Ecological Modelling 243 (2012) 81–88

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

On the "strict homeostasis" assumption in ecological stoichiometry

Hao Wang[a,*], Robert W. Sterner[b], James J. Elser[c]

[a] CAB 539, Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, AB T6G 2G1, Canada
[b] Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, United States
[c] School of Life Sciences, Arizona State University, Tempe, AZ 85287, United States

ARTICLE INFO

Article history:
Received 14 February 2012
Received in revised form 28 May 2012
Accepted 5 June 2012
Available online 15 July 2012

Keywords:
Stoichiometry
Carbon
Nitrogen
Phosphorus
StrictHomeostasis
Hard dynamical threshold
Herbivore
Phytoplankton
Turnover rates

ABSTRACT

Multiple elements including carbon (C), nitrogen (N) and phosphorus (P) are required for organismal growth, reproduction, and maintenance. Newly emerging mathematical models linking population dynamics with stoichiometric relationships among these key elements improve historic trophic interaction models and resolve some existing paradoxes. The degree to which organisms maintain a constant chemical composition in the face of variations in the chemical composition and availability of their environmental resources is referred to as "stoichiometric homeostasis". Most of these models so far have assumed constant nutrient contents in heterotrophs, called "strict homeostasis", and varied nutrient contents in autotrophs, called "non-homeostasis", due to the fact that the stoichiometric variability of heterotrophs is often much less than that of autotrophs. Our study suggests that the "strict homeostasis" assumption is reasonable when the stoichiometric variability of herbivores is less than a threshold. This threshold is independent of algal stoichiometric variability, thus the above historic reasoning for strict homeostasis in heterotrophs is not convincing. We find that the "strict homeostasis" assumption seems valid for many herbivores except for herbivores with small mortality rates. The results are nearly same in both one-nutrient and two-nutrient models, and robust to perturbation of parameter values and environmental nutrient status. Finally, the two-nutrient model shows that herbivore's survival needs higher variation in the more potentially limiting of the two elements.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Ecological stoichiometry is the study of the balance of energy and multiple nutrient elements in ecological interactions (Sterner and Elser, 2002). Mathematical models incorporating ecological stoichiometry link population dynamics with flows of energy (or C) and nutrient elements (such as N or P). Many existing stoichiometric models examine dynamics among light and nutrient-dependent phytoplankton or plants and their herbivorous predators. Most of these have assumed constant nutrient contents in herbivores, sometimes called "fixed stoichiometry" or "strict homeostasis" (Andersen, 1997; Hessen and Bjerking, 1997; Elser and Urabe, 1999; Loladze et al., 2000; Muller et al., 2001; Wang et al., 2008). Other, fewer, models examine phytoplankton–bacteria interactions and assume strict homeostasis in bacteria (Bratbak and Thingstad, 1985; Wang et al., 2007). Thus, a common feature of most existing stoichiometric models (but see below) is that they assume variable stoichiometry in autotrophs but fixed stoichiometry in heterotrophs.

Under the assumption of fixed stoichiometry of heterotrophs, these models suggested new insights into how energy flow and nutrient cycling regulate predator–prey trophic interactions. For example, when autotrophs are severely nutrient limited, heterotrophs often will also be limited by nutrients, and may even go extinct despite an abundance of food (Andersen, 1997; Hessen and Bjerking, 1997; Loladze et al., 2000; Muller et al., 2001; Wang et al., 2007, 2008). Mathematically, complex dynamics such as attracting limit cycles, bistability, or even chaos can occur because of the stoichiometric mechanisms coupled to homeostasis incorporated into these models (Loladze et al., 2000; Deng and Loladze, 2007; Wang et al., 2008, 2009).

Strict homeostasis, however, is only an approximation and is often not supported by empirical studies, as consumers consistently display some small changes in body elemental composition in response to stoichiometric variation in their diet (DeMott et al., 1998; Acharya et al., 2004; Hood and Sterner, 2010). These studies motivate us to ask how the "strict homeostasis" assumption used in stoichiometric phytoplankton–herbivore models affects dynamics. The degree of homeostasis itself ranges widely, exhibiting variation even among clones as well as among species in the model herbivore *Daphnia*. Experiments in DeMott et al. (1998), for example, showed that the P content of *Daphnia magna* decreased from 1.55% to 1.11%

* Corresponding author. Tel.: +1 780 492 8472; fax: +1 780 492 6826.
E-mail addresses: hao8@ualberta.ca, hwang@math.ualberta.ca (H. Wang).

0304-3800/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ecolmodel.2012.06.003

when feeding on P-deficient diets. Experiments in Hood and Sterner (2010) showed that the P content of *Daphnia pulex* in high-P treatments can be three times in low-P treatments. On the other hand, *Daphnia parvula* exhibited strong homeostasis under the same condition, changing less than 0.2%. Thus, although heterotrophs are generally more homeostatic than autotrophs (Persson et al., 2010), the importance of the homeostasis assumption in stoichiometric models needs to be examined because questions as to the appropriateness of the assumption of strict homeostasis have been raised.

Some more recent studies have developed a new generation of stoichiometric models with nonhomeostatic herbivores (Grover, 2003; Mulder and Bowden, 2007; Mulder, 2007). Grover (2003) developed a multinutrient chemostat (i.e. nutrient-open) model of bacterial prey and a flagellate predator by assuming that both predator and prey have variable stoichiometry. Recently, Mulder and Bowden (2007) and Mulder (2007) examined how quantitative results of existing theoretical models change after relaxing the "strict homeostasis" assumption. All these studies reach the same conclusion that theoretical results can be different if we consider nonhomeostatic elemental composition in herbivores.

The main aim of this paper is to explore how the dynamics of trophic interactions depend on the degree of stoichiometric variability in herbivores. Beyond Grover (2003), Mulder and Bowden (2007) and Mulder (2007), we discuss the dependence of dynamical turning points, such as bifurcation points, on consumer stoichiometric variability, using two closed-nutrient dynamical models. We apply these results to provide guidance for the usage of the "strict homeostasis" assumption. Intuitively, when consumer stoichiometric variability is small enough, the same or similar dynamics may be expected in both homeostatic and nonhomeostatic models. There may be a threshold for a switch of dynamics as the variability increases. With estimation of this threshold, we can better define when the "strict homeostasis" assumption is valid.

In this paper, first we model phytoplankton–herbivore interactions with only one nutrient element (P) and assume that both phytoplankton and herbivores have variable stoichiometry. The total nutrient amount of our system is a constant since most experiments for *Daphnia* are performed in closed microcosms. We explicitly examine how the stoichiometric variability of herbivores affects predator–prey dynamics, estimating the dynamical threshold (called "hard dynamical threshold") for switch of dynamics. Only when the stoichiometric variability of herbivores is less than the threshold, theoretical results from strict homeostasis models remain sound. Next, we model phytoplankton–herbivore interactions with two nutrient elements (P and N) to evaluate if similar outcomes arise and if introducing two nutrients affects the position of the hard dynamical threshold for stoichiometric variability.

2. Model derivation

To quantitatively test how "nonhomeostasis" affects trophic interactions in a food chain, we develop a closed-nutrient model and assume that there is sufficient light for algae to grow. We further assume that there is only one nutrient element, R, with four other state variables — phytoplankton carbon biomass A with P:C ratio Q_A, and herbivore carbon biomass H with P:C ratio Q_H (Table 1).

The equation of algal biomass change has three parts:

$$\frac{dA}{dt} = \text{growth} - \text{nonpredatory death} - \text{predation}.$$

The algal growth term depends on internal nutrient content (Droop, 1974):

$$\text{algal growth} = \mu_A \left(1 - \frac{Q_A^{min}}{Q_A}\right) A,$$

where Q_A^{min} is the minimal P:C ratio and μ_A is a theoretical maximal growth rate, which may not be achieved. The per capita nonpredatory death rate is a constant d_A. The predation term takes the Holling Type II functional response: predation = $f(A)H$, where $f(A) = (c_H A)/(a_H + A)$.

The equation of algal P:C ratio change has two parts:

$$\frac{dQ_A}{dt} = \text{replenishment} - \text{depletion}.$$

The replenishment rate of algal P:C ratio is the per capita nutrient uptake rate of algae:

$$\text{replenishment of algal P:C ratio} \triangleq \rho(Q_A, R)$$
$$= V_A \left(\frac{R}{a_A + R}\right) \left(\frac{Q_A^{max} - Q_A}{Q_A^{max} - Q_A^{min}}\right),$$

where V_A is the maximal per capita nutrient uptake rate of algae, $R/(a_A + R)$ is the Michaelis-Menten function, and $(Q_A^{max} - Q_A)/(Q_A^{max} - Q_A^{min})$ means that when P:C ratio is near its minimum, nutrient uptake is high, and when P:C ratio increases to its maximum, nutrient uptake decreases zero. Per capita depletion of algal P:C ratio is by growth dilution, i.e.

$$\text{depletion of algal P:C ratio} = \mu_A \left(1 - \frac{Q_A^{min}}{Q_A}\right) Q_A.$$

The equation of herbivore's biomass change has two parts:

$$\frac{dH}{dt} = \text{growth} - \text{death}.$$

The growth rate of herbivores is also assumed to follow the Droop equation:

$$\text{herbivore's growth} = \mu_H \left(1 - \frac{Q_H^{min}}{Q_H}\right) H,$$

where Q_H^{min} is the minimal P:C ratio and μ_H is a theoretical maximal growth rate, which may not be achieved. The per capita herbivore's death rate is a constant d_H.

The equation of herbivore's P:C ratio change has three parts:

$$\frac{dQ_H}{dt} = \text{replenishment} - \text{depletion} - \text{release}.$$

The per capita predation rate is $f(A)$. Since this is measured in carbon biomass, we convert it to nutrient-based per capita predation rate, $f(A)Q_A$, which is the replenishment rate of herbivore's P:C ratio. The per capita depletion rate of herbivore's P:C ratio is same as the per capita growth rate of herbivores, i.e.

$$\text{depletion of herbivore's P:C ratio} = \mu_H \left(1 - \frac{Q_H^{min}}{Q_H}\right) Q_H.$$

$$\text{nutrient release of herbivores} = \text{nutrient ingested from predation} - \text{nutrient assimilated}.$$

The nutrient ingested from predation is $f(A)Q_A$. The nutrient assimilated by herbivores takes the form proposed by Grover (2003):

$$\text{nutrient assimilated by herbivores} = f(A)Q_A \frac{Q_H^{max} - Q_H}{Q_H^{max} - Q_H^{min}},$$

which assumes that when a herbivore's P:C ratio is near its minimum, the assimilated proportion of the ingested nutrient reaches

Table 1
Variables and parameters used in simulations.

Symbol	Meaning	Unit	Value
Variables			
R	Nutrient concentration	mgP/L	I.C. 0–0.15
A	Density of algal carbon content	mgC/L	I.C. varied
Q_A	Algal P:C ratio	mgP/mgC	I.C. Q_A^{min}
H	Density of herbivore's carbon content	mgC/L	I.C. varied
Q_H	Herbivore's P:C ratio	mgP/mgC	I.C. Q_H^{min}
Parameters			
X_A	Stoichiometric variability indicator of algae	No unit	5–12
X_H	Stoichiometric variability indicator of herbivores	No unit	1–3
η_A	Stoichiometric variability of algae	No unit	$X_A - 1$
η_H	Stoichiometric variability of herbivores	No unit	$X_H - 1$
Q_A^{min}	Minimal algal P:C ratio	mgP/mgC	0.004
Q_A^{max}	Maximal algal P:C ratio	mgP/mgC	Varied with X_A
Q_H^{min}	Minimal herbivore's P:C ratio	mgP/mgC	0.025
Q_H^{max}	Maximal herbivore's P:C ratio	mgP/mgC	Varied with X_H
V_A	Maximal uptake rate of nutrient by algae	mgP/mgC/day	0.2–1
a_A	Half-saturation constant for nutrient uptake by algae	mgP/L	0.0015
c_H	Maximal predation rate	/day	0.75
a_H	Half-saturation constant for predation	mgC/L	0.25
μ_A	Theoretical maximal growth rate of algae	/day	1
d_A	Algal specific maintenance respiration loss rate	/day	0.1
μ_H	Theoretical maximal growth rate of herbivores	/day	0.5
d_H	Per capita mortality rate of herbivores	/day	0–0.2, median 0.08

Note: I.C. represents initial condition.

100%, and when the P:C ratio increases to its maximum, the assimilated proportion decreases to zero. Hence,

$$\text{nutrient release of herbivores} \triangleq \sigma_H(A, Q_A, Q_H) = f(A)Q_A\left[1 - \frac{Q_H^{max} - Q_H}{Q_H^{max} - Q_H^{min}}\right].$$

This formulation for herbivore release allows for varying degrees of homeostasis, by changing the range between Q_H^{min} and Q_H^{max}. Homeostasis has been defined formally in stoichiometry as the variation in the consumer relative to the variation in the resources, whereas homeostasis in this paper refers only to absolute variation in the consumer.

The equation of change of nutrient density in the external environment has four parts:

$$\frac{dR}{dt} = -\text{uptake by algae} + \text{release by herbivores} + \text{recycling from dead algae} + \text{recycling from dead herbivores}.$$

We can easily obtain all these four terms from the above derivations. In summary, our closed-nutrient model is

$$\begin{aligned}
\frac{dR}{dt} &= -\rho_A(Q_A, R)A + \sigma_H(A, Q_A, Q_H)H + Q_A d_A A + Q_H d_H H,\\
\frac{dA}{dt} &= \mu_A\left(1 - \frac{Q_A^{min}}{Q_A}\right)A - d_A A - f(A)H,\\
\frac{dQ_A}{dt} &= \rho_A(Q_A, R) - \mu_A\left(1 - \frac{Q_A^{min}}{Q_A}\right)Q_A,\\
\frac{dH}{dt} &= \mu_H\left(1 - \frac{Q_H^{min}}{Q_H}\right)H - d_H H,\\
\frac{dQ_H}{dt} &= f(A)Q_A - \mu_H\left(1 - \frac{Q_H^{min}}{Q_H}\right)Q_H - \sigma_H(A, Q_A, Q_H),
\end{aligned} \tag{1}$$

where

$$\begin{aligned}
\rho_A(Q_A, R) &= V_A\left(\frac{R}{a_A + R}\right)\left(\frac{Q_A^{max} - Q_A}{Q_A^{max} - Q_A^{min}}\right),\\
\sigma_H(A, Q_A, Q_H) &= f(A)Q_A\left[1 - \frac{Q_H^{max} - Q_H}{Q_H^{max} - Q_H^{min}}\right],\\
f(A) &= \frac{c_H A}{a_H + A},\\
Q_A^{max} &= X_A Q_A^{min},\\
Q_H^{max} &= X_H Q_H^{min},
\end{aligned}$$

with fixed minimal P:C ratios Q_A^{min}, Q_H^{min} because minimal P:C ratios reflect structural nutrient contents. Both algae and herbivores have variable stoichiometry with variability indicators $X_A(\geq 1)$ and $X_H(\geq 1)$, respectively. In our simulations, we plot stoichiometric variabilities as $\eta_A = X_A - 1(\geq 0)$ and $\eta_H = X_H - 1(\geq 0)$ in terms of percentages. The parameter X_A has been found to reach up to 12 (Sterner and Elser, 2002), that is, a stoichiometric variability of algae η_A of up to 1100%. The parameter X_H has been found to reach up to 3 for the model herbivore *Daphnia*, e.g. *D. pulex* in Experiment 1 of Hood and Sterner (2010); that is, a stoichiometric variability of herbivores η_H of up to 200%. A possible exception is *Daphnia mendotae* in Experiment 1 of Hood and Sterner (2010), whose X_H was not only nine times larger than for *D. mendotae* in Experiment 2 but also far larger than X_H of any other *Daphnia* species. We exclude this unusual and unduplicated data point in our consideration.

Let $TR(t) = R(t) + A(t)Q_A(t) + H(t)Q_H(t)$ be the total nutrient in the system at time t, then

$$\frac{dTR}{dt} = \frac{dR}{dt} + \frac{dA}{dt}Q_A + A\frac{dQ_A}{dt} + \frac{dH}{dt}Q_H + H\frac{dQ_H}{dt} = 0,$$

by substituting all equations into the derivatives. Hence, the total nutrient in the system follows the Law of Mass Conservation; that is, $TR(t)$ is a constant independent of t and $TR = R(0) + A(0)Q_A(0) + H(0)Q_H(0)$. We can change the total nutrient availability in the system by varying $R(0)$ in simulations.

Therefore, we can reduce the system by one dimension:

$$\begin{aligned}\frac{dA}{dt} &= \mu_A\left(1-\frac{Q_A^{min}}{Q_A}\right)A - d_A A - f(A)H,\\ \frac{dQ_A}{dt} &= \rho_A(Q_A, TR - AQ_A - HQ_H) - \mu_A\left(1-\frac{Q_A^{min}}{Q_A}\right)Q_A,\end{aligned} \tag{2}$$

$$\begin{aligned}\frac{dH}{dt} &= \mu_H\left(1-\frac{Q_H^{min}}{Q_H}\right)H - d_H H,\\ \frac{dQ_H}{dt} &= f(A)Q_A - \mu_H\left(1-\frac{Q_H^{min}}{Q_H}\right)Q_H - \sigma_H(A, Q_A, Q_H).\end{aligned}$$

3. Theoretical results

In these first simulations we take *Daphnia* as the herbivore and P as the only limiting nutrient element. We present estimation of parameters and initial conditions in Table 1. Most of these parameter values, except stoichiometric variabilities, have been estimated in existing modeling papers (Bratbak and Thingstad, 1985; Loladze et al., 2000; Wang et al., 2008, 2009).

Logical deduction suggests that nonhomeostatic herbivores will often grow better than homeostatic herbivores but never worse. The herbivore's nutrient release rate σ_H is a decreasing function of Q_H^{max} except when $Q_H = Q_H^{min}$, and thus is decreasing in X_H. This observation, together with the equation of Q_H, leads to the positive dependence of Q_H on X_H. Therefore, the growth rate of herbivores is neutrally or positively related to X_H, or η_H, but not negatively. This mathematical deduction points to a potential cost of homeostasis, emphasizing the importance of other, non-modeled, benefits of homeostasis to herbivore fitness.

Two types of dynamics occurred in our time-series simulations (Fig. 1): herbivore extinction or oscillatory coexistence between algae and herbivore. In our model, we assume sufficient light input that likely leads to severe nutrient limitation. Therefore, existing models with the "strict homeostasis" assumption, as well as its equivalence in our model with 0% of herbivore stoichiometric variability, predict herbivore extinction in a closed-nutrient environment with strong nutrient limitation. The origin (0,0) in Fig. 2(a) corresponds to this case. As we decrease the strength of herbivore homeostasis, herbivores still go extinct at low levels of stoichiometric variability (see Fig. 1(a) as an example), up until a threshold of 83% variability (Fig. 2). When the stoichiometric variability of herbivores is greater than this threshold, herbivores survive and coexist with algae (see Fig. 1(b) as an example). We refer to this bifurcation point as a "hard dynamical threshold". This threshold is mathematically defined as the value of stoichiometric variability for the stability switch of the herbivore's extinction equilibrium $(\overline{A}, \overline{Q}_A, 0, \overline{Q}_H)$, with

$$\begin{aligned}\overline{Q}_A &= \frac{\mu_A Q_A^{min}}{\mu_A - d_A},\\ \overline{A} &= \frac{(a_A + TR)\phi(\overline{Q}_A) - TR}{\overline{Q}_A(\phi(\overline{Q}_A) - 1)},\end{aligned} \tag{3}$$

$$\overline{Q}_H = \frac{f(\overline{A})\overline{Q}_A Q_H^{max} + \mu_H Q_H^{min}(Q_H^{max} - Q_H^{min})}{f(\overline{A})\overline{Q}_A + \mu_H(Q_H^{max} - Q_H^{min})},$$

where

$$\phi(\overline{Q}_A) = \frac{\mu_A(Q_A^{max} - Q_A^{min})}{V_A}\frac{\overline{Q}_A - Q_A^{min}}{Q_A^{max} - \overline{Q}_A}.$$

Fig. 3(a) shows that the hard dynamical threshold is a decreasing function of nutrient availability; that is, in a more nutrient-enriched environment, even consumers with somewhat limited stoichiometric flexibility can avoid deterministic extinction due to stoichiometric constraints. On the other hand, at low nutrient availability, the parameter space where dynamics are preserved is expanded, suggesting the strict homeostasis assumption is most valid at low nutrient availability. Most existing theoretical models assume strict homeostasis of herbivores by arguing that herbivores have much lower variability in elemental composition than primary producers. However, our analysis shows that this reasoning is invalid, because the threshold for switch of dynamics is independent of algal stoichiometric variability (see Fig. 3(b)). We observe that previous theoretical results based on the "strict homeostasis" assumption remain sound for these parameter values when the stoichiometric variability of herbivores is less than 67.6% (see Fig. 3). Above this level of variability, dynamics differ.

However, further analysis shows that the hard dynamical threshold strongly depends on herbivore traits related to turnover — mortality and growth rates. As mortality rate increases, so does the hard dynamical threshold. This increases the parameter space where the strict homeostasis assumption is valid and herbivores may go extinct (see Fig. 4(a)). We vary both mortality and growth rates of herbivores in Fig. 4(b) and determine whether the hard dynamical threshold is greater than or less than 50%. When the mortality rate is high but the intrinsic growth rate is not too large, the hard dynamical threshold is greater than 50% (see Fig. 4(b)), in which case it seems appropriate to assume strict homeostasis.

4. Extension to multiple nutrients

The extension of the one nutrient model to multiple nutrients is provided by

$$\begin{aligned}\frac{dA}{dt} &= \mu_A \min_i\left(1-\frac{Q_A^{i,min}}{Q_A^i}\right)A - d_A A - f(A)H,\\ \frac{dQ_A^i}{dt} &= \rho_A^i(Q_A^i, R^i) - \mu_A \min_i\left(1-\frac{Q_A^{i,min}}{Q_A^i}\right)Q_A^i,\end{aligned} \tag{4}$$

$$\begin{aligned}\frac{dH}{dt} &= \mu_H \min_i\left(1-\frac{Q_H^{i,min}}{Q_H^i}\right)H - d_H H,\\ \frac{dQ_H^i}{dt} &= f(A)Q_A^i - \mu_H \min_i\left(1-\frac{Q_H^{i,min}}{Q_H^i}\right)Q_H^i - \sigma_H^i(A, Q_A^i, Q_H^i),\end{aligned}$$

where

$$\begin{aligned}\rho_A^i(Q_A^i, R^i) &= V_A^i\left(\frac{R^i}{a_A^i + R^i}\right)\left(\frac{Q_A^{i,max} - Q_A^i}{Q_A^{i,max} - Q_A^{i,min}}\right),\\ R^i &= TR^i - AQ_A^i - HQ_H^i,\\ \sigma_H^i(A, Q_A^i, Q_H^i) &= f(A)Q_A^i\left[1 - \frac{Q_H^{i,max} - Q_H^i}{Q_H^{i,max} - Q_H^{i,min}}\right],\\ f(A) &= \frac{c_H A}{a_H + A},\\ Q_A^{i,max} &= X_A^i Q_A^{i,min},\\ Q_H^{i,max} &= X_H^i Q_H^{i,min},\end{aligned}$$

$i = 1, 2$ in our simulations represent P and N, respectively. The minimum functions follow the Liebig's Law of Minimum.

All P-related ($i = 1$) parameter values are same as the one nutrient case. For simplicity, all N-related ($i = 2$) parameters $Q_A^{2,min}$, $Q_H^{2,min}$, V_A^i, a_A^i, $R^i(0)$ are chosen to be P-related values multiplied by a uniform constant. Note that the herbivore species must be nutrient-limited, either by P or N. For herbivores that are less

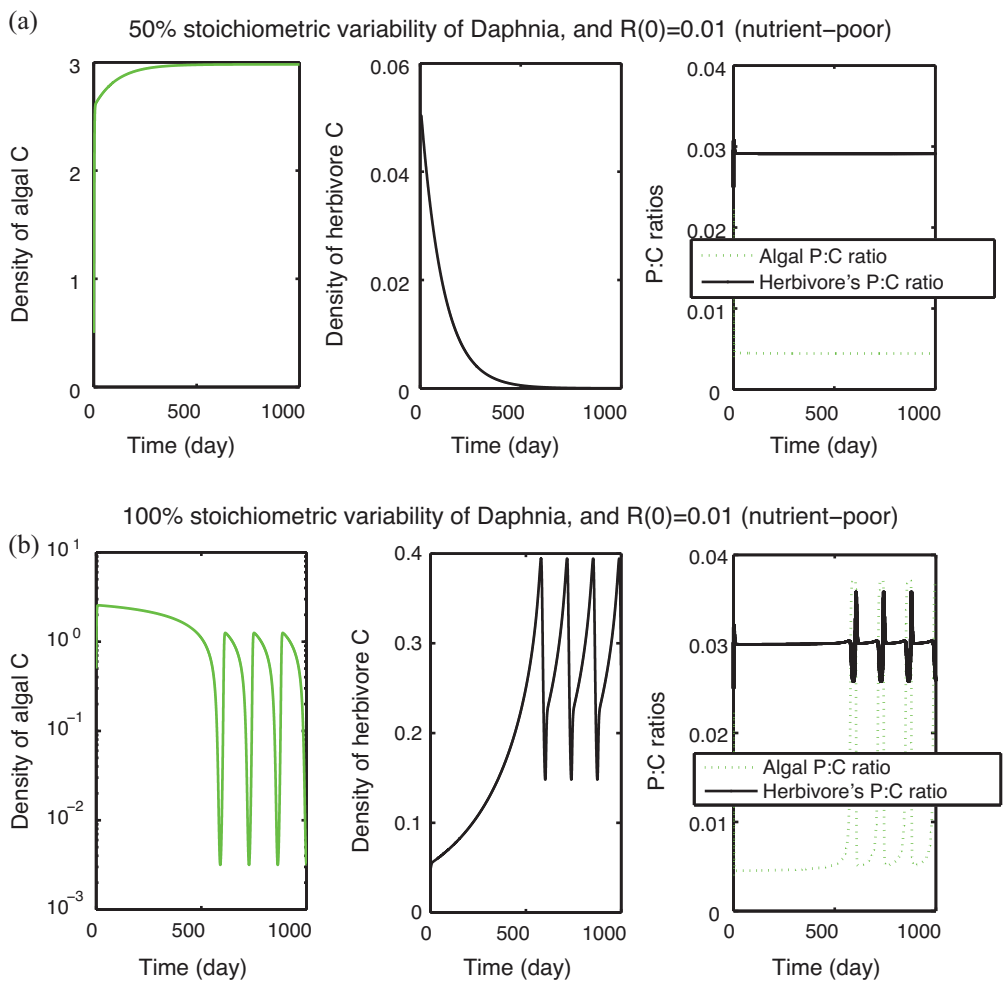

Fig. 1. Randomly picked simulations for different stoichiometric variabilities under nutrient-poor status. These time series suggest that there should be a threshold of stoichiometric variability of *Daphnia* for switch of dynamics. In these simulations, $X_A = 10$, $V_A = 0.5$, $A(0) = 0.5$, $H(0) = 0.05$ and other parameter values and initial conditions are in Table 1.

nutrient-limited, i.e. their minimum P:C ratios $Q_H^{i,min}$ ($i = 1, 2$) are lower, our hard dynamical threshold results in the next paragraph are robust.

Under various environmental N:P ratios, the hard dynamical thresholds are shown in Fig. 5 with different colors. When the environmental N:P ratio increases above the neutral ratio, the hard dynamical threshold shifts below the neutral case, i.e. dynamics are more sensitive to N-associated stoichiometric variability of herbivores. Herbivore's survival needs higher variation in P. On the other hand, when the environmental N:P ratio decreases below the neutral ratio, the hard dynamical threshold shifts to the left of the neutral case, i.e. dynamics are more sensitive to P-associated stoichiometric variability of herbivores. Herbivore's survival needs higher variation in N. For the neutral environmental N:P ratio scenario (the black star in Fig. 5), the hard dynamical threshold of P or N is about 70.6%, close to the single-nutrient case.

In the single-nutrient model, we discussed how turnover rates of herbivores determine the appropriateness of the "strict

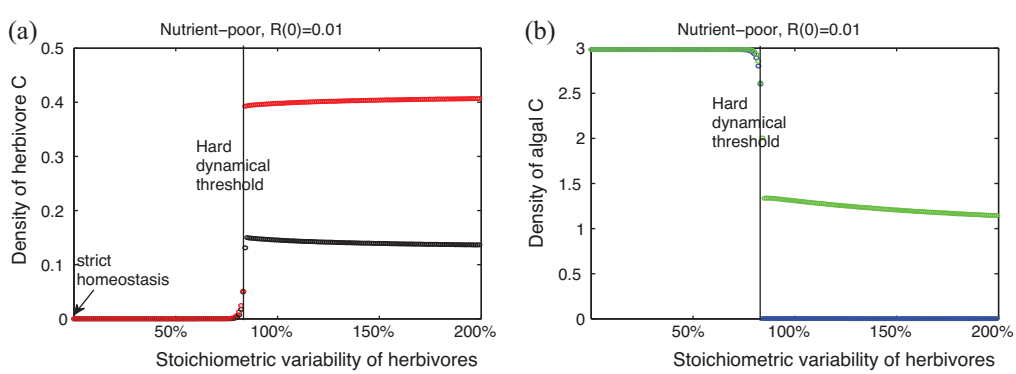

Fig. 2. The threshold of stoichiometric variability for switch of dynamics. (a) We plot maximum and minimum herbivore *C* values of the attractor (equilibrium or limit cycle) for typical solutions. (b) We plot maximum and minimum algal *C* values of the attractor (equilibrium or limit cycle) for typical solutions.

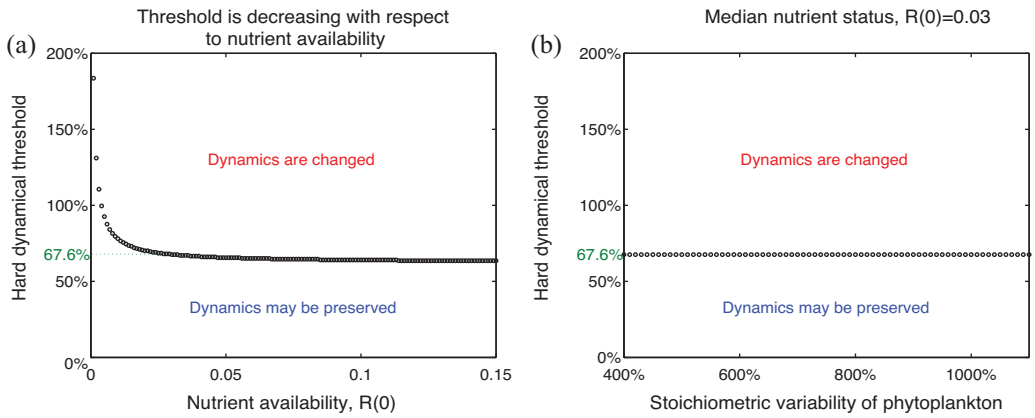

Fig. 3. The threshold of herbivore stoichiometric variability is a decreasing function of nutrient availability and independent of algal stoichiometric variability.

homeostasis" assumption. Since turnover rates are correlated in many situations, we assume turnover rates increase proportionally with a same rate, i.e. the theoretical maximal growth rate $\mu_H = 0.5\alpha$ and the per capita mortality rate $d_H = 0.08\alpha$, and then we decrease or increase α from one. We list our numerical results of thresholds for P or N with respect to various values of α in the table below:

α	0.5	0.6	0.7	0.8	0.9	1	1.1	1.2	1.3
Threshold	25.6%	31.6%	37.6%	43.6%	52.6%	70.6%	100.6%	175.6%	>200%

When the turnover multiplier α increases, the threshold increases and thus the "strict homeostasis" assumption is more likely valid. When the turnover rates are low, the sensitivity of the threshold is low; when the turnover rates are high, the sensitivity of the threshold is high.

Fig. 6 exhibits dynamics of N:P ratios in the external environment, algae, and herbivores, with respect to various levels of stoichiometric variability in herbivores and various initial N:P ratios. With a herbivore stoichiometric variability of 50%, herbivore N:P ratio eventually converges to a constant N:P ratio (panels (a) and (b)). With a capacity for stoichiometric variability of 100%, herbivores have variable N:P ratios but these variations are much smaller than the external environment or algae (panels (c) and (d)). Whether N:P ratios in the external environment, algae, or herbivores are above or below the neutral ratio depends on the initial environmental N:P ratio. Simulations in Fig. 6 illustrate the dynamical behaviors of limit cycle or chaos in the top-right region of Fig. 5. The rich dynamics of stoichiometric models have been discussed in many theoretical studies such as Deng and Loladze (2007), Wang et al. (2009) and Li et al. (2011).

5. Discussion

We develop new stoichiometric models for one nutrient and multiple nutrients after relaxing the commonly used "strict homeostasis" assumption. Our analyses show that the assumption of fixed stoichiometry of herbivores in existing models has major impacts on predicted herbivore dynamics. To examine when this assumption can be safely applied, we define a threshold (called "hard dynamical threshold") for the stoichiometric variability of herbivores. We find that this threshold is about 67.6% under realistic settings and the median nutrient availability (see Fig. 3). However this value also varies with herbivore turnover rates (see Fig. 4). When the stoichiometric variability of herbivores is less than this threshold, the "strict homeostasis" assumption can be applied. For both one-nutrient and two-nutrient models, we evaluated the robustness and sensitivity of this threshold with respect to some key parameters and environmental nutrient conditions (see Figs. 3–5, and the table in Section 4). The hard dynamical threshold strongly depended on herbivore traits such as turnover rates, but it was independent of algal stoichiometric variability (see Fig. 3). Our analyses also showed that the "strict homeostasis" assumption is more likely valid under low nutrient conditions. For the two-nutrient model, we showed how the hard dynamical threshold shifts according to the change of environmental N:P

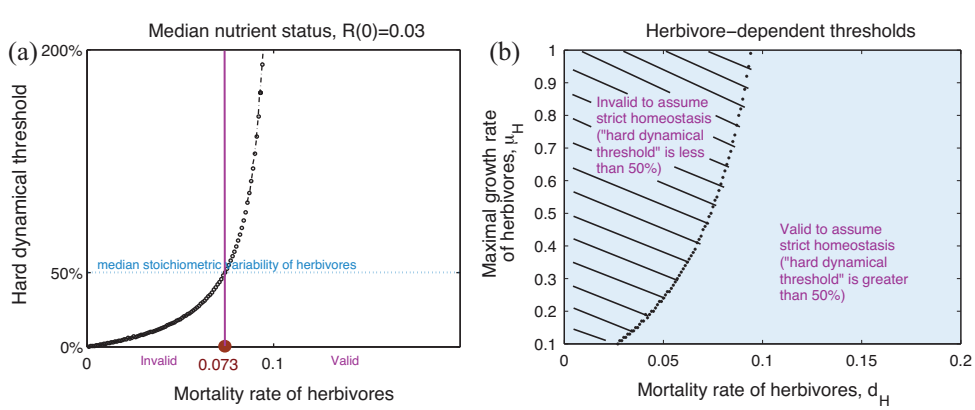

Fig. 4. (a) The threshold of herbivore stoichiometric variability strongly depends on herbivore's mortality rate. For the median stoichiometric variability, the strict homeostasis assumption is valid when the mortality rate is greater than 0.073, while the assumption is invalid when the mortality rate is less than 0.073. (b) A two-dimensional parameter space to show how the hard dynamical threshold depends on herbivore's growth and mortality rates.

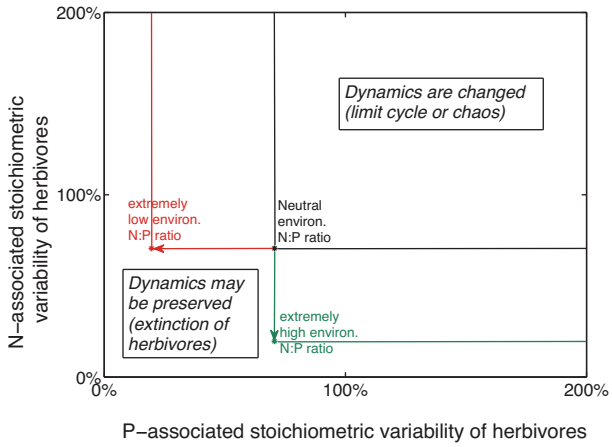

Fig. 5. The two-dimensional thresholds of P- and N-associated stoichiometric variabilities for switch of dynamics. A case with neutral environmental N:P ratio, for which the hard dynamical threshold is indicated by the black lines launched from the black star; a case with extremely low environmental N:P ratio (TR^2:TR^1 = 2), for which the hard dynamical threshold is indicated by the red lines launched from the red star; a case with extremely high environmental N:P ratio (TR^2:TR^1 = 125), for which the hard dynamical threshold is indicated by the green lines launched from the green star. The dynamics may be preserved to the left and below the threshold lines, while the dynamics are changed to the right and above the threshold lines. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

ratio (see Fig. 5). Simulations showed that chaos can occur in the case of herbivore survival (see Fig. 6). Obviously higher herbivore stoichiometric variability leads to higher dynamical complexity of the system.

Other dynamical thresholds could be obtained from models that include more environmental conditions such as light. For example, we could consider high grazer/low producer versus low grazer/high producer systems if we incorporated light intensity into the model. Under intermediate light intensities, herbivores may always survive with or without stoichiometric variability. For this scenario, we can compute the Hopf bifurcation (switching between an attracting steady state and a attracting limit cycle) to compare the case "variable C:N:P ratio of herbivores" with the case "fixed C:N:P ratio of herbivores", as well as homoclinic bifurcation after which the limit cycle vanishes. All these dynamical thresholds, including the hard dynamical threshold, provide necessary conditions for preservation of dynamics. The hard dynamical threshold we obtain in this paper is most robust because it is qualitatively defined, and most interesting because the main qualitative difference between stoichiometric predator–prey models and nonstoichiometric predator–prey models occurs at relatively high light intensities (Loladze et al., 2000; Wang et al., 2008).

Mathematically, it is interesting and intriguing to express the hard dynamical threshold explicitly. At least we can numerically express the threshold as a function of all parameters. In order to determine the conditions for existence of an attracting limit cycle, alternatively we can find the conditions for local and global stability of the herbivore extinction equilibrium. Since the model is four-dimensional, it is difficult even to find stability conditions for the herbivore extinction equilibrium. Our strategy for future analyses would be to simplify the model to be two-dimensional by applying the quasi-steady state approximation to both equations of P:C ratios because changes of P:C ratios have faster dynamics. This is an open mathematical problem.

We can easily construct open-nutrient models by incorporating chemostat-type flows (Smith and Waltman, 1995; Grover, 2003). Examination of limited parameter space shows that all results from closed-nutrient models hold when the nutrient input is small, while herbivores can survive under relatively strong light when the nutrient input is large enough. In this case, the hard dynamical threshold may disappear. However, we can still define other

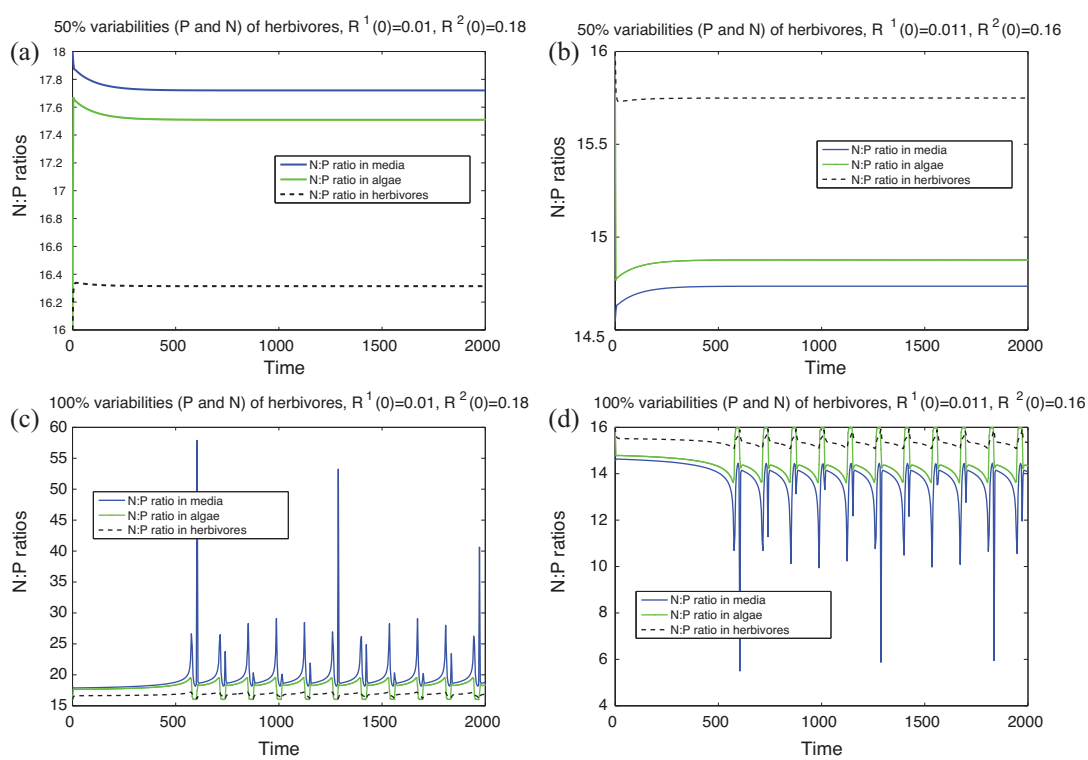

Fig. 6. Dynamics of N:P ratios in media, algae, and herbivores: (a) low stoichiometric variabilities and relatively high initial environmental N:P ratio. (b) Low stoichiometric variabilities and relatively low initial environmental N:P ratio. (c) High stoichiometric variabilities and relatively high initial environmental N:P ratio. (d) High stoichiometric variabilities and relatively low initial environmental N:P ratio.

dynamical thresholds, such as Hopf bifurcation or period-doubling bifurcation.

The assumption of strict homeostasis has been widely used in theoretical and empirical studies of the stoichiometric aspect of trophic interactions. This theoretical paper provides some answers to the following questions: Can we always assume heterotrophs have constant nutrient contents? If not, when can we make this assumption? Does the applicability depend on traits of species, environmental conditions, or some other factors? Can we express necessary or sufficient conditions explicitly? More empirical and theoretical studies need to be accumulated for the complete understanding of the applicability of the "strict homeostasis" assumption.

References

Acharya, K., Kyle, M., Elser, J.J., 2004. Biological stoichiometry of Daphnia growth: an ecophysiological test of the growth rate hypothesis. Limnology & Oceanography 49, 656–665.

Andersen, T., 1997. Pelagic Nutrient Cycles: Herbivores as Sources and Sinks. Springer, Berlin.

Bratbak, G., Thingstad, T.F., 1985. Phytoplankton–bacteria interactions: an apparent paradox? Analysis of a model system with both competition and commensalism. Marine Ecology Progress Series 25, 23–30.

Deng, B., Loladze, I., 2007. Competitive coexistence in stoichiometric chaos. Chaos 17, 033108(14 pages).

DeMott, W.R., Gulati, R.D., Siewertsen, K., 1998. Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. Limnology & Oceanography 43, 1147–1161.

Droop, M.R., 1974. The nutrient status of algal cells in continuous culture. Journal of the Marine Biological Association of the United Kingdom 54, 825–855.

Elser, J.J., Urabe, J., 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations and consequences. Ecology 80, 735–751.

Grover, J.P., 2003. The impact of variable stoichiometry on predator–prey interactions: a multinutrient approach. American Naturalist 162, 29–43.

Hessen, D.O., Bjerking, B., 1997. A model approach to planktonic stoichiometry and consumer-resource stability. Freshwater Biology 38, 447–471.

Hood, J.M., Sterner, R.W., 2010. Diet mixing: do animals integrate growth or resources across temporal heterogeneity? The American Naturalist 176, 651–663.

Li, X., Wang, H., Kuang, Y., 2011. Global analysis of a stoichiometric producer-grazer model with Holling-type functional responses. Journal of Mathematical Biology 63, 901–932.

Loladze, I., Kuang, Y., Elser, J.J., 2000. Stoichiometry in producer-grazer systems: linking energy flow with element cycling. Bulletin of Mathematical Biology 62, 1137–1162.

Mulder, K., Bowden, W.B., 2007. Organismal stoichiometry and the adaptive advantage of variable nutrient use and production efficiency in Daphnia. Ecological Modelling 202, 427–440.

Mulder, K., 2007. Modeling the dynamics of nutrient limited consumer populations using constant elasticity production functions. Ecological Modelling 207, 319–326.

Muller, E.B., Nisbet, R.M., Kooijman, S.A.L.M., Elser, J.J., McCauley, E., 2001. Stoichiometric food quality and herbivore dynamics. Ecology Letters 4, 519–529.

Persson, J., Fink, P., Goto, A., Hood, J.M., Jonas, J., Kato, S., 2010. To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. Oikos 119, 741–751.

Smith, H.L., Waltman, P., 1995. The Theory of the Chemostat: Dynamics of Microbial Competition. Cambridge Studies in Mathematical Biology, Cambridge University Press.

Sterner, R.W., Elser, J.J., 2002. Ecological Stoichiometry. Princeton University, Princeton, NJ.

Wang, H., Smith, H.L., Kuang, Y., Elser, J.J., 2007. Dynamics of stoichiometric bacteria–algae interactions in the epilimnion. SIAM Journal on Applied Mathematics 68, 503–522.

Wang, H., Kuang, Y., Loladze, I., 2008. Dynamics of a mechanistically derived stoichiometric producer-grazer model. Journal of Biological Dynamics 2, 286–296.

Wang, H., Dunning, K., Elser, J.J., Kuang, Y., 2009. Daphnia species invasion, competitive exclusion, and chaotic coexistence. Discrete and Continuous Dynamical Systems - Series B 12, 481–493.