Weak dynamical threshold for the “strict homeostasis” assumption in ecological stoichiometry

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Abstract

“Stoichiometric homeostasis” is 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. Most stoichiometric models 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. The study for the hard dynamical threshold under sufficient light in Wang et al. (2012) suggested that the “strict homeostasis” assumption is reasonable when the stoichiometric variability of herbivores is less than the hard dynamical threshold. In this paper, we explore the light-dependent case that results in homoclinic and heteroclinic bifurcations, from which we obtain the weak dynamical threshold, which is normally larger than the hard dynamical threshold. With the weak dynamical threshold, the “strict homeostasis” assumption is more likely valid, which further confirms the conclusion that strict homeostasis of herbivores can be assumed for most herbivores. Homoclinic/heteroclinic bifurcations are not only exciting dynamics in mathematics but also important indicators for the robustness of empirical studies. Experimental results are highly sensitive when homoclinic or heteroclinic orbits occur.

1. Introduction

Ecological stoichiometry is the study of the balance of energy and nutrient elements in trophic interactions (Sterner and Elser, 2002). Stoichiometric models incorporate flows of energy (or C) and nutrient elements (such as N or P) into population dynamics. Many existing stoichiometric producer–grazer models have assumed constant nutrient contents in herbivores, called “fixed stoichiometry” or “strict homeostasis” (Andersen, 1997; Hessen and Bjerkling, 1997; Elser and Urabe, 1999; Loladze et al., 2000; Muller et al., 2001; Wang et al., 2008; Peace et al., 2014). Some other models have examined phytoplankton–bacteria interactions and assumed strict homeostasis in bacteria (Bratbak and Thingstad, 1985; Wang et al., 2007; Alijani et al., 2015). As a conclusion, most existing stoichiometric models assume variable stoichiometry in autotrophs but fixed stoichiometry in heterotrophs.

Under the “strict homeostasis” assumption for 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 are often limited by nutrients as well and may even go extinct despite an abundance of food (Andersen, 1997; Hessen and Bjerkling, 1997; Loladze et al., 2000; Muller et al., 2001; Wang et al., 2007, 2008; Wang, 2010). Mathematically, complex dynamics such as attracting limit cycles, bistability, or chaos can appear under stoichiometric constraints (Loladze et al., 2000; Deng and Loladze, 2007; Wang et al., 2008, 2009).

However, strict homeostasis 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 trophic interaction models regulates population 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) showed that the P content of Daphnia magna decreased from 1.55% to 1.11% 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%. Therefore, though heterotrophs are more homeostatic than autotrophs...
variables and parameters used in simulations.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Meaning</th>
<th>Unit</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R$</td>
<td>Nutrient concentration</td>
<td>mgP/L</td>
<td>1.C.0-0.15</td>
</tr>
<tr>
<td>$A$</td>
<td>Density of algal carbon content (or density of algae measured in C)</td>
<td>mgC/L</td>
<td>I.C. varied</td>
</tr>
<tr>
<td>$Q_A$</td>
<td>Algal P:C ratio</td>
<td>mgP/mgC</td>
<td>I.C. varied</td>
</tr>
<tr>
<td>$H$</td>
<td>Density of herbivore carbon content (or density of herbivore measured in C)</td>
<td>mgC/L</td>
<td>I.C. varied</td>
</tr>
<tr>
<td>$Q_H$</td>
<td>Herbivore’s P:C ratio</td>
<td>mgP/mgC</td>
<td>I.C. or $Q_H^{min}$</td>
</tr>
<tr>
<td>$z$</td>
<td>The depth from the surface</td>
<td>m</td>
<td>0–$z_m$</td>
</tr>
</tbody>
</table>

Note: I.C. represents initial condition.

(Persson et al., 2010), the widely used homeostasis assumption in stoichiometric models needs to be carefully examined.

In the past decade, some theoretical studies have developed a new generation of stoichiometric models with nonhomeostatic herbivores (Grover, 2003; Mulder and Bowden, 2007; Mulder, 2007; Wang et al., 2012). Grover (2003) developed a chemostat multinutrient model of phytoplankton carbon biomass $A$ with P:C ratio $Q_A$, herbivore biomass $H$ with P:C ratio $Q_H$ (see Table 1).

We apply the Lambert–Beer’s law to keep track of light intensity and the Liebig’s law of minimum for multiple limiting elements (phosphorus and light/energy) for both growths of the producer and the grazer. The light-dependent algal growth term is

$$
\mu_A \min \left[ 1 - \frac{Q_A^{min}}{Q_A}, \frac{1}{z_m} \int_{z_m}^{z_m} I(z, A) \, dz \right] A,
$$

and the energy-dependent herbivore’s growth term is

$$
\mu_H \min \left[ 1 - \frac{Q_H^{min}}{Q_H}, \gamma \frac{A}{H} \right] H.
$$

Of course, the corresponding cell quota dilution terms need to be changed accordingly. Consequently, we obtain the following stoichiometric model with energy flow and nutrient P cycling:

$$
\frac{dR}{dt} = -\rho_R (Q_A, A) A + \mu_R (A, Q_A, Q_H) H + Q_A d_A A + Q_H d_H H,
$$

$$
\frac{dA}{dt} = \mu_A \min \left[ 1 - \frac{Q_A^{min}}{Q_A}, \frac{1}{z_m} \int_{z_m}^{z_m} I(z, A) \, dz \right] A - f(A) H - d_A A,
$$

Table 1
\[
\frac{dQ_A}{dt} = \rho_A(Q_A, R) - \mu_A \min \left[ 1 - \frac{Q_A^{\min}}{Q_A}, \frac{1}{\varepsilon_m} \int_0^{\varepsilon_m} \frac{I(z, A)}{T(z, A) + L} \, dz \right] Q_A,
\]
\[
\frac{dH}{dt} = \min \left[ \mu_H \left( 1 - \frac{Q_H^{\min}}{Q_H} \right), \hat{f}(A) \right] H - d_H H,
\]
\[
\frac{dQ_H}{dt} = f(A)Q_A - \min \left[ \mu_H \left( 1 - \frac{Q_H^{\min}}{Q_H} \right), \hat{f}(A) \right] Q_H - \sigma_H(A, Q_A, Q_H),
\]
where

\[
\rho_A(Q_A, R) = V_A \left( \frac{R}{a_A + R} \right) \left( \frac{Q_A^{\max} - Q_A}{Q_A^{\max} - Q_A^{\min}} \right).
\]
\[
\sigma_H(A, Q_A, Q_H) = f(A)Q_A \left[ 1 - \frac{Q_H^{\max} - Q_H}{Q_H^{\max} - Q_H^{\min}} \right].
\]
\[
I(z, A) = I_0 e^{-k(z+kA)z};
\]
\[
f(A) = \frac{\hat{C}_A A}{a_H + A};
\]
\[
Q_A^{\max} = X_A Q_A^{\min},
\]
\[
Q_H^{\max} = X_H Q_H^{\min}.
\]
Here we define the stoichiometric variability of algae as $\eta_A = X_A - 1$ and the stoichiometric variability of herbivores as $\eta_H = X_H - 1$. Let $TR(t) = R(t) + A(t)Q_A(t) + H(t)Q_H(t)$ be the total nutrient P in the system at time $t$, then

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

(12)

by substituting all equations into the derivatives. Hence, the total nutrient P 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 reduce the system by one dimension as in Wang et al. (2012), and we can change the total nutrient P availability in the system by varying $R(0)$ in simulations.

3. Theoretical results

In this paper, 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. All 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, 2012).
We run simulations for two nutrient statuses (low and high). For each nutrient status, we explore the effects of light and herbivore's stoichiometric variability on population dynamics via sample solutions and bifurcation diagrams.

Because homoclinic and heteroclinic bifurcations will occur, we pose their definitions as follows:

1. Homoclinic bifurcation is a global bifurcation which occurs when a periodic orbit coincides with a saddle point.
2. Heteroclinic bifurcation is a global bifurcation involving a heteroclinic orbit that connects two or more equilibrium points.

In the oligotrophic case $R(0) = 0.01$, we vary the light intensity and plot sample solutions in Figs. 1 and 2. Fig. 1 illustrates an approximation of a homoclinic orbit which leads to an infinite period bifurcation. One important consequence of such large oscillations is population extinction due to stochastic factors. As the light intensity increases, we can observe from Fig. 2 that the solution curves will be farther away from a homoclinic orbit. When the light intensity is not too low, the solution curves follow the regular predator–prey dynamics. Figs. 3 and 4 sketch bifurcation diagrams for a wide range and a narrow range of the light intensity. Fig. 3 shows that the amplitude of the predator–prey cycle shrinks as the light intensity increases. This new finding, opposite to results found in classical predator–prey models, partly solves Rosenzweig's paradox of enrichment. When we zoom into the low light intensity part, we can observe from Fig. 4 that several homoclinic and heteroclinic bifurcations occur. We sketch all possible homoclinic/heteroclinic bifurcations on the two-dimensional parameter space in Fig. 5. We vary both the light intensity $I_{in}$ and the stoichiometric variability of herbivores $\eta H$. We observe that homoclinic/heteroclinic bifurcations occur in the parameter region when $I_{in} > 10 \mu$mol(photon)/(m²·s) and $\eta H > 99\%$. Actually if we consider Figs. 3 and 5 together, homoclinic/heteroclinic bifurcations occur when the light intensity is between two thresholds, that is, $I_{\min} < I_{in} < I_{\max}$. Fig. 5 shows that the weak dynamical threshold is 99%, much larger than the hard dynamical threshold 67% (indicated as the yellow vertical line in Fig. 5). Hence, the hard dynamical threshold is more crucial for the validity of the "strict homeostasis" assumption for herbivores. In the region where homoclinic/heteroclinic bifurcations occur, experimental results are highly sensitive as we have encountered in Elser’s lab in 2006 (Wang et al., 2009) and in 2012 (an unpublished experiment). Even in the presence of reasonably high quality food (see the eutrophic case below), it is possible for herbivores to go extinct, via falling into a homoclinic orbit. This shows the importance of considering the stoichiometric variability of herbivores.

In the eutrophic case, we illustrate from Fig. 6 that a homoclinic orbit can occur even under strong light. In Fig. 7, we sketch a two-dimensional bifurcation diagram to show when homoclinic/heteroclinic bifurcations occur.
heteroclinic bifurcations can occur. In comparison to the low nutrient case (Fig. 5), the high nutrient case has the weak dynamical threshold 79%, closer to the hard dynamical threshold, and a larger light lower bound \( I_{\text{min}} \). The locations of homoclinic/heteroclinic bifurcations in the high nutrient case are more spread-out on the two-dimensional parameter space than in the low nutrient case. This observation means that experimental results are more sensitive in an eutrophic case than in an oligotrophic case when the stoichiometric variability of herbivores is above the weak dynamical threshold.

4. Discussion

The validity of the “strict homeostasis” assumption is worth questioning. By ignoring the potential light limitation in Wang et al. (2012), the “strict homeostasis” assumption works well when the stoichiometric variability of herbivores is less than the hard dynamical threshold. In
In this paper, we extend the stoichiometric model in Wang et al. (2012) with light/energy. Introduction of light and energy flow creates very complex and interesting dynamics such as homoclinic and heteroclinic orbits. Here we define a new threshold for the validity of the "strict homeostasis" assumption, called the weak dynamical threshold, which is defined by the appearance of homoclinic/heteroclinic bifurcations. The weak dynamical threshold for herbivore's stoichiometric variability is 79–99% as opposed to the hard dynamical threshold 67%. With the weak dynamical threshold, the "strict homeostasis" assumption is more likely valid, which further confirms the conclusion that strict homeostasis of herbivores can be assumed for most herbivores.

Homoclinic/heteroclinic bifurcations are not only exciting dynamics in mathematics but also important indicators for the robustness of experimental results. Even in the presence of reasonably high quality food, it is still possible for herbivores to go extinct (with small stochasticity) via falling into a homoclinic orbit. This is a remarkable situation for empirical studies. Experimental results can be highly sensitive when homoclinic/heteroclinic bifurcations occur as we have encountered in two almost identical stoichiometric experiments in 2006 (Wang et al., 2009) and in 2012 (an unpublished experiment). Both experiments were performed in Elser's lab, but the outcomes were quite different. In comparison, a much higher percentage of microcosms have

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**Fig. 6.** An approximation of a homoclinic orbit with high nutrient $R(0) = 0.03$ and strong light $I_\text{in} = 100 \mu\text{mol}/\text{m}^2$.

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the extinction of *Daphnia* in the 2012’s experiment than in the 2006’s experiment. These empirical studies verify our experimental robustness hypothesis on homoclinic/heteroclinic orbits.

Loladze et al. (2004) showed an apparent exception to the competitive exclusion principle: two herbivores can coexist at a stable equilibrium while preying on one species of algae and being limited by the same nutrient in the prey. We have the conjecture that the stoichiometric variability of herbivores can facilitate the coexistence of even more herbivore species on one species of algae due to the complexity of dynamics. This is an open problem for future work.

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References


