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A stoichiometric producer-grazer model incorporating the effects of excess food-nutrient content on consumer dynamics

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ABSTRACT

There has been important progress in understanding ecological dynamics through the development of the theory of ecological stoichiometry. For example, modeling under this framework allows food quality to affect consumer dynamics. While the effects of nutrient deficiency on consumer growth are well understood, recent discoveries in ecological stoichiometry suggest that consumer dynamics are not only affected by insufficient food nutrient content (low phosphorus (P): carbon (C) ratio) but also by excess food nutrient content (high P:C). This phenomenon is known as the *stoichiometric knife edge*, in which animal growth is reduced not only by food with low P content but also by food with high P content, and needs to be incorporated into mathematical models. Here we present a Lotka–Volterra type model to investigate the growth response of *Daphnia* to algae of varying P:C ratios capturing the mechanism of the stoichiometric knife edge.

1. Introduction

Recent advances towards the understanding of ecological interactions have been made through the development of the theory of ecological stoichiometry [1]. By considering the balance of multiple chemical elements in ecological interactions, this theory provides new constraints and mechanisms that can be formulated into mathematical models. These stoichiometric models incorporate the effects of both food quantity and food quality into a single framework that produces rich dynamics [2–11]. One of these models formulated by Loladze et al. [2] describes a two-dimensional Lotka–Volterra type model of the first two trophic levels of a food chain (producer-grazer). This model, called the LKE model [12], incorporates the fact that both producer and grazer are chemically heterogeneous organisms. Specifically, it explicitly tracks the amount of two essential elements, carbon (C) and phosphorus (P), in each trophic level. It allows the phosphorus to carbon ratio (P:C) of the producer to vary above a minimum value, which effectively brings food quality into the model. The production efficiency of the consumer is reduced when this producer P:C value becomes low. The LKE model assumes the producer is optimal food for the grazer if its P:C ratio is equal to or greater than the P:C of the grazer, thus incorporating the effects of low nutrient food content on grazer dynamics.

Thus, low nutrient food content causes a nutrient deficiency in grazers, the consequences of which are relatively well understood and modeled [2,13–15]. However, recent reported empirical data suggest that grazer dynamics are also affected by *excess* food nutrient content [16,17]. This phenomenon, called the *stoichiometric knife edge* reflects a reduction in animal growth not only by food with low P content but also by food with excessively high P content. Although the effects of excess nutrients have recently been receiving attention and there are several examples reporting the knife edge phenomenon for a variety of grazers (*Daphnia*, snails, insects, fish) [12,16–18], there is still little known about the general shape of the relationship between grazer growth rate and food P:C ratio. The shape of this curve may vary among different consumers. The recent data on this phenomenon motivate us to rethink our notion of optimal food. The "stoichiometric knife edge" implies that optimal food should no longer be considered just as that with sufficient nutrient content, which just accounts for avoiding deficiencies, but instead as a balanced nutrient content, avoiding both deficient and excess nutrient food content. While the effects of low food nutrient content have been incorporated into stoichiometric food web models, the model presented in this paper is the first to incorporate the effects of excess nutrient content. It describes an ecological system of algae (producer) and *Daphnia* (grazer), building on the structure of the

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LKE model. The model was briefly introduced by Elser et al.[12]; here we give more details of the model formulation and provide analytical and numerical analysis to gain insight into the dynamics of the system and their implications.

2. Mathematical model

The model aims to capture the dynamics of the stoichiometric knife edge. One possible mechanism that may cause the observed reduction in growth is the animal's feeding behavior. Plath and Boersma [19] suggested that *Daphnia* may follow a simple feeding rule: *eat until you get enough P, then stop.* High P content of food causes the animal to strongly decrease their ingestion rate, perhaps leading to insufficient C intake and thus decreased growth rate. In other words, the satiation level of *Daphnia* is dictated by P. Here we use this hypothesis to form our model.

2.1. Model construction

We start with the stoichiometric producer-grazer LKE model [2]

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{\min(K, (P-\theta y)/q)}\right) - f(x)y \tag{1a}$$

$$\frac{dy}{dt} = \hat{e}\min\left(1, \frac{Q}{\theta}\right)f(x)y - dy \tag{1b}$$

where

$$Q = \frac{P-\theta y}{x}$$

describes the variable P quota of the producer. Here $x(t)$ is the biomass of the producer, $y(t)$ is the biomass of the grazer, b is the maximum growth rate of producer, K is the producer carrying capacity, P is the total phosphorus in the system, θ is the grazer's constant P:C, q is the producer minimal P:C, $\hat{e}$ is the maximum production efficiency, and d is the grazer loss rate. The grazer's ingestion rate, $f(x)$ is taken to be a monotonic increasing and differentiable function, $f'(x) \geqslant 0$. $f(x)$ is saturating with $\lim_{x\to\infty} f(x) = \hat{f}$. The model makes the following three assumptions.

A1: The total mass of phosphorus in the entire system is fixed, i.e., the system is closed for phosphorus with a total of P (mg P/L).
A2: P:C ratio in the producer varies, but it never falls below a minimum q (mg P/mg C); the grazer maintains a constant P:C, 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.

In order to incorporate the dynamics of the knife edge, a fourth assumption is needed. The hypothesis claims the ingestion rate of the grazer depends on the P content of the producer.

A4: The grazer ingests P up to the rate required for its maximal growth but not more.

This assumption leads to a new expression for the grazer ingestion rate. Note that $f(x)$ is the grazer ingestion rate and Q is the P quota of the producer; thus the grazer would ingest P at rate $f(x)Q$ if its ingestion is never capped by the P content of the producer. However, the grazer's maximal possible growth rate expressed in P units is $\hat{f}\theta$. Using these two quantities, we define the grazer satiation level (GSL) as the ratio of $f(x)Q$ to $\hat{f}\theta$. If $GSL < 1$, then the grazer ingests at its usual $f(x)$ rate. But if $GSL \geqslant 1$, then the grazer ingests at the rate $\frac{\hat{f}\theta}{Q}$. This way the grazer's rate of P ingestion is capped at $(\frac{\hat{f}\theta}{Q})Q = \hat{f}\theta$. We incorporate the assumption A4 into a new ingestion rate as follows:

$$u(x,y) = \begin{Bmatrix} f(x) & \text{for } f(x)Q < \hat{f}\theta \\ \frac{\hat{f}\theta}{Q} & \text{for } f(x)Q > \hat{f}\theta \end{Bmatrix} = \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\}$$

The grazer's production efficiency is also modified to incorporate the effect of mandatory C losses to metabolic costs, mainly to respiration, on the post-ingested food quality. Similar to the LKE, the grazer growth rate may be limited by P; however, if P is in excess, the growth rate may be limited by the amount of available C. Q is actually the P:C ratio of the producer before ingestion. A portion of this ingested C is required for metabolic costs such as respiration. $\hat{e}$ is the maximal production efficiency in terms of carbon so that $\frac{Q}{\hat{e}}$ is the P:C ratio of the post-ingested producer representing the amount of P and C available for growth (Fig. 1). When $\frac{Q}{\hat{e}} < \theta$, there is not excess P and the grazer's growth rate is determined by the P content of the producer. The grazer ingests $u(x,y)Q$ units of P, and the grazer's growth rate, $g(x,y)$, satisfies $g(x,y)\theta = u(x,y)Q$. On the other hand, when $\frac{Q}{\hat{e}} > \theta$, there is excess P. In this situation, the grazer's growth is no longer limited by P, but by the amount of available C. The grazer ingests $u(x,y)$ units of C and $u(x,y)\hat{e}$ units of C are available for growth. The growth rate then satisfies $g(x,y) = u(x,y)\hat{e}$. The grazer's biomass growth rate is defined.

$$g(x,y) = \begin{Bmatrix} \frac{Q}{\theta}u(x,y) & \text{for } \frac{Q}{\hat{e}} < \theta \\ \hat{e}u(x,y) & \text{for } \frac{Q}{\hat{e}} > \theta \end{Bmatrix}$$
$$= \min\left\{\hat{e}, \frac{Q}{\theta}\right\}u(x,y) = \min\left\{\hat{e}, \frac{Q}{\theta}\right\}\min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\}.$$

Since $\hat{e}f(x) < \hat{f}$, we see that

$$g(x,y) = \min\left\{\hat{e}f(x), \frac{Q}{\theta}f(x), \hat{e}\frac{\hat{f}\theta}{Q}, \hat{f}\right\} = \min\left\{\frac{Q}{\theta}f(x), \hat{e}\frac{\hat{f}\theta}{Q}, \hat{e}f(x)\right\}.$$

Biologically, this translates into three cases in which growth is determined by energy limitation ($\hat{e}f(x)$), P limitation ($\frac{Q}{\theta}f(x)$), and P in excess ($\hat{e}\hat{f}\frac{\theta}{Q}$).

The result is the following modified version of LKE:

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{\min(K, (P-\theta y)/q)}\right) - \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\}y \tag{2a}$$

$$\frac{dy}{dt} = \min\left\{\hat{e}f(x), \frac{Q}{\theta}f(x), \hat{e}\hat{f}\frac{\theta}{Q}\right\}y - dy \tag{2b}$$

Where $Q = \frac{P-\theta y}{x}$. It is worth mentioning that although the above model modifies the grazer ingestion and growth rate functions of the LKE model, no new model parameters have been introduced.

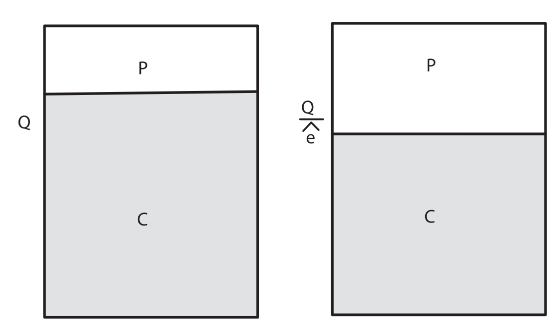

Fig. 1. This diagram depicts the carbon costs of respiration of the grazer. The left side presents the P:C of the producer prior to ingestion. Since some of the ingested C is used for respiration the P:C available for consumer growth is higher. The right figure depicts the post-ingested producer P:C, available for grazer growth.