monoculture at its carrying capacity without a consumer, and a coexistence equilibrium at $(P, C) = (P^*, C^*)$, where P^* is determined by the unique solution to $f(P) = \frac{d_C}{e}$, and $C^* = \frac{(b-d_P)P^* - l(P^*)^2}{f(P^*)}$. This coexistence equilibrium will exist as long

as the maximum predation rate r_{max} is greater than $\frac{d_C}{e}$. Equilibrium bifurcations as the birth rate b is varied are determined by computing the Jacobian and evaluating at the three equilibrium points. There is a transcritical bifurcation from a stable no-life equilibrium to a stable producer monoculture at $b = d_P = 0.1$. A second transcritical bifurcation occurs at $b = \frac{d_P r_{max} e + d_C l h - d_C d_P}{r_{max} e - d_C} \approx 0.23333$, where the stable monoculture is supplanted by a stable coexistence equilibrium. By evaluating the Jacobian at the coexistence equilibrium and solving for the b value which results in pure imaginary eigenvalues, we can determine b_H , which we use to denote an apparent Hopf bifurcation. For $b > b_H \approx 0.76667$, the system has a coexistence limit cycle which we believe to always be stable [13]. The amplitude of the limit cycle continues to grow as b is increased, but no qualitative change in system behavior has been observed.

The bifurcations involving these equilibria are illustrated in the top panel of the bifurcation diagrams of Fig. 2 in Section 4. The bifurcation diagram was computed using the continuation software AUTO [3].

2.2 Loladze, Kuang, and Elser Model

Loladze, Kuang, and Elser [9] introduced a model that has become a standard reference model for most recent stoichiometric population models. They began with the same Rosenzweig-MacArthur predator prey model as eq. (1). Stoichiometry is introduced to the model under the following assumptions:

1. The system is closed for nutrient: there is a fixed total nutrient content, N .
2. The nutrient to carbon ratio in the consumer is fixed at θ_C .
3. The nutrient to carbon ratio in the producer varies, but never falls below a minimum ratio q .
4. All nutrient in the system is divided into two pools: nutrient in the producer and nutrient in the consumer. (There is no sediment compartment.) The underlying assumption is that once the nutrient is released through the death of the consumer, it is immediately recycled back to the producer.
5. The carrying capacity of the producer has a maximum of $K = (b - d_P)/l$ (depending on system parameters such as light). This maximum K is reduced to $\frac{N - \theta_C C}{q}$, the maximum producer population that can be supported with the available producer nutrient $N - \theta_C C$ at the minimum nutrient to carbon ratio q whenever $\frac{N - \theta_C C}{q} < K$.

6. The production efficiency has a maximum value of e , which is proportionately reduced whenever the average nutrient to carbon ratio of the food (the producer) is less than the fixed ratio θ_C of the consumer.

The result, with the introduction of the two minimum functions to satisfy items 5 and 6 above, reads

$$\begin{aligned}\frac{dP}{dt} &= bP - \frac{(b - d_P)P^2}{\min(K, (N - \theta_C C)/q)} - d_P P - f(P)C \\ \frac{dC}{dt} &= e \min\left(1, \frac{(N - \theta_C C)/P}{\theta_C}\right) f(P)C - d_C C\end{aligned}\quad (2)$$

where P is the density of the producer, and C is the density of the consumer. System parameters are

- b = per capita growth rate of producer
- d_P = per capita death rate of producer
- d_C = per capita death rate of consumer
- $f(P)$ = consumer's ingestion rate
- θ_C = consumer's nutrient to carbon ratio (assumed fixed)
- N = total amount of nutrient in system
- q = minimum nutrient to carbon ratio in producer
- K = producer's carrying capacity based on light intensity without regard to stoichiometry
- e = maximal production efficiency (for sufficiently nutritious food)

We note that the system of eq. (2) is equivalent to the original equations presented in Loladze, Kuang, Elser [9]. We have rewritten it in a slightly more complicated form to simplify its comparison to the R-M model and to the elimination model developed here. Specifically, the logistic growth for the producer is split into birth $bP - lP^2$ and death $-d_P P$, the coefficient l is adjusted according to the LKE stoichiometric assumptions (assumption 5 above).

Loladze, Kuang and Elser studied their system in [9]. There are up to five equilibria: the origin (no life), a producer monoculture, and three coexistence

equilibria. Depending on parameters, there can exist zero, one, two or three coexistence equilibria in the open first quadrant. In order to illustrate the dependence of system dynamics on the parameter b , we performed a numerical bifurcation analysis using AUTO [3]. The remaining parameters were fixed at: $d_P = 0.1$, $d_C = 0.2$, $f(P) = \frac{P}{2+P}$, $\theta_P = 0.020$, $\theta_C = 0.0275$, $N = 0.15$, $q = 0.0038$. These parameter values were chosen to match the parameters in the elimination model which follows, rather than the original parameters in the LKE paper [9].

The resulting bifurcation diagram varying b is almost identical to the bifurcation diagram obtained in LKE [9] by varying K . The only difference is that in LKE [9], the saddle equilibrium and the repelling equilibrium do not disappear, at least in the parameter range displayed in Figure 4 of [9].

We find the following dynamical behavior. For $0 < b < 0.1$ neither the producer nor the consumer can survive. For $0.1 < b < 0.23333$ the system has a stable producer monoculture. For $0.23333 < b < 0.76667$, the system has a stable producer-consumer coexistence equilibrium. The bifurcations at $b = 0.1$ and $b \approx 0.23333$ are both transcritical bifurcations.

At $b \approx 0.76667$, the coexistence equilibrium undergoes a supercritical Hopf bifurcation, spawning an attracting coexistence limit cycle. The amplitude of the limit cycle increases as b increases, accompanied by an increase in the period of the limit cycle. At $b \approx 1.53893$, the limit cycle is destroyed when a saddle-node bifurcation of equilibria causes two equilibria – one saddle and the other a stable node – to appear on what was formerly the periodic limit cycle. The stable node which appears in this bifurcation becomes an attractor.

As b increases further, the producer's equilibrium density also increases (not shown) while the consumer's density decreases. At $b \approx 2.18333$, the equilibrium source and saddle come together and eliminate each other in a nonsmooth version of a saddle-node bifurcation. This bifurcation is the only qualitative difference between this modified LKE bifurcation scenario in b and the original bifurcation scenario in K presented in [9]. Finally at $b \approx 4.06364$, there is a third transcritical bifurcation after which the consumer is not able to survive. The consumer dies out beyond this third transcritical bifurcation because while there is sufficient quantity (carbon) in the food (producer), the food quality (phosphorus to carbon ratio) is diluted by the excess carbon.

These bifurcations are illustrated below in the middle panel of Fig. 2 in Section 4. Not surprisingly, since AUTO is not intended for nonsmooth systems, it was not able to continue through the nonsmooth saddle-node bifurcation, but it was able to approach the bifurcation from both sides. It is more surprising that AUTO [3] *was* able to perform continuation on the rest of this system. Some continuations did fail, but we were able to

adjust parameter values to find combinations for which the continuation did proceed.

3 A Stoichiometric Elimination Model

We develop here a new stoichiometric model for a producer-consumer system. We include a sediment compartment, with the goal of modeling nutrient cycling. We have in mind a terrestrial system, with a plant for a producer and an animal for a consumer. Examples might be cows feeding on grass, or moose feeding on brush. We keep track of carbon and one limiting nutrient, such as nitrogen, or possibly phosphorus, in each of the three compartments. Carbon can be thought of as a surrogate for biomass or energy.

The resulting state variables are as follows, with upper-case variables referring to carbon and lower-case variables referring to nutrient.

- P = density per unit area of producer carbon
- p = density per unit area of producer nutrient
- C = density per unit area of consumer carbon
- c = density per unit area of consumer nutrient
- S = density per unit area of sediment carbon
- s = density per unit area of sediment nutrient

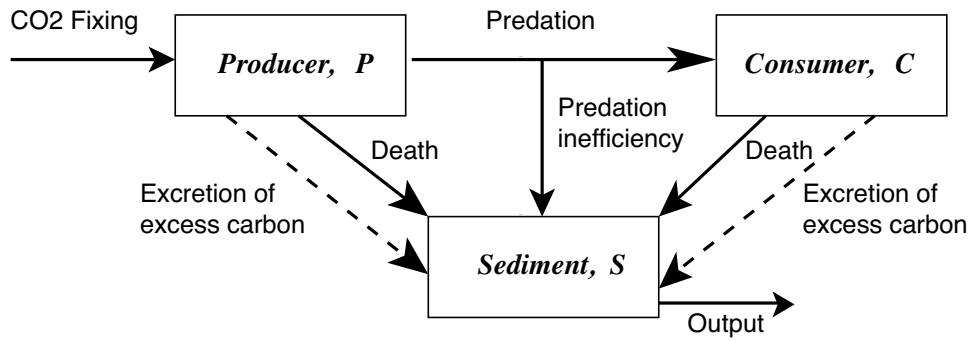
Model assumptions are described in words below, flowcharts in Fig. 1, and in equations eq. (3).

We make the following assumptions for the flow of carbon and nutrient. The related terms in the differential equations are in parentheses.

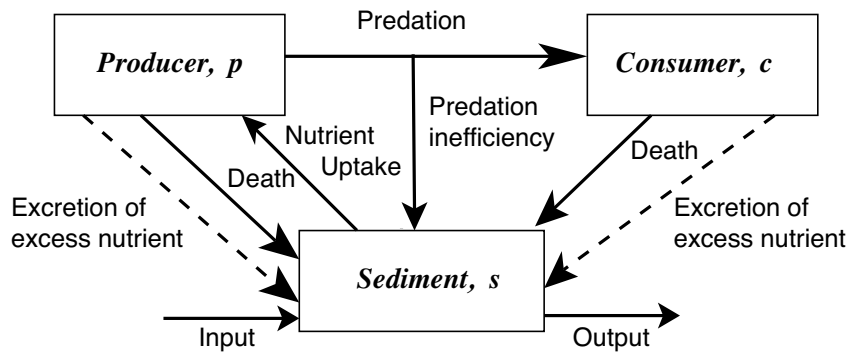
1. Carbon input to the system is entirely due to photosynthesis by the producer. ($bP - lP^2$). (See item 2 following eq (3) below.)
2. Nutrient enters the system via the sediment compartment, due, for example, to rainfall. (IN)
3. Carbon removal from the system is only from the sediment, for example being washed away with rain runoff. Linear outflow is assumed. ($d_S S$) (See item 3 following eq (3) below.)
4. As with the carbon, nutrient removal from the system is only from the sediment. ($d_S s$) (See item 3 following eq (3) below.)

Figure 1: Carbon and nutrient flowcharts of the elimination model. The dashed lines illustrate the stoichiometric elimination of excess carbon or nutrient.

Carbon:



Nutrient:



5. Carbon and nutrient are taken together from the producer when the consumer eats. Only a fraction $(ef(P)C, ef(P)Cp/P)$ gets transferred to the consumer; the remainder $((1 - e)f(P)C, (1 - e)f(P)Cp/P)$ is assumed to go to the sediment due to inefficient consumption by the consumer.
6. Carbon and nutrient are transferred together from the producer or consumer to the sediment when either dies. Linear death rates are assumed. $(d_P P, d_{Pp}, d_C C, d_{Cc})$
7. Nutrient uptake is assumed to be proportional to the density of the producer, and the density of the nutrient in the sediment. $(\mu P s)$
8. **Stoichiometry assumption.** Both the producer and consumer are assumed to have target structural nutrient-to-carbon density ratios (θ_P, θ_C) . When these target ratios are not matched, the element that is in excess is eliminated, by excretion, for example. The elimination rates are assumed to be proportional to the difference between the actual densities present and the densities which would be present if the producer (or consumer) were exactly at its target ratio. This results in four stoichiometric elimination terms. Only two of them can be active at any instant – either the elimination of excess carbon from the producer, *or* the elimination of excess nutrient from the producer. Similarly, only one of the two elimination terms for the consumer is active at any instant. Specifically,

- $m_1(P - \frac{p}{\theta_P})^+$ is the excretion rate of excess producer carbon, active when $p : P$ is below θ_P
- $m_2(C - \frac{c}{\theta_C})^+$ is the excretion rate of excess consumer carbon, active when $c : C$ is below θ_C
- $m_3(p - \theta_P P)^+$ is the excretion rate of excess producer nutrient, active when $p : P$ is above θ_P
- $m_4(c - \theta_C C)^+$ is the excretion rate of excess consumer nutrient, active when $c : C$ is above θ_C .

We have used the notation

$$x^+ = \begin{cases} x & \text{if } x \geq 0 \\ 0 & \text{if } x < 0 \end{cases}$$

to denote the “positive part” of the quantity x .

The full six-dimensional system reads

$$\begin{aligned}
\frac{dP}{dt} &= bP - lP^2 - f(P)C - d_P P - m_1(P - \frac{p}{\theta_P})^+ \\
\frac{dC}{dt} &= ef(P)C - d_C C - m_2(C - \frac{c}{\theta_C})^+ \\
\frac{dS}{dt} &= d_P P + d_C C - d_S S + (1 - e)f(P)C + m_1(P - \frac{p}{\theta_P})^+ + m_2(C - \frac{c}{\theta_C})^+ \\
\frac{dp}{dt} &= \mu P s - d_P p - \frac{p}{P} f(P)C - m_3(p - \theta_P P)^+ \\
\frac{dc}{dt} &= ef(P)C \frac{p}{P} - d_C c - m_4(c - \theta_C C)^+ \\
\frac{ds}{dt} &= d_C c + d_P p + IN - d_S s - \mu P s + (1 - e)f(P)C \frac{p}{P} + m_3(p - \theta_P P)^+ \\
&\quad + m_4(c - \theta_C C)^+ \tag{3}
\end{aligned}$$

There are several simplifying assumptions made in the construction of this model that should be pointed out.

1. We note the the producer birth rate $bP - lP^2$ does not explicitly depend on the nutrient available in the soil. However, if the producer is growing in a nutrient-limited environment, it will soon eliminate the excess carbon to the sediment. So the effect is similar (but not identical, as we point out in the next item) to reducing net growth – especially since the sediment carbon does not affect the rest of the compartments.
2. In the model we are explicitly separating producer birth and death terms. This split was unnecessary in the R-M and LKE models because both models depended only on the difference $b - d_P$ of the birth and death rates of the producer. In our model, however, because reduction in producer birth reduces only the producer carbon (P), while producer death causes transfer of nutrient as well as carbon to the sediment (P to S and p to s), reduction of birth and increase of death are not equivalent. Consequently, one might take the positive part of the birth term $bP - lP^2$, or use a more process based birth term such as in [4]. It is clear, however, from the first equation of the system (3) that the producer carbon levels cannot leave the region $bP - lP^2 \geq 0$. Hence, it suffices to proceed under the assumption that $bP - lP^2 \geq 0$, rendering restriction to the positive part unnecessary.
3. There is no explicit carbon loss term in either the producer or consumer due to respiration. For the producer, this can be justified by viewing

the birth term $bP - lP^2$ as representing *net* production: photosynthesis minus respiration. For the consumer, respiration is neglected purely for simplicity. The system appears to have the same qualitative behavior with or without an explicit respiration term. (See, however, item 1 of Section 5.)

4. In contrast to the LKE study [9], we have explicitly elected to vary the producer per capita birth rate rather than its carrying capacity. It seems to be more process oriented to have the birth rate determine the carrying capacity, rather than the other way around.
5. The nutrient uptake term, $\mu P s$, is the same as in simple foraging models. Alternatively, one might assume this uptake term to be proportional to the birth of the producer, $bP - lP^2$ rather than its current density P . Additionally, the uptake might plausibly depend on the stoichiometry of the sediment, $\frac{s}{S}$, rather than merely on the sediment nutrient s . (Limited numerical simulations show the same bifurcation sequences in both cases.)

Since we are comparing the elimination model with the LKE model, some comments about the dimensionality of the two models are of interest. Because the stoichiometric mechanisms in the two models are different, the six-dimensional elimination model does not appear to directly reduce to the two-dimensional LKE model. One could, however, start with the two-dimensional LKE model, and track assumptions from the elimination model to see which ones lead to the extra four dimensions:

- two dimensions are added with the inclusion of the sediment class, one for carbon and one for nutrient,
- one additional dimension is necessary to allow the consumer nutrient to carbon ratio to float,
- a final additional dimension is necessary to allow the nutrient system to be open.

There is, of course, a tradeoff between the extra dimensions and the flexibility of the model. Our experience suggests that the most critical difference in the two models is that the elimination model is open to nutrient flow, while the LKE model is closed. The inclusion of the nutrient sediment class appears to be significant to model nutrient cycling as well. We note that because the carbon sediment population (S) does not affect any of the other five populations (see eq. (3)), it could easily be ignored. Constraining the consumer

nutrient to carbon ratio at a constant would likely not change the qualitative behavior of the model. In summary, we could have fixed the consumer ratio, and ignored the S population and worked with a four-dimensional system. However, since the system can be numerically investigated just as easily with six dimensions as with four, and since any dimension beyond three is impossible to visualize, we have elected to proceed with the full six-dimensional model.

4 Model Analysis

We now proceed to analyze the elimination model (3). Because of the number of cases to consider (due to the four stoichiometric terms which can be turned on or off according to the stoichiometric ratios of the producer and consumer), performing an analytic equilibrium analysis is not straightforward. In our numerical exploration, we found three equilibrium points: one with nutrient but no life, one producer monoculture without any consumer, and one coexistence equilibrium with positive values for both producer and consumer. However, all three equilibria are not always physically relevant – some components can be negative, depending on the parameter values chosen.

4.1 Numerical Results

The primary parameter we vary in our numerical experiments is the producer birth rate b . We also vary a secondary parameter, the nutrient input level IN . As we will show, when IN is very small, there is not enough nutrient in the system to support a consumer. At the other end of the spectrum, when IN is large, the system essentially reverts to the Rosenzweig-MacArthur predator-prey system, at least for small to moderate values of b . The most interesting dynamics happens for midrange values of IN , illustrated by our choice of $IN = 0.01$.

Parameter values were chosen carefully to simultaneously satisfy the following five conditions:

1. All parameter values for terms which corresponded in the LKE and elimination models were the same ($l, f(P), d_P, e, d_C, \theta_C$),
2. AUTO continuation worked on the nonsmooth LKE system (eq. (2)),
3. AUTO continuation worked on a “minimally smoothed” version (described below) of the nonsmooth elimination model (eq. (3)),

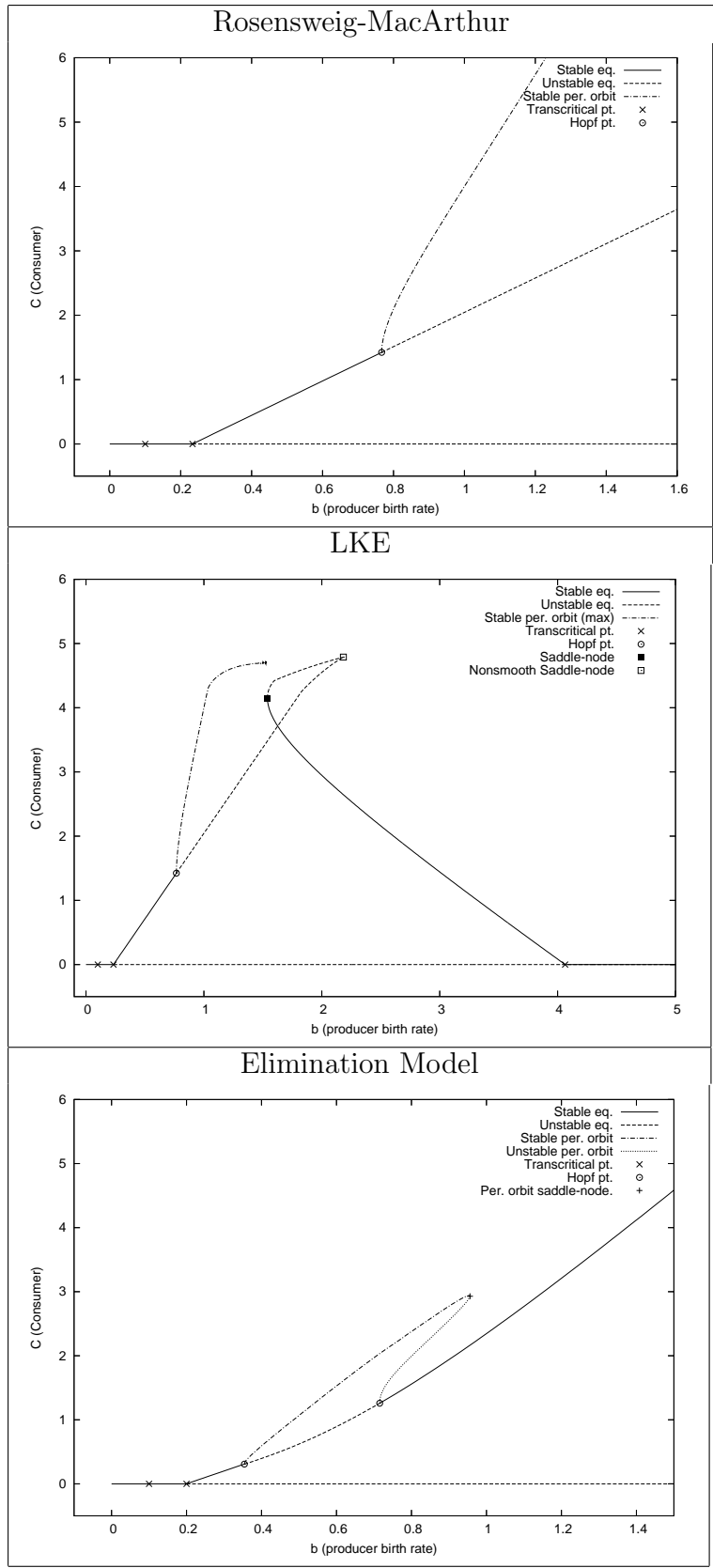


Figure 2: Comparison of bifurcation diagrams: Consumer C versus Producer birth rate b .

4. the behavior of the LKE model along our one-parameter cut in b qualitatively matched the behavior of the LKE model along the one-parameter cut in K presented in [9],
5. the behavior of the elimination model along the one-parameter cut in b matched the (interesting) behavior observed in [16].

Note that parameter q in the LKE model is a minimum nutrient-to-carbon ratio for the producer, while θ_P in the elimination model is a target ratio, which should be larger than the minimum. Indeed, our $\theta_P = 0.02 > q = 0.0038$. The other parameters were fixed as follows: $l = 0.2$, $d_P = 0.1$, $e = 0.8$, $d_C = 0.2$, $d_S = 0.3$, $\mu = 0.2$, $m_1 = m_3 = .0001$, $m_2 = m_4 = 1.0$, $\theta_P = 0.020$, $\theta_C = 0.0275$, and $f(P) = \frac{P}{1+2P}$. Note that the elimination rate for excess carbon or nutrient is much higher for consumers ($m_1 = m_3 = 1$) than it is for producers ($m_2 = m_4 = .0001$). This is consistent with herbivores being able to eliminate excess carbon or nutrient much more quickly than the plants they eat.

4.1.1 One-parameter cut in b for $IN = 0.01$

We used the continuation software AUTO [3] to compute a one-parameter bifurcation diagram in b . Many of the initial continuation attempts, however, failed. We speculate this failure was for at least two reasons. First, the system of differential equations, because of the elimination terms, is continuous, but not smooth. AUTO is not designed to handle nonsmooth systems. This is especially a problem with periodic solution continuation because the periodic solution may (and often does) pass across boundaries of the phase space where the vector field is not smooth. Second, the periodic solutions that are born in the first Hopf bifurcation grow in both amplitude and period. Portions of the periodic orbits often are forced close to the $P = 0$ hyperplane. Since several terms in the system (eq. (3)) are divided by P , this results in possible division by a number close to zero.

We did not try compensate for the latter problem (such as converting to the “stoichiometric form” by keeping track of $Q = p/P$ instead of P), but we did compensate for the nonsmoothness as follows. First note that from small $\beta > 0$, a smooth approximation to x^+ is $s_\beta(x) = \begin{cases} 0 & \text{if } x \leq 0 \\ xe^{-\beta/x} & \text{if } x > 0. \end{cases}$ Furthermore, the smooth functions $s_\beta(x) \rightarrow x^+$ uniformly as $\beta \rightarrow 0$. We used this smooth approximation and replaced $\frac{m_1}{\theta_P}(\theta_P P - p)^+$ with $\frac{m_1}{\theta_P} s_\beta(\theta_P P - p)$. The seven other nonsmooth terms in equation (3) were similarly replaced. This resulted in AUTO being able to compute both the one-parameter bifurcation diagram in Fig. 2 as well as the two-parameter bifurcation dia-

grams in Fig. 4. The numerical b values of the bifurcations changed significantly with the smoothing parameter β . Consequently, a significant amount of experimenting was required to find a minimal value of β for which the one-parameter continuation in AUTO worked. The reported results used a smoothing parameter of $\beta = .0005$.

We found the following behavior. For $0 < b < 0.1$ neither the producer nor the consumer can survive. For $0.1 < b < 0.199995$ the system possesses a stable producer monoculture. For $0.199995 < b < 0.354296$, the system possesses a stable producer-consumer coexistence equilibrium. The bifurcations at $b = 0.1$ and $b \approx 0.199995$ are both transcritical bifurcations.

At $b \approx 0.354296$, the coexistence equilibrium undergoes a supercritical Hopf bifurcation, spawning an attracting coexistence limit cycle. The amplitude and period of the limit cycle both increase as b increases. The next bifurcation distinguishes the behavior of our model from both the R-M and LKE models. At $b \approx 0.715174$, the coexistence equilibrium undergoes a second Hopf bifurcation, this time restabilizing the coexistence equilibrium and spawning a second (unstable) limit cycle. This bifurcation results in a bistable regime: the restabilized equilibrium along with the stable limit cycle which already existed. The stable manifold of the unstable limit cycle presumably separates the respective basins of attraction. This second periodic limit cycle grows in amplitude with increasing b until $b \approx 0.9562$, where it coalesces with the attracting limit cycle and both limit cycles disappear in a saddle-node of limit cycles. For b values beyond this, the coexistence equilibrium appears to be globally attracting. See the resulting bifurcation diagram in the bottom panel in Fig. 2. Compare these bifurcations with Fig. 2 of Diehl [4] as well; that model is similar because it has a second Hopf bifurcation, but it differs because it has no bistable region, and it has the extinction of the consumer with high light levels, as is common for closed nutrient systems.

Since the bistable behavior appears to be a unique feature among the stoichiometric models with which we are familiar, we numerically illustrate — using a representative parameter value of $b = 0.81$ — in Fig. 3.

4.1.2 Two-parameter bifurcation diagram in b and IN

In order to better understand the context of our single one-parameter cut described in the previous subsection, we computed a two-parameter bifurcation diagram in b and IN . The remaining parameters were unchanged from those used in the one-parameter cut and listed above. Results are summarized in Fig. 4. The bifurcations corresponding to the original $IN = 0.01$ one-parameter cut are indicated on the figure for reference. The accompany-

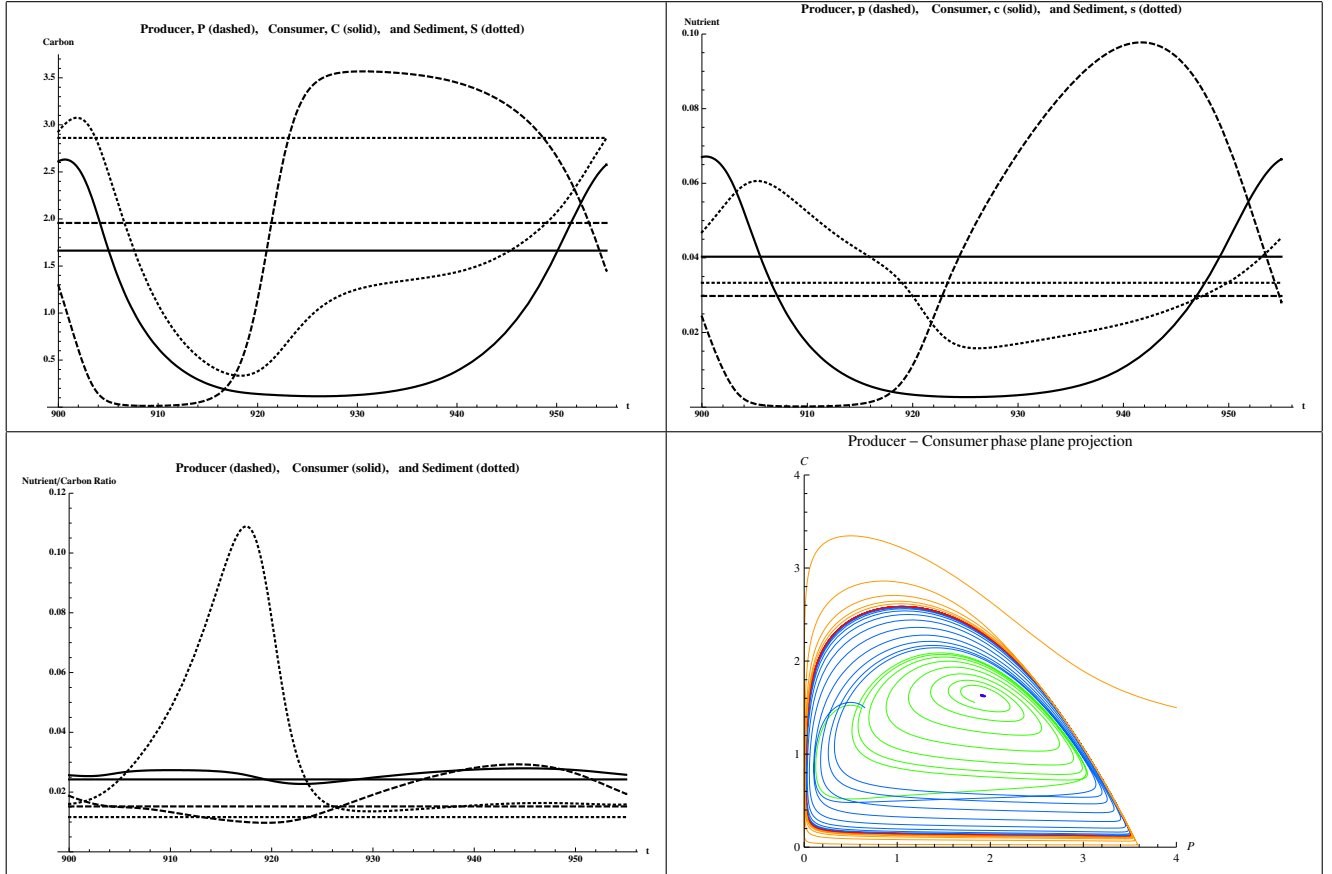


Figure 3: Bistability: attracting equilibrium and attracting limit cycle. Parameters: $b = 0.82$, $IN = 0.01$, no smoothing. Solutions were numerically generated with *Mathematica*. Top-left: time series without initial transients for the three carbon variables for both the attracting periodic orbit and the attracting equilibrium. Top-right: same as top-left, but showing the nutrient values instead of the carbon values; Bottom-left: same as top-left and top-right, but for the three stoichiometric ratios $p : P$, $c : C$ and $s : S$. Compare with the target ratios for producer (0.02) and consumer (0.0275). Bottom-right: projection of phase space to P - C plane for three orbits, starting at $(P, C) = (0.6, 1.5)$, $(0.65, 1.5)$, and $(4.0, 1.5)$, respectively; the green and blue orbits start almost together, but the green approaches the attracting equilibrium, while the blue approaches the attracting (red) limit cycle; the orange orbit also approaches the limit cycle, but from the “outside”. The crossing of orbits is a reminder that this is a projection from the full six-dimensional phase space.

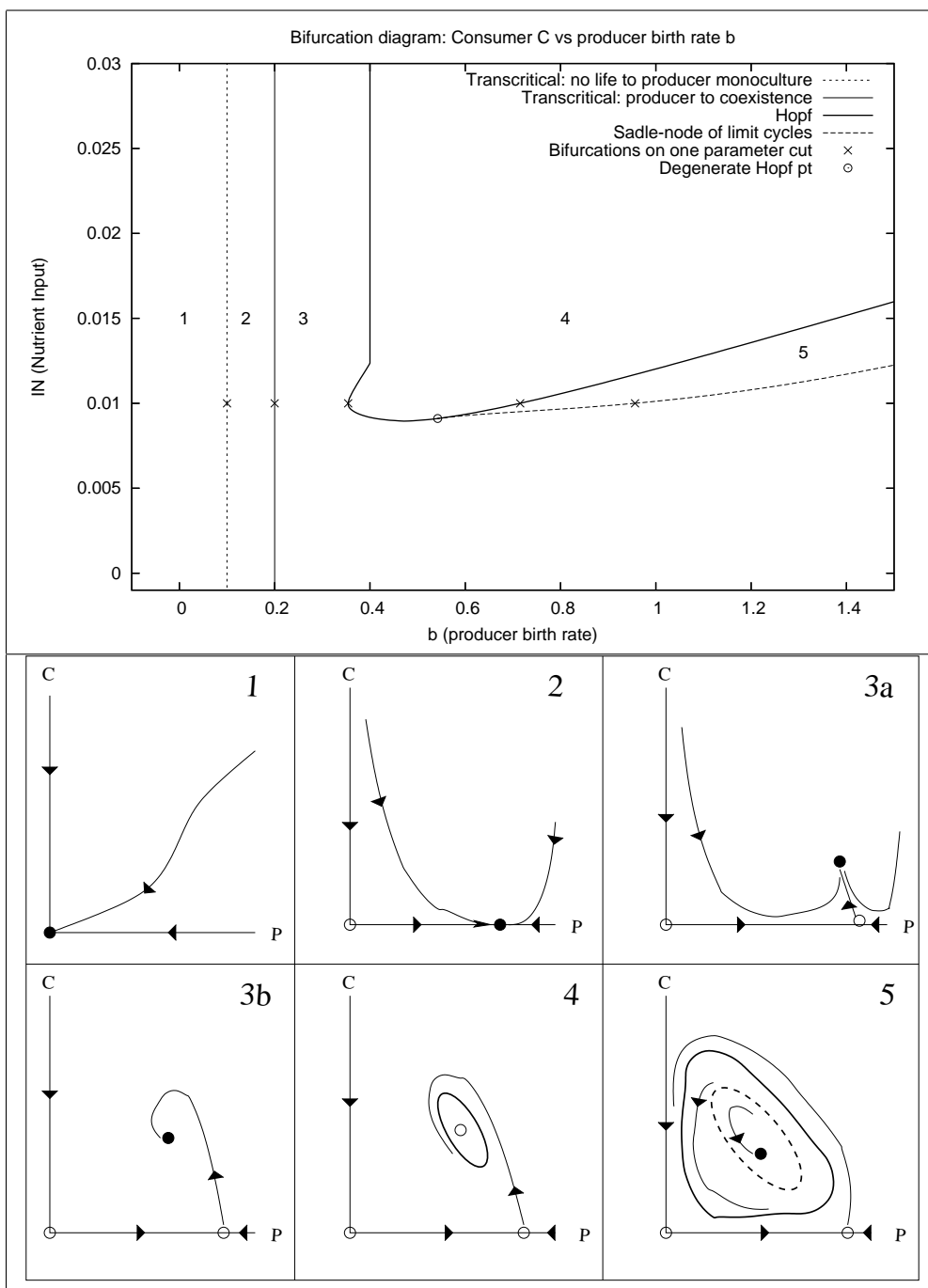


Figure 4: Top: two-parameter bifurcation diagram: IN vs b; bottom: *conceptual* phase portraits projected to the (P, C) plane for the corresponding regions.

ing “phase portraits” are conceptual only. They represent possible behaviors when projected from the six-dimensional phase space to the two-dimensional (P, C) plane.

There is a transcritical bifurcation curve at $b = 0.1$ independent of IN . This can be analytically verified as the parameter value where the origin changes from an attracting node to a saddle. Schematic phase portrait 1 gives way to schematic phase portrait 2. The producer monoculture becomes attracting as the origin becomes repelling. The second transcritical curve is parallel to the first: the attracting producer monoculture equilibrium is supplanted by an attracting coexistence equilibrium: phase portrait 2 changes to phase portrait 3. Phase portraits 3a and 3b are topologically equivalent, but are geometrically distinguished by the “straight” approach to the attracting equilibrium corresponding to real eigenvalues (3a) versus the spiral approach corresponding to complex eigenvalues (3b). The two are separated by a curve (not shown) corresponding to equal eigenvalues of the coexistence equilibrium. The Hopf bifurcation curve is the most interesting. It is roughly “V” shaped. The left-hand branch, roughly vertical, corresponds to a supercritical bifurcation. There is a codimension-two degenerate Hopf bifurcation point at approximately $(b, IN) = (0.542, 0.0091)$, where the Hopf bifurcations change from supercritical to subcritical. Consistent with the unfolding of this degenerate Hopf bifurcation point [5], the curve of saddle-nodes of limit cycles emanates from this point, tangent to the Hopf curve. Inside the “V” (region 4) there is a single attracting limit cycle. Below the right-hand branch of the Hopf curve and above the saddle-node of limit cycles curve is the bistable region 5. Passing the saddle-node of limit cycle curve from region 5, the two limit cycles coalesce and disappear, leaving only an attracting coexistence equilibrium corresponding to phase portrait 3 again.

The two-parameter bifurcation diagram illustrates the possible bifurcation sequences for one-parameter cuts in b for fixed values of IN . If IN is less than (approximately) 0.005, then the cut misses the Hopf curves altogether. If IN is above that, it appears that any one-parameter cut in b will cross in succession the two transcritical bifurcations, the supercritical Hopf bifurcation, and then the subcritical Hopf bifurcation. Without further continuation of the saddle-node of limit cycles curve, it is difficult to predict whether horizontal cuts will cross this curve or not. It is clear, however, that the larger IN , the larger the parameter range (of b values) corresponding to an attracting limit cycle - as we see in the R-M model. This is consistent with the observation that if there is a sufficient supply of nutrient, the stoichiometric models should approach the non-stoichiometric R-M model behavior.

5 Discussion

In the process of working on this paper, several issues which are related to stoichiometry have surfaced. We point them out here.

1. **Paradox of energy enrichment.** Many stoichiometric population models refer to the paradox of energy of enrichment: increase in energy (birthrate of the producer in our elimination model) does not necessarily result in a corresponding increase in the consumer populations [9, 4]. The LKE [9] and Diehl [4] models exhibit a strong version of this paradox: energy increase eventually results in the extinction of the consumer. Both these models assume closed nutrient pools. The difference between systems that are open versus closed for nutrient appears to be critical. In nutrient-closed systems, the increase in energy results in an increase in producer biomass. Since there is a fixed amount of nutrient, this results in a decrease in food quality, which, in turn, results in a decrease in the consumer population which can be supported. Eventually, the food quality is too low to support the consumer at all. Our elimination model is open to nutrient, and while the stoichiometry restricts the parameters for which a limit cycle can exist, the value of the consumer at the coexistence equilibrium appears to grow roughly linearly with the producer birth rate b . (See the bottom panel of fig. 2.)

We note that [16] did include an explicit respiration term for the consumer. Numerical continuations in b revealed exhibited qualitatively similar bifurcation phenomena, but the asymptotic value of the consumer equilibrium seemed to approach an asymptotic value with increase in b . We elected to leave this respiration term out because it kept the model as simple as possible, while retaining the same qualitative bifurcation structure. It is not clear which model is most appropriate for natural systems, or to what extent natural systems exhibit the paradox of energy enrichment.

2. **Range of stoichiometric variation.** An interesting behavior of the model is the failure of either the consumer or the producer to equilibrate to its target stoichiometric ratio (Fig. 5). Moreover, the producer equilibrium ratios vary more than the consumer ratios. For example, as b increases in Fig. 5, the producer ratio seems to be approaching approximately 57% of its target value, while the consumer ratio is approaching approximately 80% of its target ratio. In addition, the stoichiometric ratio of the producer varies over a much larger range than that of the producer during transient dynamics and along periodic orbits

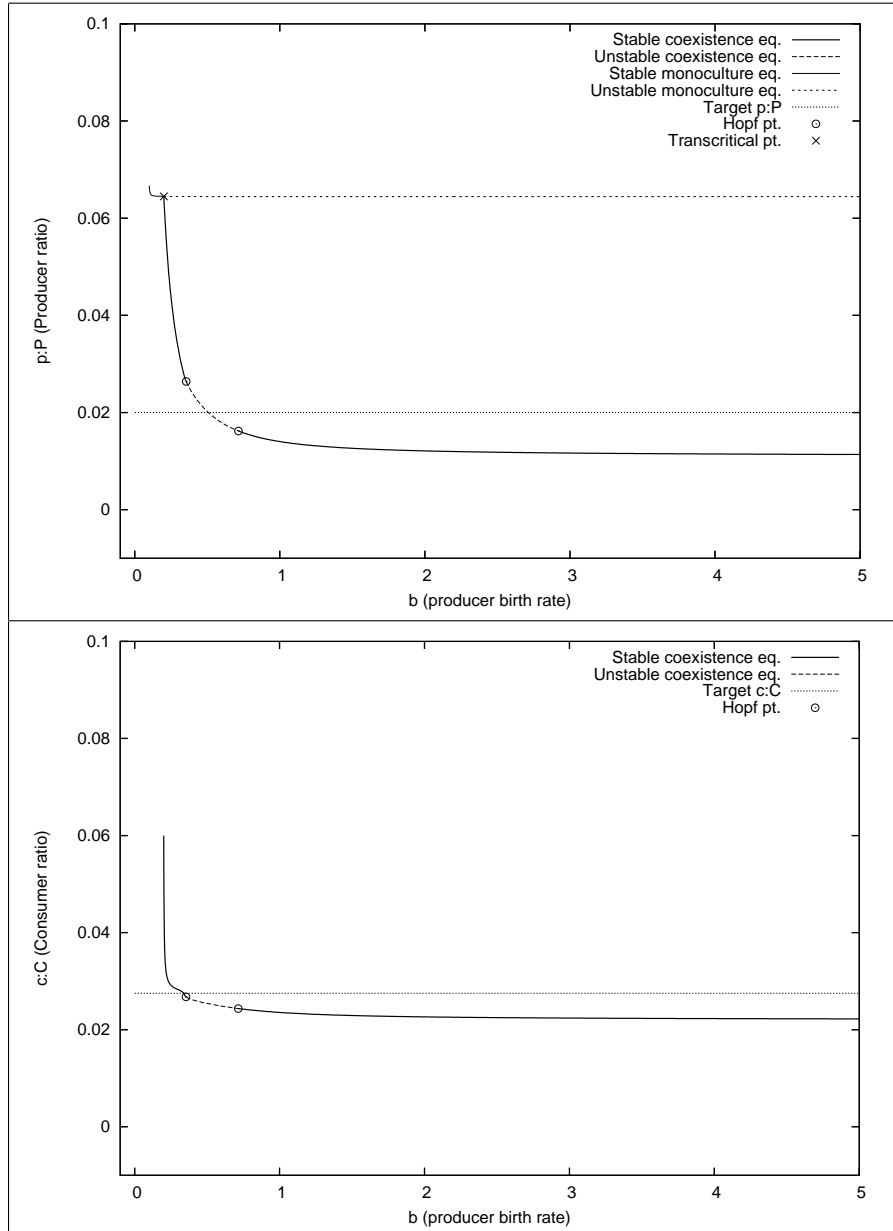


Figure 5: Top: Plant stoichiometric ratio along the producer monoculture and coexistence equilibria versus b ; Bottom: Consumer stoichiometric ratio along the coexistence equilibrium versus b . Compare with the bottom panel of fig 2.

(Fig. 3, lower-left). Producers typically have lower stoichiometric ratios and their nutrient concentrations vary much more widely than those of consumers (Sterner and Elser 2002 [12]), as is the case in our model. We surmise this is because the producer elimination rate is several orders of magnitude lower than that of the consumer, so it is less able to adjust its stoichiometry by the excretion mechanism we model. The qualitative similarity of the model predictions with the stoichiometric behavior of real producers and consumers is encouraging, and suggests that large differences between producers and consumers in elimination rates may be one reason for their wide differences in stoichiometric ratios.

3. **Stoichiometric model compartments.** When stoichiometry is considered in a model, the decisions about what compartments are necessary, as well as when carbon and/or nutrient is to be considered in a certain compartment, is not always clear. For example, do we need to separate sediment nutrient into mineralized and nonmineralized compartments as in nutrient decomposition and recycling models [2]? When a consumer eats food, when is it considered as consumer biomass: when it is bitten, when it is swallowed, or when it is converted to structural biomass? Ingested food and structural biomass might need to be separated into distinct compartments. Similarly, urine and fecal matter might need to be considered separately: excess nutrient is typically excreted in urine, while excess carbon is typically excreted as fecal matter. When biomass is assumed to be homogeneous, these issues are not necessary to deal with because it is assumed that carbon and nutrient are cycled together. Whether or not the introduction of any of these additional classes results in new and/or changed dynamics remains to be seen.
4. **Nonsmooth models.** Many stoichiometric mechanisms are modelled by systems that are not smooth, as is implicit in the widespread use of a minimum function in both the elimination model presented here, as well as the LKE model and others [4, 7, 9] How these nonsmooth models behave and whether they are realistic demands further study.
5. **Experimental Implications.** The two-parameter bifurcation diagram for birth rate and nutrient input (Fig. 4) suggests some possible experimental tests of our model. The experiments could vary either birth rate (b) or nutrient input (IN) or both to see if an experimental system can be pushed across one or more of the bifurcations. Varying birth rate could be done by using different species, each with its own

intrinsic birth rate. However, differences in birth rates could also be confounded with differences in other species parameters, so such experiments may not be straightforward. Varying nutrient input rate is far easier and, because nutrient input is independent of species, it would not be confounded with other parameters. The most interesting region to explore would be the bifurcations between regions 3 and 4 with region 5 of Fig. 4, where our model predicts a bistability of equilibria depending on initial amounts of C and P . For our parameter values, this would happen between values of 1.0 and some value greater than 1.5 for b . In this region, low nutrient inputs (below 0.01) result in a stable fixed point equilibrium of C and P (region 3). Higher nutrient inputs (above about 0.015) results in a stable limit cycle (region 4). Either increasing nutrient inputs from low values or decreasing it from high values should cause the system to enter a bistable regime (region 5). The eventual behavior of the system would either be a coexistence equilibrium or a stable coexistence limit cycle, depending on initial amounts of C and P . Therefore, the experiment should consist of a gradient of nutrient inputs crossed with various initial values of C and P in a complete factorial design. Many ecological experiments are designed to vary one or more parameters and do not often test the effect of different initial conditions. However, testing for the presence of bistable regions, as in region 5, requires that initial conditions also be varied. If bistability is a general property of stoichiometric models, then experimenters need to be aware of this possibility when setting up and interpreting their experimental results.

6 Summary

We have constructed and numerically analyzed a simple producer-consumer stoichiometric model, keeping track of carbon (biomass) and one limiting nutrient in producer, consumer and sediment compartments. The system is open for both carbon and nutrient. Stoichiometry is effected in a mechanistically simple manner: the producer and consumer populations each have target structural ratios of nutrient to carbon. Whenever either population's stoichiometry is out of balance, the chemical substance in excess is eliminated.

The resulting six-dimensional model behaves differently from the basic R-M producer-consumer model which keeps track of only biomass (carbon), and from the LKE model in which stoichiometric ratios are achieved by a different mechanism, and in which the system is closed to the nutrient. In

contrast to the LKE model, the consumer is not driven to extinction at high productivity. We hypothesize that this is because the influx of nutrients along with carbon influx prevents the quality of the producer “food” from becoming prohibitively low for consumer growth. We suggest that the extinction of the consumer at high productivity in the LKE model is an unrealistically strong behavior of that model which may be rectified by opening the system to nutrients as well as carbon, and by incorporating the elimination mechanism of adjusting stoichiometric ratios as modelled here.

For the elimination model considered here, the primary effect of stoichiometry appears to be to suppress oscillations, especially at high producer birth rates. Such oscillations in nonstoichiometric models (R-M) typically have a growth in the producer, followed by a growth in the consumer. With stoichiometry, the growth of the producer results in lower food quality for the consumer, so the consumer’s subsequent increase is tempered, either decreasing the amplitude of the oscillation, or suppressing it altogether. This damping effect is most significant when nutrient is input into the system at moderate levels. Low nutrient input levels don’t even allow a consumer to persist at all: as producer growth level increases the only bifurcation is from no life to a producer-only monoculture. A high nutrient input level allows both producer and consumer to grow without the stoichiometric limitations, at least up to very high producer birth rates. The system then essentially reverts to the standard producer-consumer system without stoichiometry: as producer levels increase the systems transitions from no life, to producer-only monoculture, to stable producer-consumer equilibrium, to stable producer-consumer limit cycle.

In the intermediate range of nutrient input levels, however, the stoichiometric elimination plays a significant role. For small to moderate producer birth rates, the system behaves similarly to the nonstoichiometric producer-consumer model: increase in producer birth rate causes transitions from no life to producer monoculture to coexistence equilibrium to coexistence limit cycle. As producer birth rate increases further, however, the system exhibits bistability – a stable coexistence equilibrium in addition to the stable coexistence limit cycle – and then the loss of the stable limit cycle in a saddle-node bifurcation of limit cycles. Continued increases in birth rate seem to effect no further qualitative changes. The producer equilibrium level continues to increase with its birth rate, while the consumer equilibrium appears to level off. In conclusion, it is necessary to consider food quality as well as food quantity to understand the stoichiometric inhibition of large amplitude limit cycles in a nutrient-limited setting.

References

- [1] T. Andersen, J.J. Elser, and D.O. Hessen, (2004), Stoichiometry and Population Dynamics, *Ecology Letters* 7, 884-900.
- [2] A.M. Cates,(2000), A mathematical investigation of the decomposition of leaf litter, Applied and Computational Mathematics Master's project, University of Minnesota Duluth.
- [3] E. Doedel, A. Champneys, T. Fairgrieve, Y. Kuznetsov, B. Sandstede and X. Wang, (1997), AUTO97: Continuation and bifurcation software for ordinary differential equations (with HomCont), Technical report, Concordia University.
- [4] S. Diehl, (2007), Paradoxes of Enrichment: effects of Increased Light versus Nutrient Supply on Pelagic Producer-Grazer Systems, *The American Naturalist* 169(6), E173-E191.
- [5] M. Golubitsky and D. Schaeffer, *Singularities and Groups in Bifurcation Theory, Vol I*, Appl. Math. Sci. 51, Springer-Verlag, New York, 1985.
- [6] J.P. Grover, Stoichiometry, herbivory and competition for nutrients: simple models based on planktonic ecosystems, *J. Theor. Biol.* 214, 599-618.
- [7] C.A. Klausmeier, E. Litchman and S.A. Levin, (2004), Phytoplankton growth and stoichiometry under multiple nutrient limitation, *Limnol. Oceanogr.* 49 (4, part 2), 1463-1470.
- [8] Y. Kuang, J. Huisman and J.J. Elser (2004), Stoichiometric Plant-Herbivore Models and Their Interpretation, *Mathematical Biosciences and Engineering* 1, 215-222.
- [9] I. Loladze, Y. Kuang, and J.J. Elser, (2000), Stoichiometry in Producer-Grazer Systems: Linking Energy Flow with Element Cycling, *Bulletin of Mathematical Biology* 62, 1137-1162.
- [10] I. Loladze, Y. Kuang, J.J. Elser and W. Fagan, (2004), Competition and stoichiometry: coexistence of two predators on one prey, *Theoretical Population Biology* 65, 1-15.
- [11] M.L. Rosenzweig, and R.H. MacArthur (1963), Graphical Representation and Stability Conditions of Predator-Prey Interactions, *American Naturalist* 97, 209-223.

- [12] R.W. Sterner, and J.J. Elser, (2002), *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*, Princeton University Press, Princeton, NJ.
- [13] P. Waltman, (1983), *Competition Models in Population Biology*, CBS-NSF Regional Conference Series in Applied Mathematics, Society for Industrial and Applied Mathematics, Philadelphia, PA.
- [14] H. Wang, Y. Kuang, I. Loladze, (2008), Dynamics of a mechanistically derived stoichiometric producer-grazer model, *Journal of Biological Dynamics*, to appear.
- [15] H. Wang, H.L. Smith, Y. Kuang, J.J. Elser, (2007), Dynamics of Stoichiometric Bacteria-Algae interactions in the epilimnion, *SIAM J. Applied Math.* 68, p.503-522.
- [16] L. Zimmermann, (2006) A Producer-Consumer Model with Stoichiometry, Applied and Computational Mathematics Master's Project (supervised by Peckham B B, Pastor J, and Stech H S), Technical Report TR 2006-5, University of Minnesota Duluth, Department of Mathematics and Statistics.