

## 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 Bjerking, 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 Bjerking, 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

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**Table 1**  
Variables and parameters used in simulations.

Symbol	Meaning	Unit	Value
<i>Variables</i>			
$R$	Nutrient concentration	mgP/L	I.C.0–0.15
$A$	Density of algal carbon content (or density of algae measured in C)	mgC/L	I.C. varied
$Q_A$	Algal P:C ratio	mgP/mgC	I.C. $Q_A^{\min}$
$H$	Density of herbivore carbon content (or density of herbivore measured in C)	mgC/L	I.C. varied
$Q_H$	Herbivore's P:C ratio	mgP/mgC	I.C. $Q_H^{\min}$
$z$	The depth from the surface	m	0– $z_m$
<i>Parameters</i>			
$I_{in}$	Light intensity at surface	$\mu\text{mol}(\text{photons})/(\text{m}^2 \cdot \text{s})$	300
$K_{bg}$	Background light attenuation coefficient	$\text{m}^{-1}$	0.3–0.9
$k$	Specific light attenuation coefficient of algal biomass	$\text{m}^2/\text{mgC}$	0.0003–0.0004
$L$	Half-saturation constant for light-dependent algal production	$\mu\text{mol}(\text{photons})/(\text{m}^2 \cdot \text{s})$	120
$X_A$	Stoichiometric variability indicator of algae	No unit	5–12
$X_H$	Stoichiometric variability indicator of herbivores	No unit	1–3
$\eta_A$	Stoichiometric variability of algae	No unit	$X_A-1$
$\eta_H$	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
$\hat{e}$	Maximal conversion rate of the grazer	No unit	0.74
$\mu_A$	Theoretical maximal growth rate of algae	/day	1
$d_A$	Algal specific maintenance respiration loss rate	/day	0.1
$\mu_H$	Theoretical maximal growth rate of herbivores	/day	0.5
$d_H$	Per capita mortality rate of herbivores	/day	0.2, median 0.08
$z_m$	The depth of the water column	m	0.1

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 bacterial prey and a flagellate predator by assuming that both predator and prey have variable stoichiometry. Mulder and Bowden (2007), Mulder (2007) examined how quantitative results of existing theoretical models change after relaxing the “strict homeostasis” assumption. Recently, with sufficient light, Wang et al. (2012) obtained the hard dynamical threshold below which the “strict homeostasis” assumption is reasonable. This threshold is independent of algal stoichiometric variability, thus the historic reasoning for strict homeostasis in heterotrophs is not convincing. This study suggested that the “strict homeostasis” assumption is valid for many herbivores except for herbivores with small mortality rates, and this assumption is more likely valid in nutrient poor environments. The two-nutrient model in Wang et al. (2012) showed that herbivore's survival needs higher variation in the more potentially limiting of the two elements. All these studies reach the same conclusion that theoretical results can be different if we consider nonhomeostatic elemental composition in herbivores.

The main goal of this paper is to explore how the dynamics of trophic interactions depend on the degree of stoichiometric variability in herbivores when the light dependence is considered. Incorporating light into the stoichiometric model leads to homoclinic and heteroclinic bifurcations, and we explore their dependence on consumer stoichiometric variability. The obtained threshold is called weak dynamical threshold which is normally larger than the hard dynamical threshold in Wang et al. (2012). Experimental results become highly sensitive when homoclinic or heteroclinic cycles appear.

In this paper, we first incorporate the light dependence explicitly into our model in Wang et al. (2012). We then examine how the

stoichiometric variability of herbivores affects predator–prey dynamics, estimating the weak dynamical threshold for the appearance of homoclinic and heteroclinic cycles.

## 2. Model derivation

We explicitly incorporate light and energy flow into the closed-nutrient model with variable consumer stoichiometry in Wang et al. (2012). The variables are the concentration of the nutrient element (P, phosphorus)  $R$ , phytoplankton carbon biomass  $A$  with P:C ratio  $Q_A$ , and herbivore carbon 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

$$\mu_A \min \left[ 1 - \frac{Q_A^{\min}}{Q_A}, \frac{1}{z_m} \int_0^{z_m} \frac{I(z, A)}{I(z, A) + L} dz \right] A,$$

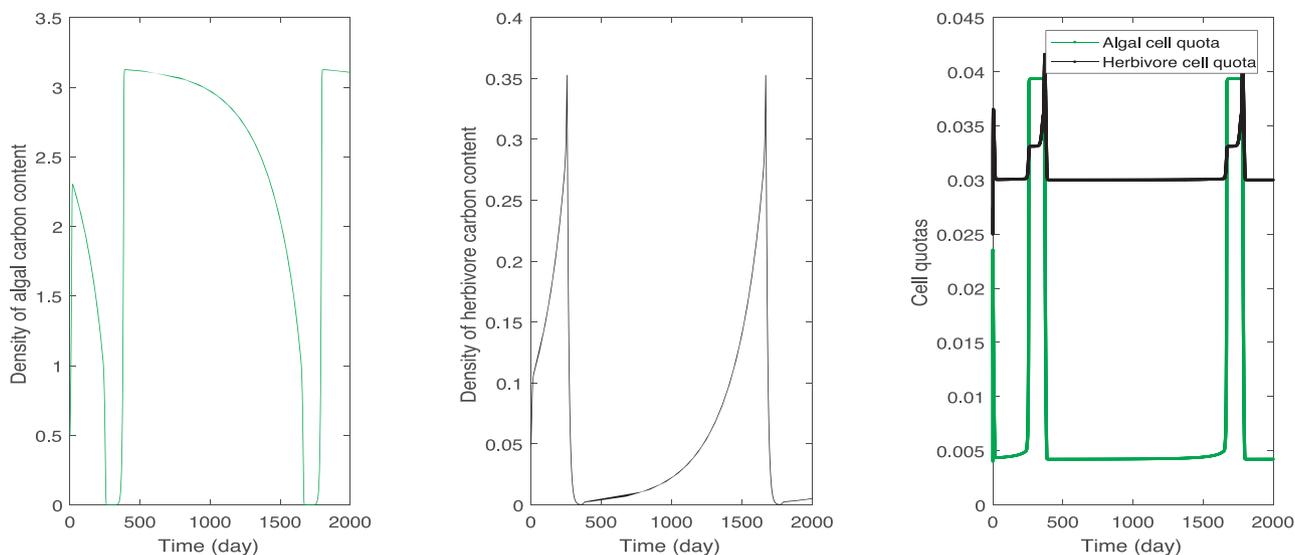
and the energy-dependent herbivore's growth term is

$$\min \left[ \mu_H \left( 1 - \frac{Q_H^{\min}}{Q_H} \right), \hat{e} f(A) \right] H.$$

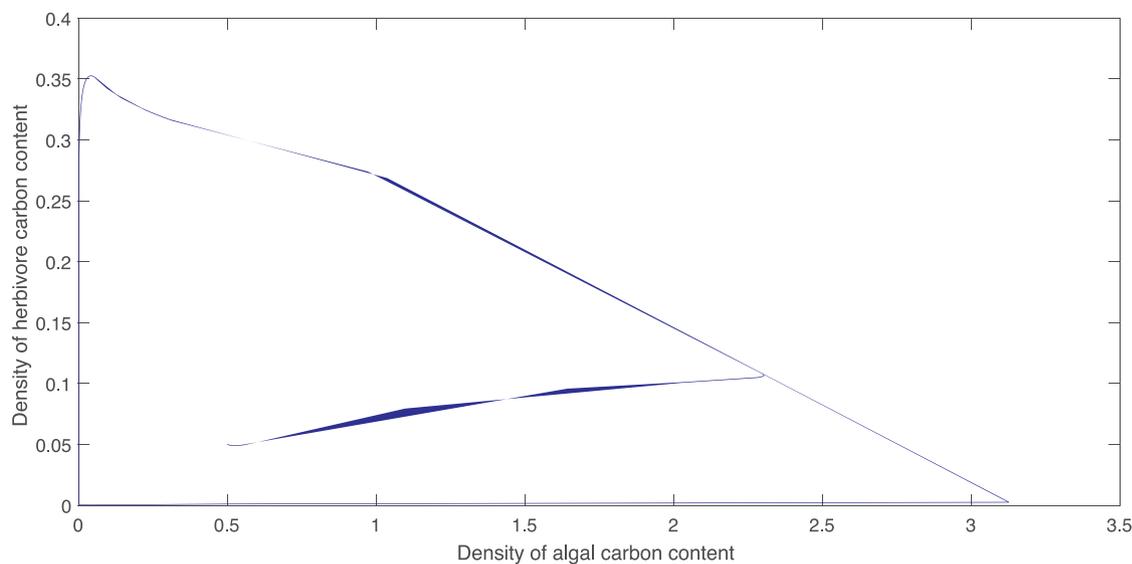
Of course, the corresponding cell quota dilution terms need to be changed accordingly. Consequently, we obtain the following stoichiometric model with energy flow and nutrient P cycling:

$$\frac{dR}{dt} = -\rho_A(Q_A, R)A + \sigma_H(A, Q_A, Q_H)H + Q_A d_A A + Q_H d_H H, \quad (1)$$

$$\frac{dA}{dt} = \mu_A \min \left[ 1 - \frac{Q_A^{\min}}{Q_A}, \frac{1}{z_m} \int_0^{z_m} \frac{I(z, A)}{I(z, A) + L} dz \right] A - f(A)H - d_A A, \quad (2)$$



(a)



(b)

Fig. 1. An approximation of a homoclinic orbit with low nutrient  $R(0) = 0.01$  and weak light  $I_{in} = 30 \mu\text{mol}/\text{m}^2$ .

$$\frac{dQ_A}{dt} = \rho_A(Q_A, R) - \mu_A \min \left[ 1 - \frac{Q_A^{\min}}{Q_A}, \frac{1}{z_m} \int_0^{z_m} \frac{I(z, A)}{I(z, A) + L} dz \right] Q_A, \tag{3}$$

$$\rho_A(Q_A, R) = V_A \left( \frac{R}{a_A + R} \right) \left( \frac{Q_A^{\max} - Q_A}{Q_A^{\max} - Q_A^{\min}} \right), \tag{6}$$

$$\frac{dH}{dt} = \min \left[ \mu_H \left( 1 - \frac{Q_H^{\min}}{Q_H} \right), \hat{e}f(A) \right] H - d_H H, \tag{4}$$

$$\sigma_H(A, Q_A, Q_H) = f(A) Q_A \left[ 1 - \frac{Q_H^{\max} - Q_H}{Q_H^{\max} - Q_H^{\min}} \right], \tag{7}$$

$$I(z, A) = I_{in} e^{-(K_{bg} + kA)z}, \tag{8}$$

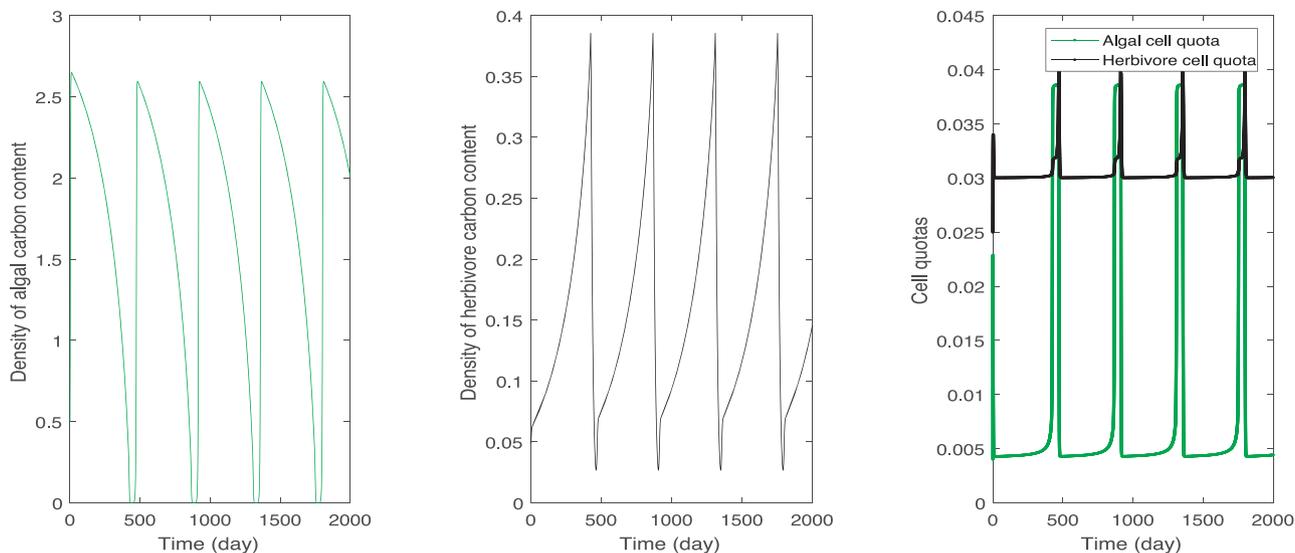
$$\frac{dQ_H}{dt} = f(A) Q_A - \min \left[ \mu_H \left( 1 - \frac{Q_H^{\min}}{Q_H} \right), \hat{e}f(A) \right] Q_H - \sigma_H(A, Q_A, Q_H), \tag{5}$$

$$f(A) = \frac{c_H A}{a_H + A}, \tag{9}$$

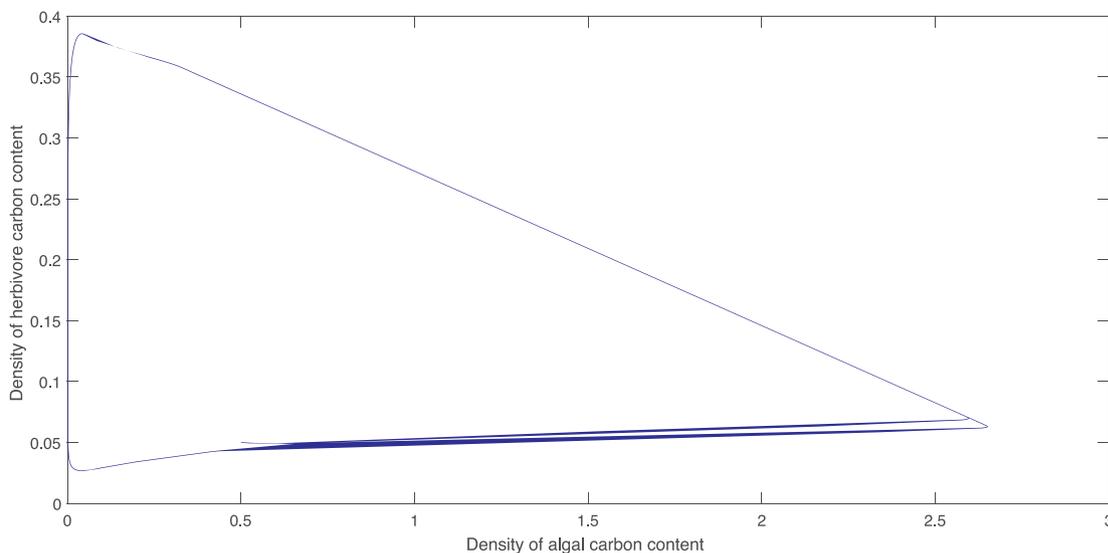
$$Q_A^{\max} = X_A Q_A^{\min}, \tag{10}$$

$$Q_H^{\max} = X_H Q_H^{\min}. \tag{11}$$

where



(a)



(b)

Fig. 2. A sample periodic solution with low nutrient  $R(0) = 0.01$  and strong light  $I_{in} = 100 \mu\text{mol}/\text{m}^2$ .

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  $TR(t) = R(t) + A(t)QA(t) + H(t)QH(t)$  be the total nutrient P in the system at time  $t$ , then

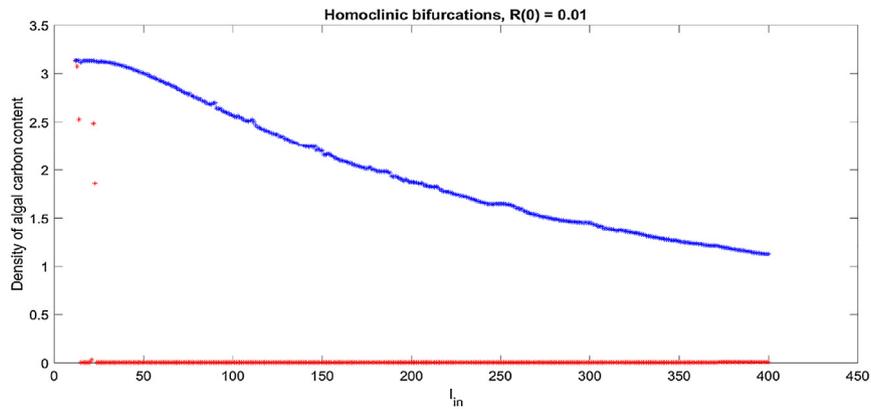
$$\frac{dTR}{dt} = \frac{dR}{dt} + \frac{dA}{dt}QA + A\frac{dQA}{dt} + \frac{dH}{dt}QH + H\frac{dQH}{dt} = 0, \tag{12}$$

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  $TR = R(0) + A(0)QA(0) + H(0)QH(0)$ . We can reduce the system by one dimension as in Wang et al.

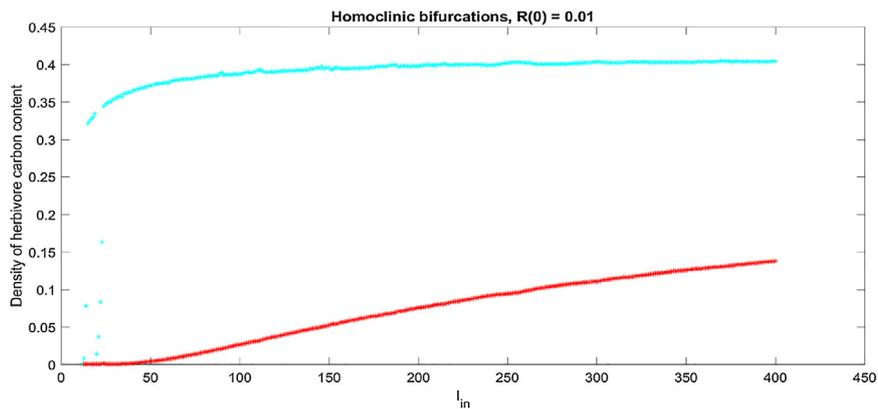
(2012), and we can change the total nutrient P availability in the system by varying  $R(0)$  in simulations.

### 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).



(a)



(b)

**Fig. 3.** Bifurcation diagram for a wide range of the light intensity with low nutrient  $R(0) = 0.01$ . The curves above (blue for algae and light blue for herbivores) are for maximum values of periodic orbits, while the red curves below are for minimum values of periodic orbits. (For interpretation of the references to color in this legend, the reader is referred to the web version of the article.)

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.

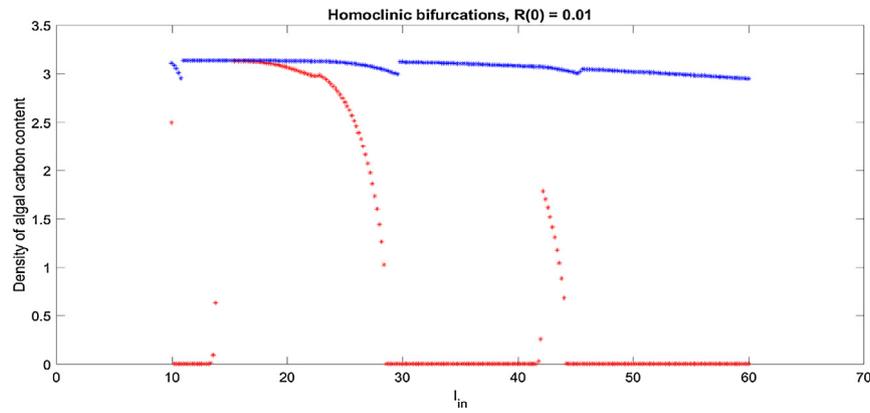
Because homoclinic and heteroclinic bifurcations will occur, we pose their definitions as follows:

- (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.

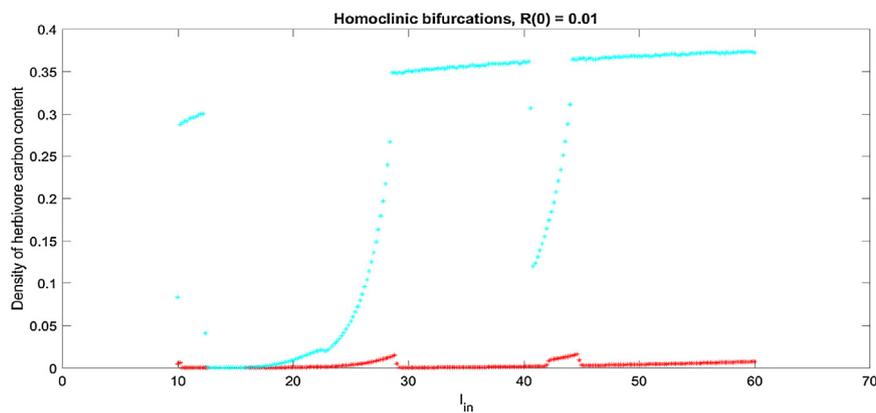
In the oligotrophic case  $R(0) = 0.01$ , we vary the light intensity and plot sample solutions in Figs. 1 and 2. Fig. 1 illustrates an approximation of a homoclinic orbit which leads to a infinite period bifurcation. One important consequence of such large oscillations is population extinction due to 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 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/

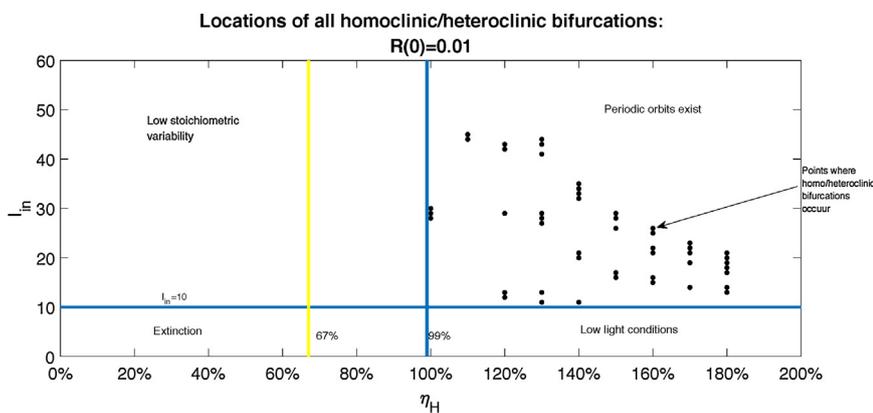


(a)



(b)

**Fig. 4.** Bifurcation diagram for a narrow range of the low light intensity with low nutrient  $R(0) = 0.01$ . The curves above (blue for algae and light blue for herbivores) are for maximum values of periodic orbits, while the red curves below are for minimum values of periodic orbits. (For interpretation of the references to color in this legend, the reader is referred to the web version of the article.)



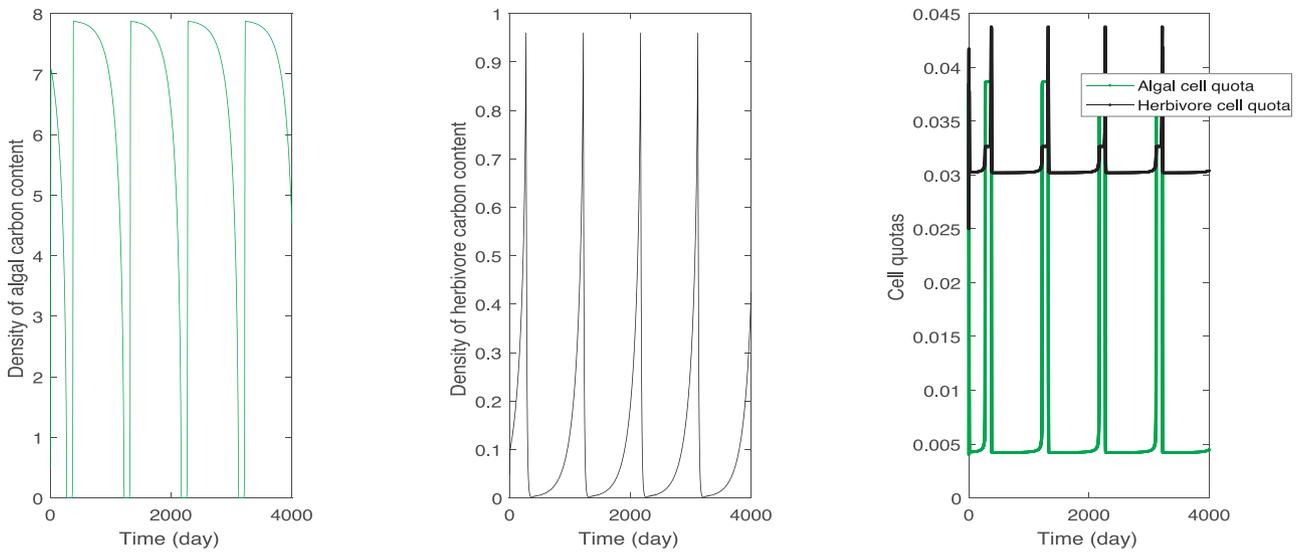
**Fig. 5.** Locations of homoclinic/heteroclinic bifurcations on the two-dimensional parameter space  $(\eta_H, I_{min})$  with low nutrient  $R(0) = 0.01$ . The horizontal blue line represents the threshold of the light intensity for generating homoclinic/heteroclinic bifurcations. The vertical blue line represents the threshold of herbivore's stoichiometric variability for generating homoclinic/heteroclinic bifurcations, called weak dynamical threshold. The vertical yellow line represents the hard dynamical threshold of herbivore's stoichiometric variability, which was found in Wang et al. (2012). (For interpretation of the references to color in this legend, the reader is referred to the web version of the article.)

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  $I_{min}$ . 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

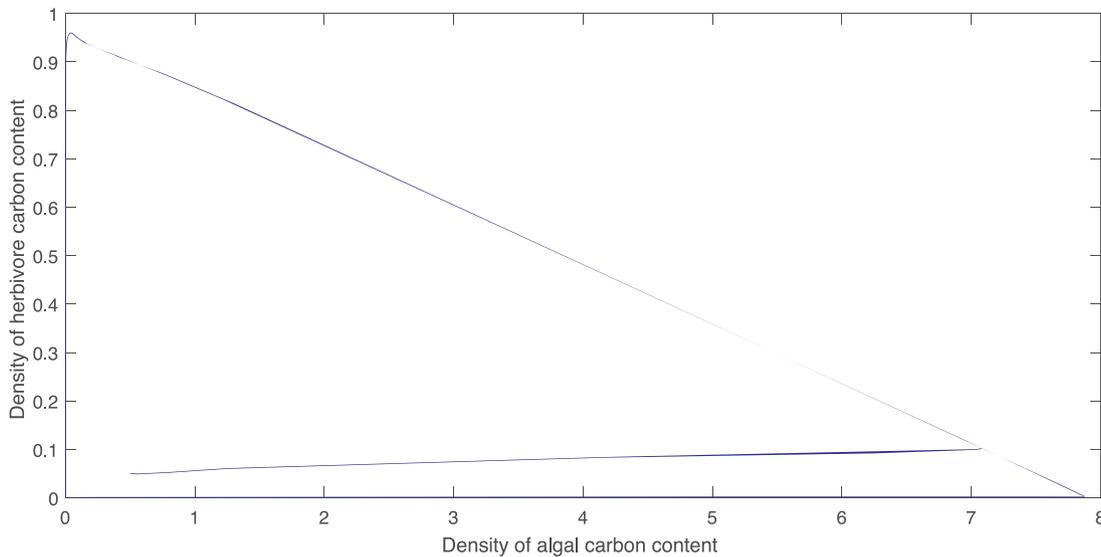
above the weak dynamical threshold.

#### 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



(a)

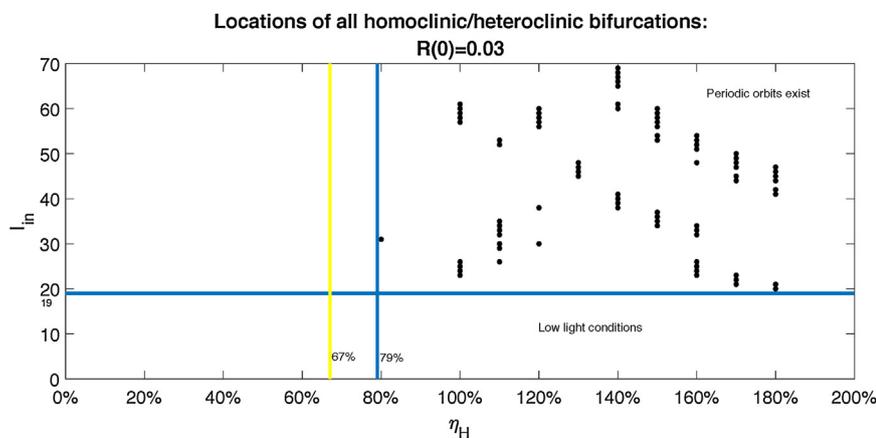


(b)

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

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



**Fig. 7.** Locations of homoclinic/heteroclinic bifurcations on the two-dimensional parameter space  $(\eta_H, I_H)$  with high nutrient  $R(0) = 0.03$ . The horizontal blue line represents the threshold of the light intensity for generating homoclinic/heteroclinic bifurcations. The vertical blue line represents the threshold of herbivore's stoichiometric variability for generating homoclinic/heteroclinic bifurcations, called weak dynamical threshold. The vertical yellow line represents the hard dynamical threshold of herbivore's stoichiometric variability, which was found in Wang et al. (2012). (For interpretation of the references to color in this legend, the reader is referred to the web version of the article.)

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

- Acharya, K., Kyle, M., Elser, J.J., 2004. Biological stoichiometry of *Daphnia* growth: an ecophysiological test of the growth rate hypothesis. *Limnol. Oceanogr.* 49, 656–665.
- Alijani, M.K., Wang, H., Elser, J.J., 2015. Modeling the bacterial contribution to planktonic community respiration in the regulation of solar energy and nutrient availability. *Ecol. Complex.* 23, 25–33.
- 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. *Mar. Ecol. Prog. Ser.* 25, 23–30.
- Deng, B., Loladze, I., 2007. Competitive coexistence in stoichiometric chaos. *Chaos* 17, 033108 14 pp.
- DeMott, W.R., Gulati, R.D., Siewertsen, K., 1998. Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnol. Oceanogr.* 43,

1147–1161.

- 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. *Am. Nat.* 162, 29–43.
- Hessen, D.O., Bjerking, B., 1997. A model approach to planktonic stoichiometry and consumer-resource stability. *Freshw. Biol.* 38, 447–471.
- Hood, J.M., Sterner, R.W., 2010. Diet mixing: do animals integrate growth or resources across temporal heterogeneity? *Am. Nat.* 176, 651–663.
- Loladze, I., Kuang, Y., Elser, J.J., 2000. Stoichiometry in producer–grazer systems: linking energy flow with element cycling. *Bull. Math. Biol.* 62, 1137–1162.
- Loladze, I., Kuang, Y., Elser, J.J., Fagan, W.F., 2004. Coexistence of two predators on one prey mediated by stoichiometry. *Theor. Popul. Biol.* 65, 1–15.
- Mulder, K., Bowden, W.B., 2007. Organismal stoichiometry and the adaptive advantage of variable nutrient use and production efficiency in *Daphnia*. *Ecol. Model.* 202, 427–440.
- Mulder, K., 2007. Modeling the dynamics of nutrient limited consumer populations using constant elasticity production functions. *Ecol. Model.* 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. *Ecol. Lett.* 4, 519–529.
- Peace, A., Wang, H., Kuang, Y., 2014. Dynamics of a producer–grazer model incorporating the effects of excess food nutrient content on grazer's growth. *Bull. Math. Biol.* 76, 2175–2197.
- 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.
- 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 J. Appl. Math.* 68, 503–522.
- Wang, H., Kuang, Y., Loladze, I., 2008. Dynamics of a mechanistically derived stoichiometric producer–grazer model. *J. Biol. Dyn.* 2, 286–296.
- Wang, H., Dunning, K., Elser, J.J., Kuang, Y., 2009. *Daphnia* species invasion, competitive exclusion, and chaotic coexistence. *DCDS-B* 12, 481–493.
- Wang, H., 2010. Revisit brown lemming population cycles in Alaska: examination of stoichiometry. *IJNAM-B* 1, 93–108.
- Wang, H., Sterner, R.W., Elser, J.J., 2012. On the “strict homeostasis” assumption in ecological stoichiometry. *Ecol. Model.* 243, 81–88.