DAPHNIA SPECIES INVASION, COMPETITIVE EXCLUSION, AND CHAOTIC COEXISTENCE

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Abstract. The cladoceran *Daphnia lumholtzi* has invaded many US rivers and lakes. To better understand the ecological factors and consequences associated with *D. lumholtzi* invasion, we carried out a microcosm experiment evaluating competition of *D. lumholtzi* with a widespread native daphnid, *D. pulex*. We applied two light treatments to these two different microcosms and found strong context-dependent competitive exclusion in both treatments. We observed that *D. lumholtzi* out-competed *D. pulex* in the high light treatment, while *D. pulex* out-competed *D. lumholtzi* in the low light treatment. To better understand these results we developed and tested a mechanistically formulated stoichiometric population interaction model. This model exhibits chaotic coexistence of the competing species of *Daphnia*. The rich dynamics of this model allow us to suggest some plausible strategies to control the invasive species *D. lumholtzi*.

1. **Introduction.** *Daphnia* are small crustacean herbivores feeding on algae and organic detritus in various freshwater environments in which they are an important food source for larval and juvenile fish. However, not all *Daphnia* species are suitable food for young fish. For example, *D. lumholtzi* has a much longer head and tail spines than do most *Daphnia*. The long spines make it difficult for young fish to consume. *D. lumholtzi* is an exotic species from Africa, southwest Asia, and Australia, and was first discovered in North America in 1991 [10]. It has since spread to many regions in the south and southwest USA and may soon invade Lake Michigan [4]. Scientists are afraid that *D. lumholtzi* may replace the native *Daphnia* species and thus in doing so, the amount of food available to young fish may be severely reduced. Hence, it is critical to better understand the interactions between *D. lumholtzi* and other species of *Daphnia*.

In this paper, we investigate how key environmental conditions affect the result of competition between *D. lumholtzi* and native *Daphnia* species in both experimental and theoretical arenas. Light intensity and nutrient availability are two environmental conditions we consider here. Many researchers ([3, 16, 23]) have explicitly incorporated energy flow and nutrient cycling in their plant-herbivore interaction models. These are referred as stoichiometric population growth models [21]. The nutrient cycling and nutrient limitations on *Daphnia* growth have been tested in many recent experiments [7, 1]. Here, we examined the effects of light intensity on *Daphnia* competition in a microcosm experiment. We also develop and analyze a stoichiometrically explicit model [23] of algae-*Daphnia* interactions to better understand and generalize the experimental findings.

2. **Microcosm experiment and hypothesis.** We experimentally studied the competition between *D. pulex* and *D. lumholtzi* with a single food source, the green alga *Scenedesmus acutus*. There were two light conditions: high intensity and low intensity. We applied each light treatment to four test cases: a control lacking *Daphnia*, *D. pulex* monoculture, *D. lumholtzi* monoculture, and *D. pulex* and *D.lumholtzi* together in competition.

2.1. **Methods.** We used the chlorophyte algae, *Scenedesmus obliquus*, as the food source for two *Daphnia* species, *D. pulex* and *D. lumholtzi*, in 3-liter microcosms. Two light conditions were applied. In the high light condition, an average intensity of $218\mu E/m^2/s$ at the surface of the corresponding microcosms was achieved through multiple fluorescent lights. In the low light condition, $21.8\mu E/m^2/s$ at the surface of the corresponding microcosms was achieved through screen shading that blocked 90% of the light. We set a timer on the lighting to provide a daily cycle with 16 hours of light and 8 hours of darkness. Temperature was held constant at 25.6 ^oC. In order to avoid any discrepancy in temperature or light intensity, all jars were moved to random positions after every sampling cycle. All microcosms had the same initial nutrient concentrations with an N:P ratio of 5. Nutrient-replete algae from a chemostat were inoculated into each jar at a target concentration of $1mgC/L$ and allowed to grow under high light or low light conditions for two weeks before the introduction of *Daphnia*.

Each light treatment was applied to four test cases: a control lacking *Daphnia*, *D. pulex* monoculture, *D. lumholtzi* monoculture, and *D. pulex* and *D. lumholtzi* together in competition. There were 3 replicates for each treatment combination. Each jar began with 10 *Daphnia* individuals. In competition jars, we added five individuals of each species. These individuals were selected randomly from a large population of neonates that were less than 12 hours old.

Twice a week, the total population of each *Daphnia* species in each jar was counted manually. We picked some sample *Daphnia* to determine body size and fecundity (counting egg numbers) using a dissecting microscope, and then returned them alive to original jars. All jars were stirred twice a day to keep the algae in suspension and to assure that the system was well mixed. 250 mL of the suspension in each jar was replaced with fresh media every week. The removed suspension was filtered onto pre-combusted glass filters that were frozen for later analysis of carbon and phosphorus. The whole process continued for six weeks.

2.2. **Experimental results.** Algal C:P ratios were significantly higher in high light than in low light (Figure 1). In each light treatment, the algal C:P ratio in
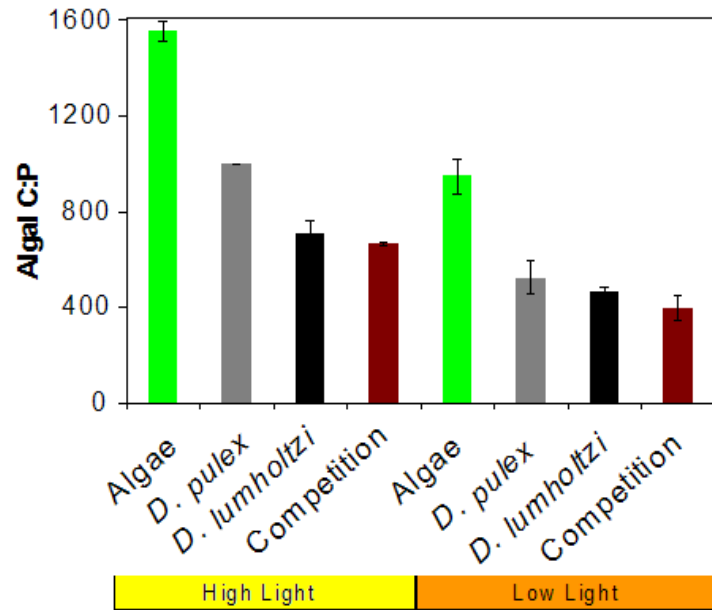
FIGURE 1. Algal C:P ratios in all 8 test cases, measured at the end of the experiment.

Daphnia-free jars was highest while the algal C:P ratio in competition jars was the smallest. If we compare the monoculture test cases, the algal C:P ratio in *D. pulex* alone jars was larger than the algal C:P ratio in *D. lumholtzi* alone jars. This observation implies that *D. pulex* sequestered more nutrients than *D. lumholtzi*.

The dynamics of the *Daphnia* populations are shown in Figure 2. In monocultures, *Daphnia* grew much better in high light than in low light. In competition microcosms, *D. lumholtzi* grew well in high light but was excluded by *D. pulex* in low light. In contrast, *D. pulex* grew well in low light but was excluded by *D. lumholtzi* in high light. Thus, it appears that *D. pulex* can grow very well in high light monoculture but could not persist in the high light competition microcosms, indicating that the invasive species, *D. lumholtzi*, is very competitive in high light treatments. We can see competitive exclusions more directly by examining the values of percentage of total *Daphnia* comprised by the two species under high and low light intensity (Figure 3). *D. lumholtzi* won the competition in high light after 2 weeks while *D. pulex* dominated in low light after 1 month.

2.3. **Hypothesis.** The data show that *Daphnia* populations achieved greater populations in high light than in low light. Furthermore, in all low light treatments, *D. lumholtzi* went extinct while *D. pulex* survived at a small population level. While *D. pulex* grew well in its high light monoculture, it was excluded by *D. lumholtzi* in high light competition treatments. Hence, *D. lumholtzi* out-competed *D. pulex* in high light, while *D. pulex* out-competed *D. lumholtzi* in low light. To explain these results, we propose that *D. lumholtzi* has higher metabolic carbon (or energy) requirements, while *D. pulex* has higher metabolic phosphorus requirements. This
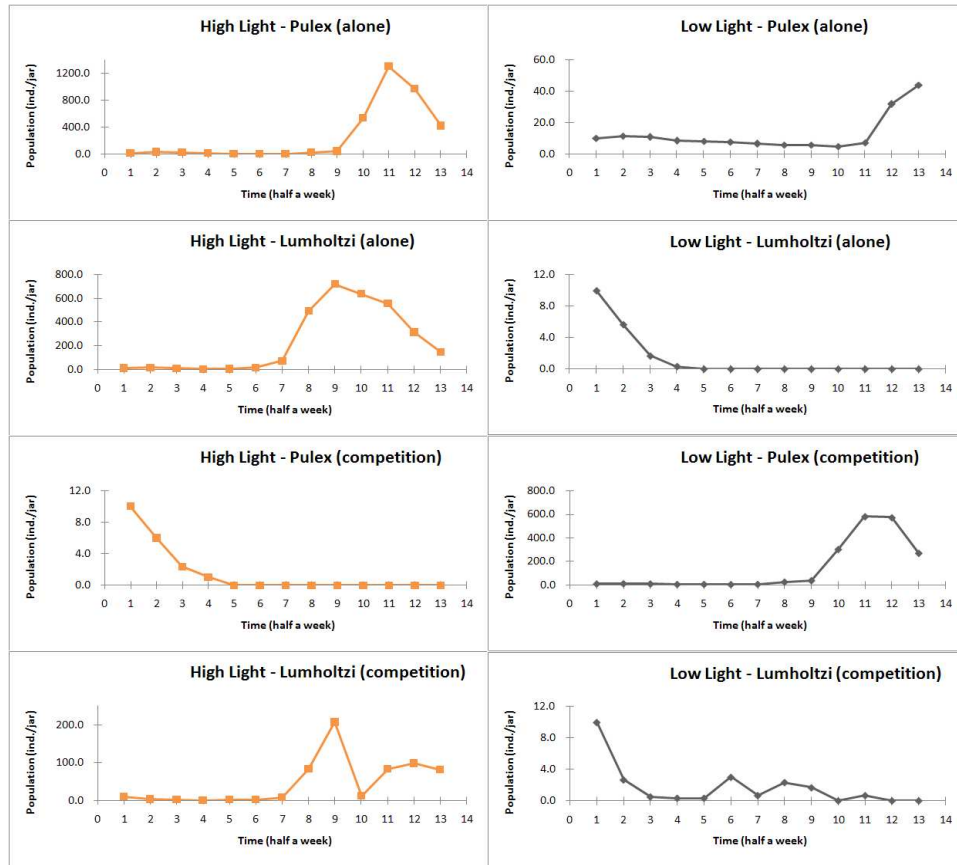
FIGURE 2. Time series of *Daphnia* populations in monocultures
and competition microcosms with the high or low light intensity.

hypothesis is equivalent to saying that *D. lumholtzi* is more likely to be limited by
food quantity (in carbon biomass) than *D. pulex*, while *D. pulex* is more likely to
be limited by stoichiometric food quality (algal nutrient content) than *D. lumholtzi*.
Thus, under low light intensity, *D. pulex* could be more competitive because of the
absence of nutrient (P) limitation and because low light intensity likely results in
low algal concentrations that may be insufficient to support the added energetic
costs of *D. lumholtzi*'s defensive head and tail spines. In contrast, under high light
intensity with higher algal C:P ratio, *D. lumholtzi* is more competitive because of
severe nutrient limitation that excludes *D. pulex*.

3. **Hypothesis testing by a stoichiometric model.** Ecologists have long known
that herbivores are coupled to plants not only through their grazing but also through
their nutrient cycling [21]. Recently, many stoichiometric explicit models on trophic
interactions have been formulated [3, 13, 16, 22, 23]. Frequently, addition of stoi-
chiometric constraints enrich the dynamics of such population models [14, 17, 6].

The model in this section is a natural extension of the one-prey one-predator
stoichiometric model in [23]. There are five variables for our theoretical model:
algal carbon biomass x, algal phosphorus biomass p, *D. pulex* carbon biomass y_1,
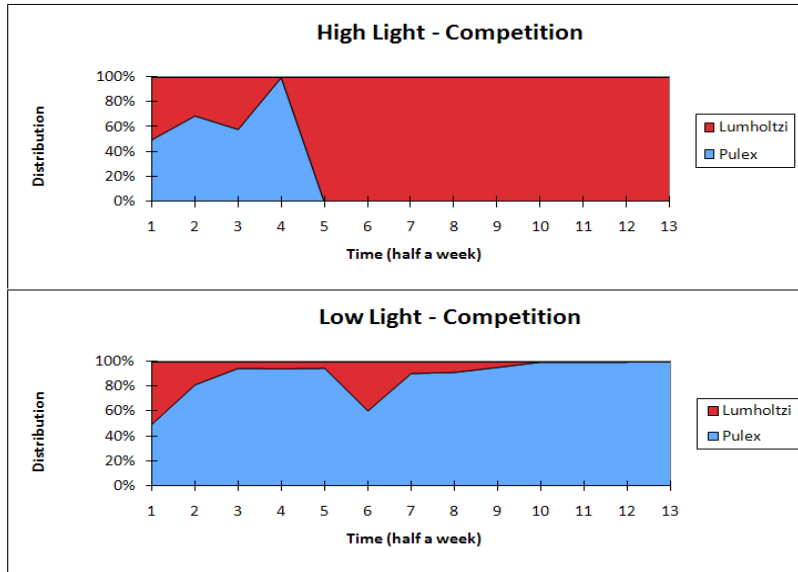
FIGURE 3. Population percentages of *D. lumholtzi* and *D. pulex* in competition microcosms. This figure clearly shows competitive exclusions in the high light treatment and in the low light treatment.

D. lumholtzi carbon biomass y_2, and available media phosphorus P. The model is developed upon the main biological assumption that algae have highly variable nutrient contents while *Daphnia* have relatively fixed nutrient contents. Thus, following previous models we assume that the $P : C$ ratio in algal cells is a variable and coupled to algal growth rate and that the $P : C$ ratio in each *Daphnia* species is constant.

We assume that the carrying capacity of algae, K, is positively related to the light intensity, then the logistic growth factor, $1 - \frac{x}{K}$, represents the light limitation. $1 - \frac{q}{p/x}$ is the Droop equation for nutrient-based specific algal growth. The minimum function in algal equation stems from the Liebig's Minimum Law. $f_i(x)y_i$ are predation terms, where $f_i(x)$'s take the Michaelis-Menten (Monod) form, i.e. $f_i(x) = \frac{c_i x}{x + a_i}$. e_i's are conversion efficiencies of algal carbon biomass to *Daphnia*'s carbon biomass. $\min\left\{1, \frac{p/x}{\theta_i}\right\}$'s express the food quality limitations on *Daphnia* growth. There exists a food quality limitation on the growth of species i when $p/x < \theta_i$. $g(P)x$ is the algal phosphorus uptake from media, where $g(P) = \frac{c_3 P}{P + a_3}$ takes the Michaelis-Menten form. We assume that phosphorus in all dead organisms including algae and *Daphnia* is recycled to media immediately and we also assume that *Daphnia* return the excess phosphorus taken from algae to media.

$$\frac{dx}{dt} = \underbrace{rx \min\left\{1 - \frac{x}{K}, 1 - \frac{q}{p/x}\right\}}_{\text{algal growth limited by light and nutrient}} - \underbrace{\sum_{i=1}^{i=2} f_i(x)y_i,}_{\text{ingestion by Daphnia}} \quad (1)$$

$$\frac{dy_1}{dt} = \underbrace{e_1 \min\left\{1, \frac{p/x}{\theta_1}\right\} f_1(x)y_1}_{\text{D. pulex growth limited by algal quantity and quality}} - \underbrace{d_1 y_1,}_{\text{D. pulex mortality}} \tag{2}$$

$$\frac{dy_2}{dt} = \underbrace{e_2 \min\left\{1, \frac{p/x}{\theta_2}\right\} f_2(x)y_2}_{\text{D. lumholtzi growth limited by algal quantity and quality}} - \underbrace{d_2 y_2,}_{\text{D. lumholtzi mortality}} \tag{3}$$

$$\frac{dp}{dt} = \underbrace{g(P)x}_{\text{algal P uptake}} - \underbrace{\frac{p}{x}\sum_{i=1}^{i=2} f_i(x)y_i}_{\text{P loss due to grazing}} - \underbrace{dp,}_{\text{P loss due to algal recycling}} \tag{4}$$

$$\frac{dP}{dt} = \underbrace{-g(P)x}_{\text{algal P uptake}} + \underbrace{dp}_{\text{algal P recycling}} + \underbrace{\sum_{i=1}^{i=2} \theta_i d_i y_i}_{\text{P recycling from dead Daphnia}}$$

$$+ \underbrace{\sum_{i=1}^{i=2} \left(\frac{p}{x} - e_i \min\left\{\theta_i, \frac{p}{x}\right\}\right) f_i(x)y_i.}_{\text{P recycling from Daphnia wastes}} \tag{5}$$

The total phosphorus of the system is conserved, since $d(\theta_1 y_1 + \theta_2 y_2 + p + P)/dt = 0$. Let $T = \theta_1 y_1 + \theta_2 y_2 + p + P$ be the total phosphorus which is a constant depending on the initial condition. Then $P(t) = T - p(t) - \theta_1 y_1(t) - \theta_2 y_2(t)$. Hence, the above mathematical model is reduced to be

$$\frac{dx}{dt} = rx \min\left\{1 - \frac{x}{K}, 1 - \frac{q}{p/x}\right\} - \sum_{i=1}^{i=2} f_i(x)y_i, \tag{6}$$

$$\frac{dy_1}{dt} = e_1 \min\left\{1, \frac{p/x}{\theta_1}\right\} f_1(x)y_1 - d_1 y_1, \tag{7}$$

$$\frac{dy_2}{dt} = e_2 \min\left\{1, \frac{p/x}{\theta_2}\right\} f_2(x)y_2 - d_2 y_2, \tag{8}$$

$$\frac{dp}{dt} = g(T - p - \theta_1 y_1 - \theta_2 y_2)x - \frac{p}{x}\sum_{i=1}^{i=2} f_i(x)y_i - dp. \tag{9}$$

With biologically meaningful initial data, it can be shown, as in [23], that these systems generate bounded non-negative solutions. In limiting but biologically relevant cases, they produce dynamics similar to that of LKE model and its various variations and extensions [13, 16, 23]. This includes complex dynamics with multiple positive equilibria, where limit cycle dynamics, bistability and deterministic extinction of the grazer are possible. The system dynamics are confined to a region naturally bounded by biological constraints.

The hypothesis we describe above can be mapped to some restrictions on the parameters of our stoichiometric model. That is, the assumption that *D. lumholtzi* has higher metabolic carbon requirements means that $a_2 > a_1$ in the model. The assumption that *D. pulex* has higher metabolic phosphorus requirements means that $\theta_1 > \theta_2$ in the model. With these connections, we can test the consequences of these hypothesized differences using our stoichiometric model. Parameters of algae can be estimated from experimental time series. For convenience and simplicity,
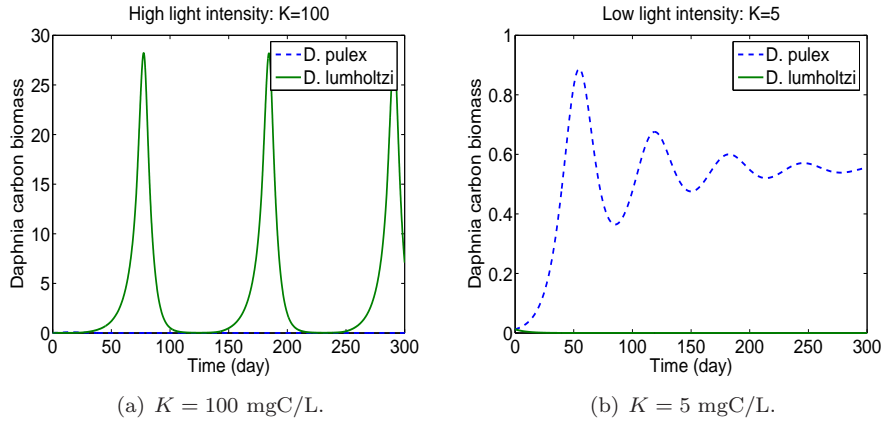
(a) $K = 100$ mgC/L.   (b) $K = 5$ mgC/L.

FIGURE 4. Competitive exclusions occur both in high light and in low light with the initial condition $x(0) = 5$ mgC/L, $y_1(0) = 0.0125$ mgC/L, $y_2(0) = 0.0125$ mgC/L, $p(0) = 0.01$ mgP/L. These results are consistent with the microcosm experiment.

the parameters of *Daphnia*, except a_i's and θ_i's, are assumed to be equal for both *D. pulex* and *D. lumholtzi*. By varying the light intensity parameter, K, we can qualitatively compare our simulation findings with the experimental observations.

Our model simulations (Figure 4) show competitive exclusions in both high and low light intensities: *D. lumholtzi* wins the competition in the high light environment while *D. pulex* wins the competition in the low light environment. These results are consistent with the experimental observations, and therefore provide qualitative support for the hypothesized physiological mechanisms. Panel (a) of Figure 5 gives a global view of competitive results under different light conditions. The low light condition of our experiment is equivalent to the second region while the high light condition would be associated with the fourth region. Again, this bifurcation diagram confirms the conditions that resulted in competitive exclusion in the microcosm experiment and thus supports the physiological hypothesis we propose.

4. **Chaotic coexistence.** Many modeling results support the competitive exclusion principle, which states that at most n species can coexist on n food resources [9, 15, 8]. However, this mathematical principle fails to answer the fundamental question of biodiversity: why can so many species coexist on a limited number of food resources? To explain this intriguing paradox in community ecology, various mechanisms have been proposed that might facilitate coexistence. One of the mechanisms to enhance coexistence is the introduction of nutrient cycling. [17], suggesting that stoichiometric principles might help understand how biodiversity is promoted. We show below that our mechanistically derived model here exhibits possible chaotic coexistence in suitable light intensities.

Our simulation results (Figure 6 and Figure 7) illustrate the chaotic coexistence of two-herbivores on a single food source (algae) for some parameter regions. Figure

(a) K varies from 0 to 200 mgC/L.
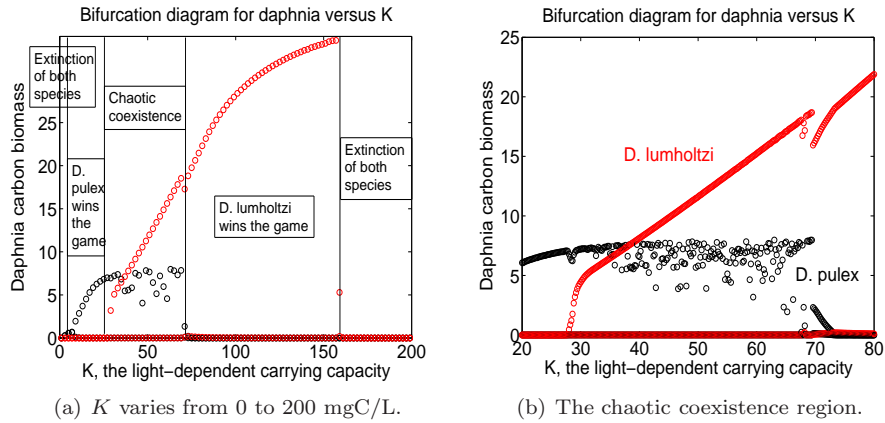

(b) The chaotic coexistence region.

FIGURE 5. Bifurcation diagrams for different light-dependent carrying capacities. The red points show the local minima and maxima of *D. lumholtzi* carbon biomass and the black points show the local minima and maxima of *D. pulex* carbon biomass, plotted during the period from t=2000 to t=3000 days, as functions of K. The chaotic coexistence region of (a) is magnified in (b).
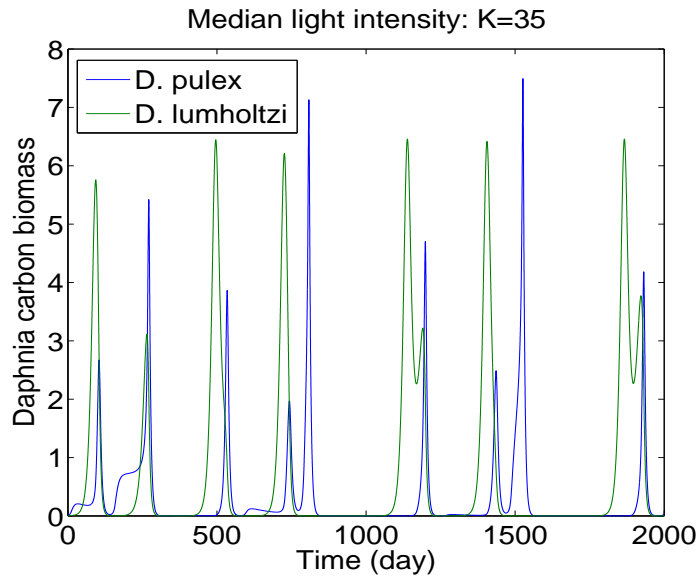

FIGURE 6. The chaotic coexistence with $K = 35$ mgC/L and the initial condition $x(0) = 5$ mgC/L, $y_1(0) = 0.0125$ mgC/L, $y_2(0) = 0.0125$ mgC/L, $p(0) = 0.01$ mgP/L.

TABLE 1. Parameters (P.) of the stoichiometric model. Here exp. stands for experiment

P.	Meaning	Value	Unit	Source
r	intrinsic growth rate of algae	0.15	day^{-1}	exp.
K	algal light-dependent carrying capacity	0 – 200	mgC/L	exp.
q	minimal P:C ratio of algae	0.0004	mgP/mgC	[21]
c_1	maximal ingestion rate of *D. pulex*	0.8	day^{-1}	[16]
c_2	maximal ingestion rate of *D. lumholtzi*	0.8	day^{-1}	[16]
a_1	half-saturation constant of algal consumption by *D. pulex*	3	mgC/L	exp.
a_2	half-saturation constant of algal consumption by *D. lumholtzi*	20	mgC/L	exp.
e_1	maximal conversion efficiency of *D. pulex*	0.6	no unit	
e_2	maximal conversion efficiency of *D. lumholtzi*	0.6	no unit	
θ_1	constant P:C ratio of *D. pulex*	0.02	mgP/mgC	[21]
θ_2	constant P:C ratio of *D. lumholtzi*	0.004	mgP/mgC	[21]
d_1	loss rate of *D. pulex*	0.2	day^{-1}	[17]
d_2	loss rate of *D. lumholtzi*	0.2	day^{-1}	[17]
c_3	maximal phosphorus uptake rate of algae	0.1	mgP/mgC/day	[23]
a_3	half-saturation constant of phosphorus uptake by algae	0.1	mgP/L	
d	phosphorus loss rate of algae	0.05	day^{-1}	[23]
T	total phosphorus in the system	0.3	mgP/L	exp.

7 gives an evolutionary observation of the global attractor as light (K) increases. The attractor changes from a boundary limit cycle to a smooth internal limit cycle, then to a non-smooth twisted limit cycle, and later to period-doublings, and finally to a chaotic attractor. This evolution clearly shows a transition to chaos through period-doublings. Panel (b) of Figure 5 also exhibits chaotic behavior in the intermediate region of light intensity. Dynamics of all four Lyapunov exponents and the Kaplan-Yorke dimension [12, 19] are shown in Figure 8. The maximal Lyapunov exponent and the Kaplan-Yorke fractal dimension of the strange attractor are positive; thus, this system is chaotic for some parameter regions. The differential equation-based chaos is both mathematically and biologically interesting as has been shown in [5, 11]. Mathematically, chaos gives rich dynamics of a differential equation system. Biologically, chaos shows possible mechanistically based complex coexistence in natural ecosystems. That is, modeled populations of *D. pulex* and *D. lumholtzi* can coexist when the light intensity is located in the third region of Figure 5 (a). The "window size" of coexistence is large in proportion and hence these two *Daphnia* species can coexist with a relatively large probability. Actually, there are two types of coexistence depending on parameter regions: a limit cycle or a chaotic attractor of a differential equation system. We do not show the case of coexistence via limit cycle here, a result that is more easily obtained.
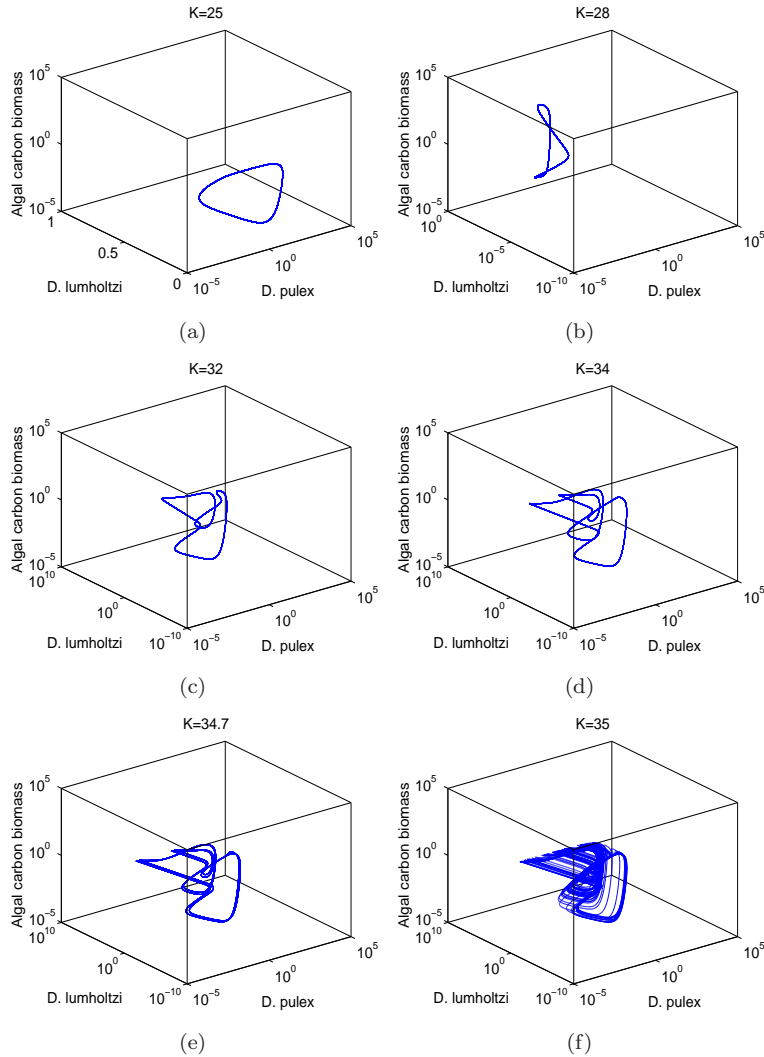
FIGURE 7. Attractors projected to 3-dimensional space. All attracting trajectories are plotted from the period from t=80000 to t=100000 days. (e) depicts period-doubling, and (f) illustrates a chaotic attractor.

Finally, we observe that both *Daphnia* species go extinct when the light intensity is too high or two low. When the light intensity is too low in the first region, there is too little food to allow either species to survive. When the light intensity is too high in the fifth region, there is more than enough food whose nutrient contents are very low ("junk food"). Under this condition, neither species can persist because neither can grow rapidly enough to offset its loss processes.

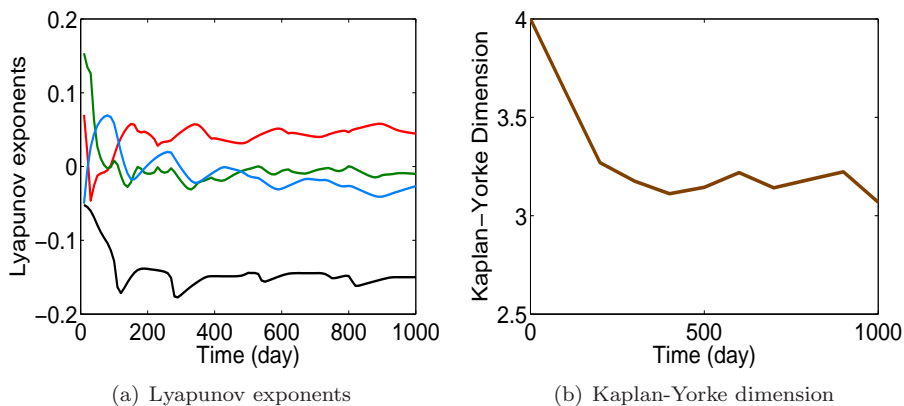(a) Lyapunov exponents

(b) Kaplan-Yorke dimension

FIGURE 8. Dynamics of lyapunov exponents and the Kaplan-Yorke dimension [12, 19].

5. **Discussion.** As our experiment and our mathematical model suggest, the success of *D. lumholtzi* is reduced under low light intensity (which results in low food abundance) and thus we would suggest that its invasive success might be reduced in lakes with deep mixed layers or high inorganic turbidity, both of which should result in lower light intensities. This interpretation places emphasis on *D. lumholtzi*'s greater sensitivity to low food abundance. However, our results also suggest that the native daphnid *D. pulex* does well in competition with *D. lumholtzi* when algal C:P ratio is low (the algae are P-rich). Thus, *D. pulex* may do better in persisting in the presence of *D. lumholtzi* in more eutrophic lakes, which tend to have lower seston C:P ratios [20].

In our experiment, *D. lumholtzi* had higher metabolic demands than *D. pulex*. This result is contrary to [2] which showed that %RNA (dry mass) of *D. lumholtzi* was significantly higher than the tested native species. We speculate that these different results may be caused by other distinct environmental conditions than nutrients and light, such as temperature, mixed status, and the original environments where tested *Daphnia* came from. In addition, we observed resting eggs in our experiment when "times are bad". This observation has been noted in previous studies [18].

For future work, we propose to conduct longer and more sophisticated experiments to be able to more comprehensively test our model with data, and to develop more mechanistic and realistic models. For example, our model predicts oscillatory behavior; however, the experimental period of six weeks is less than half a period of the oscillations observed in the model. To really test our model, we need to obtain experimental data for at least four to six months. Also, while counting the algal density in our experiment, we could not differentiate between living algal cells and detritus. This results in a potentially serious overestimate of the living algal density. We also had to count *Daphnia* individually, and may have injured many of them and introduced mortality not accounted for in our model. To avoid this, automated

image analysis methods may allow fast and non-destructive counts. Moreover, the microcosm experiment includes bacteria in addition to algae; these bacteria likely also utilized nutrients and may have influenced the observed dynamics. We propose to explicitly include bacteria into the model, and thus create, analyze, and experimentally test the effects of light and nutrients on a *Daphnia*-algae-bacteria system. Finally, it would be interesting to test for chaotic coexistence experimentally by providing the intermediate light intensity in the third region of Figure 5 (a). Showing chaos in laboratory experiments is difficult because of naturally occurring stochastic variations and will require an experiment with very long duration in order to confirm the chaotic behavior.

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