ENRICHMENT EFFECTS IN A SIMPLE STOICHIOMETRIC PRODUCER-CONSUMER POPULATION GROWTH MODEL

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In Honor of Drumi Bainov.

ABSTRACT. A rudimentary predator-prey model is considered that is stoichometric, in that the nutrient content of the producer species affects the ability of the consumer to produce biomass. We show that the model supports biologically important dynamical properties that differ from the corresponding non-stoichiometric model. Specifically, under the assumption of Holling II-type functional response, for all sufficiently high system nutrient levels energy enrichment of the producer induces the loss of stability for the consumer-free (producer "monoculture") system and the transcritical creation of a non-trivial coexistence equilibrium. Under further energy enrichment, this equilibrium undergoes a loss of stability (generically via Hopf bifurcation.) The model then supports a non-trivial periodic coexistence solution. In contrast to the non-stoichiometric case, here further energy enrichment induces restabilization of the monoculture equilibrium. Moreover, under sufficiently high energy enrichment, the system supports no nontrivial periodic solutions. The details of the bifurcation structure are computed for a simple case. Our results suggest that the energy-induced loss of periodic coexistence state can be attributed to the dilution of a consumer-limiting nutrient when the producer population is large, resulting in a carbon-rich / nutrient-poor food source that cannot sustain the consumer's nutrient needs.

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1. INTRODUCTION

In 1971, Rosenzweig [24] pointed out that energy/carbon enrichment in predator-prey systems [25] can destabilize a system's coexistence equilibrium state, inducing the creation of an oscillatory coexistence state. In the modification of the classical

Lotka-Volterra model that assumes Holling II-like saturation of the consumer foraging rate [4], the amplitude of oscillation increases with enrichment, and the periodic solution persists for all large energy levels. In such non-stoichiometric models (which only track the flow of carbon in the system) enrichment is modeled as an increase in producer carrying capacity.

More recently, the impact of energy enrichment has been considered in stoichiometric producer consumer models. Stoichiometric models differ from their non-stoichiometric analogues in that in such models producer and consumer biomass production depend both on the carbon:nutrient properties of the producer, as well as the carbon:nutrient requirements of the consumer species. For example, Droop [6] considered the effects of nutrients on producer primary productivity. Methods for modeling the dependence of consumer biomass conversion efficiency on the nutrient content of the producer population were first considered in the work of Andersen [2] and Hessen & Bjerkeng [11], and subsequently in [3], [14], [23] and [26].

The effects of enrichment in stoichiometric producer-consumer systems began with the paper of Loladze, Kuang & Elser [20]. In stoichiometric models, enrichment must be modeled more mechanistically in order to distinguish between (say) increasing ambient light and increasing total system nutrient levels. The LKE model introduced stoichiometric effects to the usual realization of the Rosenzweig-MacArthur model [25] that assumes Holling II-type predation. They take the system to be nutrient-closed (that is, it possesses a fixed total nutrient budget) for a single nutrient that is partitioned between the producer and consumer populations. The nutrient concentration of the producer population is variable, with higher nutrient levels affecting both producer primary productivity and consumer biomass conversion efficiency. Numerical simulations of the LKE model (parameterized for algae–*Daphnia* system with phosphorous viewed to be the limiting nutrient) suggested that with increasing energy enrichment, a stable, producer monoculture gives way to a stable coexistence equilibrium state. Like the Rosenzweig model, with further enrichment this coexistence equilibrium can lose stability, resulting in a stable, attracting, periodic, co-existence state. However, in contrast to the non-stoichiometric case, the periodic state persists until energy enrichment has attained a critical level, at which point the periodic state is apparently lost. Under further enrichment, all (in a generic sense) solutions of the system eventually approach the carrying-capacity equilibrium associated with the monoculture (consumer-free) system.

Subsequent to the LKE study, a number of authors have proposed alternate stoichiometric producer-consumer models ([3], [5], [8] [15], [16], [17], [19], [21], [28], [29], [30].) These models typically support many of the energy-enrichment induced behaviors seen in the LKE model. A general class of producer-consumer models is presented in [26]. The goal of that work has been to construct a general model that

is justified on the basis of the underlying biological processes, but one that is also amenable to rigorous analysis [27].

However, one can argue that the very generality of recent models tends to obscure the underlying causes of the dynamic changes observed in numerical and analytic studies of energy enrichment. For example, in [26] nutrient limitation is allowed to affect (through a flexible producer nutrient reserve pool which supports growth) both producer primary productivity and consumer biomass conversion. Moreover, the sizes of both the producer and consumer populations indirectly affect the producer nutrient reserve in that both populations sequester nutrients, leaving only the remainder available for producer uptake. The model also allows a variety of ways to describe the producer's uptake of environmental nutrients.

Our goal here is to gain insight into the root causes of the energy-induced dynamical changes observed in stoichiometric producer-consumer models, rather than pursue a model that is biologically fully accurate. We therefore consider a model that is intentionally simple in construction. The model can be viewed as an approximation of those considered in the literature, but includes only a single stoichiometric effect, the influence of producer nutrient:carbon ratio on the consumer's efficiency in converting producer biomass to consumer biomass. We will rigorously show that this single stoichiometric mechanism leads to many of the enrichment-induced effects observed in previous studies, including the loss of periodic solutions under high energy enrichment.

We present the model in the next section, with a discussion of the assumptions made of the constituent functions. The dynamical properties of the model are examined in Section 3, including an analysis of system nullclines, the stability properties of equilibria, and the existence (and non-existence) of periodic solutions. Section 4 focuses on a numerical treatment of a specific realization of the model, using parameters associated with algae-*Daphnia* systems. We conclude in the final section with a summary of our findings and their ecological implications.

2. MODEL DERIVATION

As in [26], [27], we consider a system consisting of a producer population, $P(t)$, and consumer population, $C(t)$ as described in terms of their spatial carbon densities. In contrast to the highly mechanistic model in those references, we here consider the simple system

$$P' = [g(P,e) - f(P)C]P \tag{2.1}$$

$$C' = [\delta\mu(n/P)f(P)P - d]C \tag{2.2}$$

where functions g, f and μ are smooth and satisfy assumptions described below. The function $g(P,e)$ represents the per capita (specific) net growth rate of the producer

population, which is assumed affected by ambient energy levels, denoted by $e \geq 0$. Per capita (specific) predation by the consumer population is assumed to be a saturating function $f(P)P$ of producer population size, as typified by Holling-II predation. The parameter $\delta > 0$ denotes the maximal biomass conversion efficiency for the consumer, while $d > 0$ is the specific death rate for the consumer population.

The parameter $n \geq 0$ represents the spatial density of the total nutrient level in the system, which is assumed to be constant. Producer growth is here assumed independent of n, and all system nutrient is assumed immediately sequestered by the producer, resulting in a producer nutrient:carbon ratio of n/P. This fraction describes the "food quality" that the producer presents to the consumer. This is an approximation to the more realistic case considered in [26], [27], but is justified when the producer primary productivity is not nutrient-limited, and the amounts of nutrient sequestered by the consumer is a small fraction of the total system nutrient pool.

The function $0 \leq \mu(n/P) \leq 1$ describes a stoichiometry-induced constraint on the consumer's ability to convert producer biomass to consumer biomass. We remark that a possible generalization might seemingly involve taking an efficiency factor of the form $\mu(P, n)$. However, this factor should be independent of the spatial units used to measure producer carbon density, P, and system nutrient concentration, n. That is, $\mu(P, n) = \mu(sP, sn)$ for any scaling factor $s > 0$. Selecting $s = 1/P$, we arrive (heuristically) at $\mu(P, n) = \mu(1, n/P)$, which is the form we have assumed in (2.2). Replacing $\mu \equiv 1$ recovers the non-stoichiometric model of Rosenzweig and MacArthur [24], [25].

Conditions on g, f and μ are given below. Throughout, we use primes to denote differentiation with respect to P.

H_g: *For all $e > 0$, $g(P, e)$ is assumed to be non-increasing in P. We assume that for $e > 0$ there exists a value $P_m = P_m(e) > 0$ with $g(P_m, e) = 0$, $g'(P_m, e) < 0$ and $g(P, e) > 0$ on the interval $0 \leq P < P_m$. Without loss of generality, we assume that $\lim_{e \to 0^+} P_m(e) = 0$.*

The value $P_m(e) < \infty$ designates the e-dependent carrying capacity ("monoculture" equilibrium) for the system in the absence of the consumer population. By construction, this equilibrium is globally attracting of all positive solutions to the monoculture system.

The assumptions on the predation term are motivated by the classic Holling II response function $f(P)P = \alpha P/(h + P)$.

H_f: *For all $P \geq 0$, $f(P)P$ is assumed to be increasing in P and $f'(P) < 0$. Moreover, $\lim_{P \to \infty} f(P)P < +\infty$ and $\lim_{P \to \infty} f(P) = 0$.*

The assumptions on μ are motivated by [26]. In particular, that reference includes a derivation of the properties expected of μ based on a generalization of the consumer biomass "synthesizing unit" of Kooijman [14].

H_μ: *The biomass conversion efficiency function $\mu(Q)$ is a non-decreasing function of $Q > 0$, with $\mu(0) = 0$ and normalized with $\mu(+\infty) = 1$. Moreover, we assume that there exists a constant $q > 0$ independent of e and n such that $\mu(Q) \leq Q/q$.*

The inequality imposed on $\mu(Q)$ reflects a stoichiometric constraint on consumer biomass conversion. The efficiency of consumer biomass conversion cannot be greater than the ratio of the producer nutrient:carbon ratio, $Q = n/P$, to the consumer population nutrient:carbon ratio, q (assumed fixed.) Specifically, one unit of consumed producer will contain n/P units of nutrient, which will generate at most n/Pq units of consumer biomass. That is, $\mu(Q) \leq Q/q$. Hypothesis H_μ is satisfied, for example, by the Monod function $\mu(Q) = 1/(1 + q/Q)$, the "Poisson Arrival Time" model $\mu(Q) = 1/(1 + q/Q - (1 + Q/q)^{-1})$ of [14], [23], as well as by the Liebig form $\mu(Q) = \min[1, \ Q/q]$ used in [20].

Based on hypothesis H_μ we see that biomass conversion efficiency will increase as total system nutrient increases: For each $P > 0$, $\lim_{n\to\infty} \mu(n/P) = 1$. The effect of energy enrichment is modeled through the dependence of g on e. We assume:

H_e: *For each $P \geq 0$, $g(P, e)$ is assumed to be increasing in e, with $\lim_{e\to\infty} g'(P,e)/g(P,e) = 0$ and $\lim_{e\to\infty} P_m(e) = +\infty$.*

The first limit of H_e can be interpreted to mean that energy enrichment eventually has a diminishing return in its impact on the producer specific growth rate. It can be satisfied in two enrichment scenarios. First, the limit follows if $\lim_{e\to\infty} g'(P, e) = 0$, which corresponds to a saturation of the net producer growth rate under high-energy enrichment. Second, the limit holds if $g'(P, e)$ is bounded as $e \to \infty$ (energy enrichment does not significantly impact the sensitivity of self-limitation on net producer growth) and $\lim_{e\to\infty} g(P, e) = \infty$ (energy enrichment increases producer productivity without bound.) Hypotheses H_g and H_e are satisfied by the classic logistic growth function $g(P, e) = r(b - P/K)$ for either $e = b$ or $e = K$. The more mechanistic growth model of Huisman and Weissing [12], [13], [31] has the form

$$g(P, e) = \frac{r}{z} \int_0^z \frac{I_0 e^{-(\kappa P + \kappa_b)s}}{a + I_0 e^{-(\kappa P + \kappa_b)s}} ds - d_p,$$

where in pelagic settings z denotes the depth of the water column and I_0 measures light intensity at surface level, [5]. Hypothesis H_e is satisfied for either $e = 1/z$ or $e = I_0$ since for each $P \geq 0$ $\lim_{z\to 0} g(P, 1/z) = r\frac{I_0}{a+I_0} - d_p$ and $\lim_{I_0\to\infty} g(P, I_0) = r - d_p$, both implying that $\lim_{e\to\infty} g'(P, e) = 0$.

3. MODEL PROPERTIES

In this section we analyze the dynamic properties of the model, focusing on the effects that the increases of nutrient and energy levels have on the existence of system equilibria and periodic states. It is not difficult to show that system (2.1, 2.2) is well-posed for biologically reasonable initial conditions, and that all solutions eventually enter the region $P \leq P_m$. Moreover, solutions will also be (ultimately uniformly) bounded in C, with a bound that is independent of e and n. This can be verified by showing that an orbit that is bounded in P but unbounded in C, must have unbounded $\frac{dC}{dP}$. This can be ruled out (arguing by contradiction) since along any solution trajectory with C large

$$\frac{dC}{dP} = \frac{\delta\mu(n/P)f(P)P - d}{g(P,e)P/C - f(P)P}.$$

The producer nullcline is given by $C = g(P,e)/f(P)$, which by H_g and H_f is positive on $0 \leq P < P_m$ and intersects the P axis at $P = P_m$ with $\frac{dC}{dP}\big|_{P'=0} < 0$. Observe that the producer nullcline is independent of n.

As a clear necessary condition for consumer persistence, we proceed under the assumption that $\lim_{P\to\infty} \delta f(P)P > d$. When they exist, the consumer nullclines are vertical, and satisfy $\delta\mu(n/P)f(P)P = d$. By H_f and H_μ the function $\delta\mu(n/P)f(P)P$ vanishes at $P = 0^+$ and at $P = +\infty$. Moreover, for all n sufficiently small $\delta\mu(n/P)f(P)P < d$ holds for all P, and (2.2) gives that $C(t) \to 0$ as $t \to \infty$. It follows that under all sufficiently low nutrient levels the producer monoculture equilibrium is globally attracting to all nonzero solutions.

Conversely, for all sufficiently large n there will exist nullclines $P = P_h(n)$ and $P = P_l(n)$ ($P_h < P_l$) with the property that $\delta\mu(n/P)f(P)P < d$ when $P < P_h$ or $P > P_l$. In contrast to the producer nullclines, the consumer nullclines are independent of e. With increasing n, $P_h(n)$ decreases and approaches the unique solution of $\delta f(P)P = d$, while $P_l(n)$ increases and approaches $P = +\infty$. It follows that for all n sufficiently large $(\mu(n/P)f(P)P))'|_{P=P_h} > 0$. We proceed under the generic expectation that $(\mu(n/P)f(P)P))'|_{P=P_l} < 0$.

Regarding the stability of equilibria, we compute the Jacobian for (2.1, 2.2) as

$$J = \begin{pmatrix} g(P,e) - f(P)C + (g'(P,e) - f'(P)C)P & -Pf(P) \\ \delta(\mu(n/P)f(P)P))'C & \delta\mu(n/P)f(P)P - d \end{pmatrix}. \quad (3.1)$$

For $e > 0$ the "no life" equilibrium $(P,C) = (0,0)$ is an unstable saddle since the associated Jacobian has eigenvalues $g(0,e) > 0$ and $-d < 0$. At the monoculture equilibrium $(P,C) = (P_m,0)$ the associated Jacobian has eigenvalues $g'(P_m,e)P_m < 0$ and $\delta\mu(n/P_m)f(P_m)P_m - d$. By our previous discussion, P_m will be locally asymptotically stable if either $P_m < P_h$ or $P_m > P_l$. By H_e, with increasing energy the producer

monoculture equilibrium loses stability when $P_m(e)$ increases past $P = P_h$, resulting in a transcritical bifurcation of ("high food quality") coexistence equilibrium (P_h, C_h). With further energy enrichment the producer monoculture equilibrium re-stabilizes when $P_m(e)$ increases past P_l, and remains locally asymptotically stable for all higher energy levels. This final change in stability corresponds to the transcritical creation of a second ("low food quality") coexistence equilibrium (P_l, C_l).

At coexistence equilibria the characteristic polynomial of the associated Jacobian matrix reads $\lambda^2 - (g'(P, e) - f'(P)C)P\lambda + \delta(\mu(n/P)f(P)P))'CPf(P)$. It follows that the coexistence equilibrium (P_l, C_l) will generically be an unstable saddle. The coefficient of λ can be written as

$$-(g'(P,e)/g(P,e) - f'(P)/f(P))g(P,e)P = -f(P)P \left.\frac{dC}{dP}\right|_{P'=0}. \qquad (3.2)$$

Thus, the stability of the equilibrium (P_h, C_h) will be determined by the slope of the producer nullcline at $P = P_h$. At its transcritical creation, this equilibrium is locally stable since $-(g'(P_h, e) - f'(P_h)C_h)P_h = -g'(P_h, e)P_h > 0$. However, under our energy enrichment hypothesis H_e, $-(g'(P_h, e)/g(P_h, e) - f'(P_h)/f(P_h))g(P_h, e)P_h \to f'(P_h)/f(P_h)g(P_h, e)P_h < 0$ as $e \to +\infty$.

Thus coexistence equilibrium (P_h, C_h) will generically lose stability at a Hopf bifurcation. The direction (stability) of this bifurcation can be computed with the algorithm of [10], but since it is known [32] that in the non-stoichiometric case $\mu \equiv 1$ system (2.1, 2.2) supports (depending on g and f) both sub- and super-critical bifurcations, we anticipate that this will also be the case here, as well.

The theory of global Hopf bifurcation [1] implies that the one-parameter family of periodic orbits associated with this generic Hopf bifurcation will either terminate at a second point of Hopf bifurcation, or become unbounded in at least one of amplitude, bifurcation parameter, e, or period. The uniform bound on solutions to (2.1, 2.2) eliminates the first alternative. The following proposition rules out the second possibility by showing that there is a finite energy level beyond which system (2.1, 2.2) cannot support non-constant periodic orbits.

Proposition 3.1. *If the producer nullcline is monotone on the interval $0 \le P \le P_l$, then system (2.1, 2.2) admits no non-constant periodic orbit.*

Proof. Assume that (2.1, 2.2) has a non-constant periodic orbit. By considering the configuration of the system nullclines, one can show that any periodic orbit must lie within the region $0 < P < \min[P_l, P_m]$. We apply Dulac's criterion, using multiplier $1/f(P)PC$. One computes that

$$\frac{\partial}{\partial P}\left(\frac{1}{f(P)PC}[g(P,e) - f(P)C]P\right) + \frac{\partial}{\partial C}\left(\frac{1}{f(P)PC}[\delta\mu(n/P)f(P)P - d]C\right) = \frac{1}{C}\frac{d}{dP}\left(\frac{g(P,e)}{f(P)}\right),$$

which (when of constant sign) contradicts the existence of periodic orbits.

$\square$

By H_e and (3.2), the hypothesis of this proposition will hold for all sufficiently large e. We conclude that the one-parameter family of periodic solutions that (generically) is created at the change of stability of (P_h, C_h) will either terminate in a second Hopf bifurcation or in a homoclinic bifurcation. Without further technical conditions, both possibilities can hold. In fact, for the closely related (and more realistic) stoichiometric producer consumer model of [26], [27] both Hopf and homoclinic terminations have been observed, dependent on total system nutrient level, n.

In the simple case where the function $\mu(n/P)f(P)P$ is unimodal in P (as in the example of the next section), there are only two coexistence equilibria, (P_l, C_l) and (P_h, C_h), and for all e sufficiently large both are unstable. Thus, a subsequent Hopf bifurcation (which by our eigenvalue analysis must occur at (P_h, C_h)), is ruled out. We conclude that (2.1, 2.2) must admit a homoclinic bifurcation involving (P_l, C_l). Any such homoclinic bifurcation will be locally stable, as determined by the trace of the Jacobian matrix at (P_l, C_l), which is given by $f(P_l)P_l \frac{dC}{dP}\big|_{P'=0} < 0$. See [10], [18].

4. A NUMERICAL EXAMPLE

To illustrate the results of the previous section, we provide the details for a particular realization of the stoichiometric producer consumer model (2.1, 2.2). Specifically, we select $g(P, e) = r(e - P/K)$ (logistic producer growth), $f(P)P = \alpha P/(h + P)$ (Holling II predation term) and $\mu(n/P) = 1/(1 + qP/n) = n/(n + qP)$ (Monod consumer biomass nutrient conversion factor.) System (2.1, 2.2) becomes

$$P' = r(e - P/K)P - \alpha CP/(h + P) \tag{4.1}$$

$$C' = [\delta(n/(n + qP))\alpha P/(h + P) - d]C. \tag{4.2}$$

The hypotheses of Section 2 hold. Under these selections, model (2.1, 2.2) is remarkably tractable. Our results are summarized in the figures that follow. The producer transcritical bifurcation occurs at $e = 0$. The producer nullcline takes the classic "parabolic" form

$$C = \frac{r}{\alpha}(e - P/K)(h + P), \tag{4.3}$$

with horizontal intercept at producer monoculture carrying capacity $P_m = eK$.

The existence of consumer nullclines is determined by the function $\delta\mu(n/P)f(P)P$, which is unimodal, and with maximum occurring at $P = \sqrt{qh/n}$. The necessary condition for consumer persistence $\lim_{P \to \infty} \delta f(P)P > d$ of the previous section becomes $\rho \equiv \alpha\delta/d > 1$. The quantity ρ is often referred to as the consumer reproductive number.

Using the algebraic forms of f and μ, it is easily shown that the consumer null-clines satisfy

$$(1 + qP/n)(h + P) = \rho P. \tag{4.4}$$

This quadratic equation has two, distinct, real solutions $0 < P_h(n) < P_l(n)$ for all $n > qh/(\sqrt{\rho} - 1)^2$. With decreasing n these two roots coalesce, causing a saddle-node bifurcation of equilibria at $n = qh/(\sqrt{\rho} - 1)^2$. As pointed out in Section 3 for the general model, the effects of nutrient and energy enrichment on consumer and producer nullclines (respectively) are uncoupled.

Consumer transcritical bifurcations occur when $n > qh/(\sqrt{\rho} - 1)^2$ and when the producer carrying capacity $P_m = eK$ satisfies (4.4). Thus, at consumer transcritical bifurcations n can be computed in terms of e as

$$n = \frac{q(eK + h)}{\rho - 1 - h/eK} \tag{4.5}$$

for $e > \frac{h}{K(\rho - 1)}$.

Coexistence steady state (P_h, C_h) is destabilized in a Hopf bifurcation when the producer nullcline peak (which occurs at $P = (eK - h)/2$) crosses the consumer nullcline $P = P_h$. Thus, using (4.4), at Hopf bifurcations n can be computed in terms of e as

$$n = \frac{q/2}{\rho/(h + eK) + 1/(h - eK)} \tag{4.6}$$

for $h(\rho + 1)/K(\rho - 1) < e < h(\sqrt{\rho} + 1)/K(\sqrt{\rho} - 1)$. As e approaches the upper limit of this interval the value of n from (4.4) approaches $n = qh/(1 - \sqrt{\rho})^2$, the value at which P_l and P_h coincide at a saddle-node bifurcation. When viewed in the e, n parameter plane, at $e = h/K(\sqrt{\rho} - 1)$ this saddle-node curve intersects the consumer transcritical curve at a "transcritical saddle-node" point. The intersection of the saddle-node curve and Hopf curve defines a Takens-Bogdanov point, explicitly computable as $TB = (h(\sqrt{\rho} + 1)/(K(\sqrt{\rho} - 1)),\ qh/(\sqrt{\rho} - 1)^2)$.

Finally, we note that the segment of the curve (4.6) with $h(\sqrt{\rho}+1)/K(\sqrt{\rho}-1) < e$ (dashed in Figure 1) corresponds to values where the peak of the producer nullcline occurs at $P = P_l$. By Proposition 3.1, for $n > qh/(\sqrt{\rho} - 1)^2$, equation (4.6) implicitly defines an upper bound on the energy levels for which (4.1, 4.2) can support periodic solutions. A representative two-parameter (e, n) bifurcation diagram for (4.1, 4.2) is given in Figure 1. Model parameters are based on the algae/*Daphnia* system considered in [26], with $r = .88$ day^{-1}, $K = 1.25$ mg producer carbon/liter, $\alpha = .8$ mg producer /mg consumer/day, $h = .2$ mg producer carbon/liter, $d = .24$ day^{-1}, and $\delta = .8$ (unitless.) The consumer reproductive number is computed to be $\rho = \alpha\delta/d = 3.333$. In this context, n refers to system phosphorous, measured in units of mg/liter. We assume a consumer population with biologically reasonable phosphorous/carbon ratio of $q = .0375$. See [2].
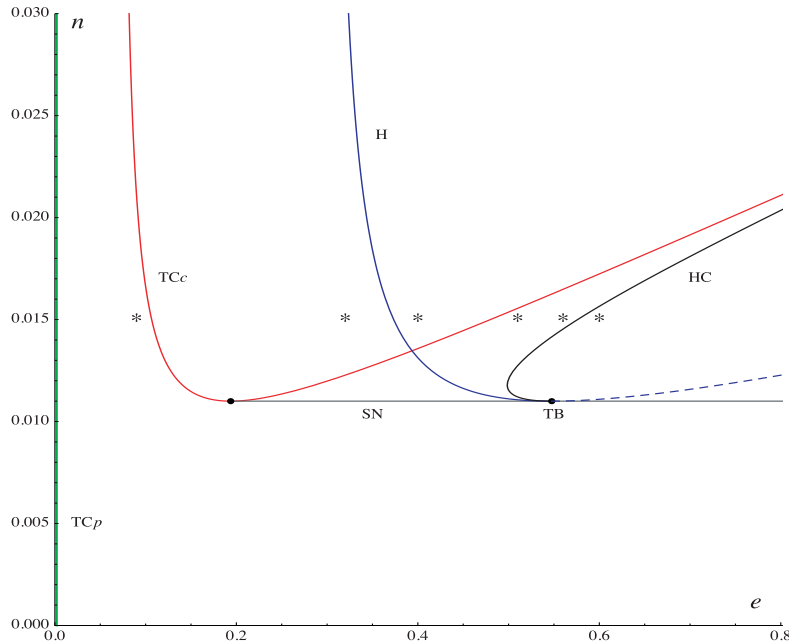
FIGURE 1. Two-parameter bifurcation diagram for (4.1, 4.2). Transcritical bifurcations of the monoculture producer and co-existence equilibria are denoted by TC_P and TC_C, respectively. With increasing n, pairs of co-existence equilibria are created via saddle-node bifurcations along the curve SN. Hopf bifurcation (H) and homoclinic bifurcation curves (HC) meet along the saddle-node curve at a Takens-Bogdanov point, TB [9]. The dashed segment is not a bifurcation curve, but corresponds to (for fixed n) the energy upper bound beyond which Proposition 3.1 proves the system to not have periodic orbits. In Figure 3, phase planes are shown for the six points distinguished points, where $n = .015$, and $e = .09, .40, .32, .51, .56,$ and $.60$.

With the exception of the homoclinic bifurcation curve, all elements of Figure 1 are computed using the formulae derived in this section. As a global bifurcation phenomenon, there is no simple algebraic description of the curve of homoclinic bifurcations. The curve in Figure 1 was computed with AUTO [7], which also confirmed the other bifurcation curves. Figure 2 shows the one-parameter bifurcation diagrams for (4.1, 4.2) obtained when nutrient levels are held at $n = .015$ and energy levels vary. These diagrams illustrate the general behavior of (2.1, 2.2) when nutrient levels are high enough to support (with increasing energy levels) the creation of coexistence equilibria. Specifically, the monoculture equilibrium $P_m = eK$ loses, then regains, its stability at $e = .100667$ and $e = .48$, respectively, as computed from
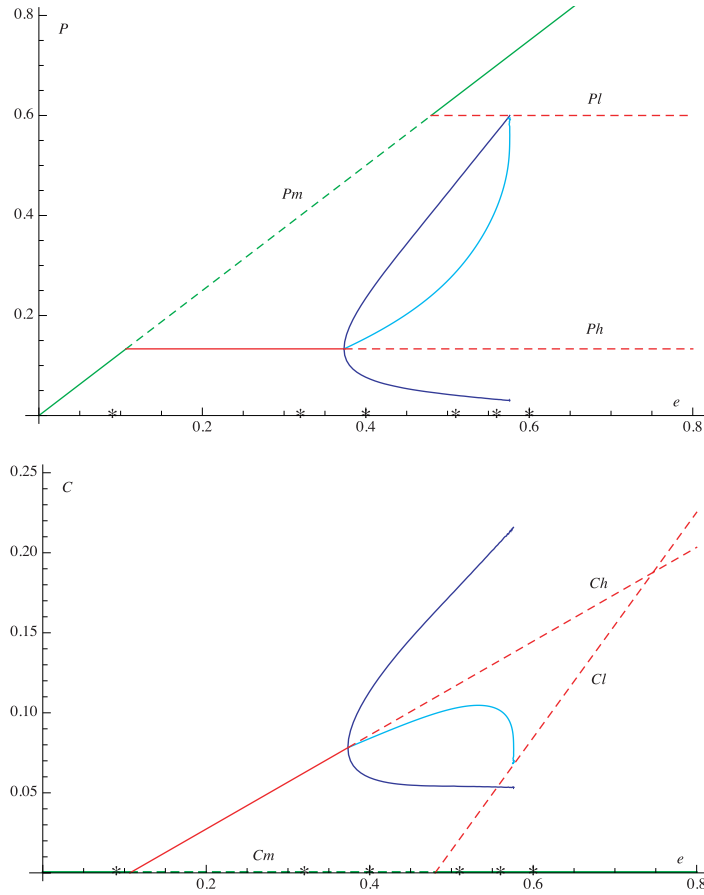
FIGURE 2. Energy enrichment bifurcation diagram for (4.1, 4.2) with $n = .015$. Upper panel shows e vs. P; Lower panel shows e vs. C. Green curves refer to the monoculture equilibrium; red curves refer to the coexistence equilibria (P_h, C_h) (emerging at $e = .100667$) and (P_l, C_l) (emerging at $e = .48$.) The max/min values along the family of periodic orbits are shown in blue, with the average values across cycles shown in cyan. Solid curves indicate stable objects; dashed curves indicate unstable. Figure 3 shows the phase planes for the six distinguished energy levels on the horizontal axis.

(4.5). The coexistence equilibria are found by solving (4.4) for P, then using these in (4.3) to evaluate C. The Hopf bifurcation for the system occurs at $e = .37333$, as computed from (4.6). The parametric family of periodic orbits was computed using AUTO, and was observed to terminate in a homoclinic bifurcation near $e = .5758$. For $.48 < e < .5758$ the system supports bistability.
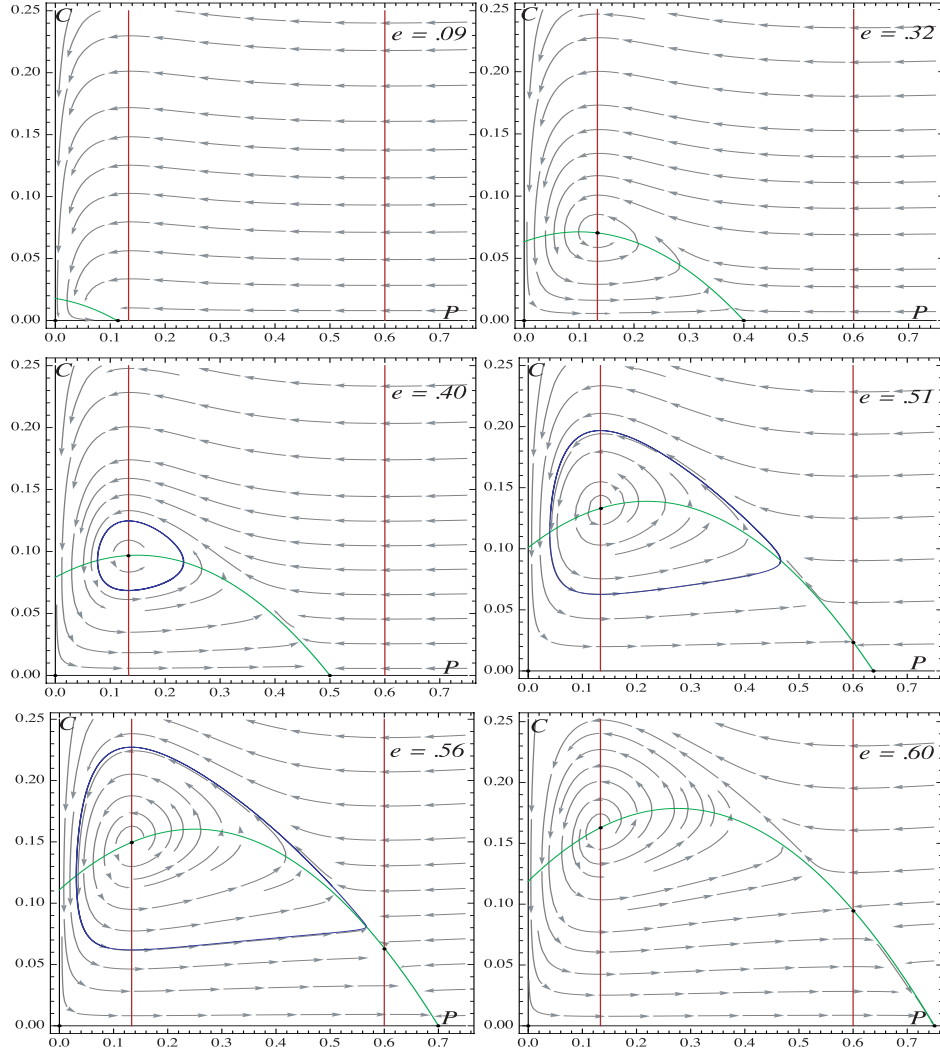
FIGURE 3. Representative phase planes for system (4.1, 4.2) with
$n = .015$ and the energy levels indicated by * in Figure 1. Left and
right red vertical lines correspond to producer nullclines $P = P_h$ and
$P = P_l$, respectively. The consumer nullcline is shown in green. Its in-
tersection with the horizontal axis defines the monoculture equilibrium
$(P_m, 0)$, while its intersections with the producer nullclines defining the
high food quality equilibrium (P_h, C_h) and low food quality equilibrium
(P_l, C_l), respectively. Periodic cycles are shown in blue.

The global dynamics for (4.1, 4.2) are best understood in terms of the system's
phase planes. These are shown in Figure 3 for $n = .015$, and the energy levels
distinguished in Figure 1. All plots were computed using *Mathematica* [22]. As

observed in [20], [26] and [27], the homoclinic bifurcation signals an abrupt change in the asymptotic behavior of system trajectories initiated near the equilibrium (P_h, C_h). The loss of periodic orbit is coincident to a loss of the system's bistability.

5. CONCLUSIONS

The model considered here supports many of the main effects that the inclusion of variable producer stoichiometry has been observed to have on models of nutrient-constrained, energy enriched systems. Beyond a minimal critical system nutrient level, energy enrichment induces the creation of a monoculture (producer only) equilibrium state. Under all sufficiently high nutrient levels, energy enrichment causes this monoculture equilibrium to lose stability, simultaneous to the emergence of a locally attracting high food quality coexistence equilibrium, (P_h, C_h). With further energy enrichment, this coexistence equilibrium looses stability, and the system can support a periodic coexistence state. Energy enrichment also induces the re-stabilization of the monoculture equilibrium at the creation of a subsequent (unstable) low food quality coexistence equilibrium state, (P_l, C_l).

We remark that the re-stabilization of the producer monoculture equilibrium can occur either before or after the creation of a periodic coexistence state. Figure 3 points out that the re-stabilized monoculture equilibrium always attracts not only all solutions with sufficiently small C (an Allee-like effect), but also all solutions initiated with *large* consumer or small producer populations. This corresponds to the following ecological scenario: Predation by an initially large consumer population drives the producer population to near-extinction. Due to low producer levels the consumer population consequently falls to near-extinction. With the resulting reduction of predation, the producer population then rebounds and approaches levels near the carrying capacity of the consumer-free system. Under high energy levels (relative to the fixed system nutrient pool), the producer population presents a nutrient-poor food source to the consumer population. Despite the high abundance of its producer resource, the consumer population is eventually driven to extinction due to the poor quality of its food source and its corresponding low biomass conversion efficiency. Ultimately, the producer population then approaches the carrying capacity of the consumer-free system.

We have rigorously shown that for all sufficiently high energy levels the system cannot support any periodic solution. Generically, all solutions to the system are then attracted to the monoculture equilibrium (the producer approaching the consumer-free carrying capacity.) The methods used here are motivated by the results of [32]. In fact, (2.1, 2.2) is similar to that of non-stoichiometric predator-prey systems where the prey population exhibits a "group defense" strategy. However, in contrast to our assumptions, in [32] the predator's functional response $f(P)P$ is no longer assumed

monotone in prey population size and the predator-specific biomass production rate is taken to be proportionate to the specific predation rate.

The work of Rosenzweig [24] pointed out the potential perils of enrichment in producer-consumer systems. For the non-stoichiometric models considered there, energy enrichment induces a loss of stability of the system's (unique) coexistence steady-state, and causes the creation of a corresponding periodic coexistence state. This oscillatory state is considered to make the system more prone to extinction due to possible random losses at times of low producer or consumer population levels. The possibility that energy enrichment might actually imperil the system is often referred to as the "paradox of enrichment."

In contrast, the enrichment-induced route to consumer extinction described here does not rely on any such exogenous stochastic effect, but rather it is a deterministic consequence of the stoichiometry of the system. In its (intentional) omission of certain stoichiometric processes in producer-consumer systems, our model suggests that the energy enrichment-induced collapse of consumer population in closed stoichiometric predator-prey systems can be attributed to the dilution of total system nutrient across the producer population, and does not rely on other nutrient-related processes.

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