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Spatial coexistence of phytoplankton species in ecological timescale

Abstract The species diversity of phytoplankton is usually very high in wild aquatic systems, as seen in the paradox of plankton. Coexistence of many competitive phytoplankton species is extremely common in nature. However, experiments and mathematical theories show that interspecific competition often leads to the extinction of most inferior species. Here, we present a lattice version of a multi-species Lotka–Volterra competition model to demonstrate the importance of local interaction. Its mathematical equilibrium is the exclusion of all but one superior species. However, temporal coexistence of many competitive species is possible in an ecological time scale if interactions are local instead of global. This implies that the time scale is elongated many orders when interactions are local. Extremely high species diversity of phytoplankton in aquatic systems may be maintained by spatial coexistence in an ecological time scale.

Keywords Competition · Species diversity · Lattice model · Phytoplankton

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Introduction

Species diversity of phytoplankton is usually very high in natural aquatic ecosystems. Coexistence of many competitive species is extremely common in natural aquatic ecosystems (Hutchinson 1961 ; Ogawa and Ichimura 1984; Ogawa 1988). In spatially competitive communities, the coexistence of species is highly limited unless interspecific competition is weaker than intraspecific competition. Simulation studies usually exhibit the dominance of a single species, leading to the exclusion of all the rest (inferior species). At equilibrium, all but one species is persistent. This theoretical prediction (competitive exclusion) is often supported by the experimental results using chemostats (Tilman 1977, 1982; Takeya et al. 2004; Kuwata and Miyazaki 2000). Thus, local coexistence of multiple species is usually impossible without additional extrinsic factors. Many studies, therefore, proposed to include some extrinsic factors such as climatic changes, immigration, dormancy and spatial heterogeneity of habitats, and chaotic dynamics (Richerson et al. 1970; Levins 1979; Sommer 1985; Padisák et al. 1993; Huisman and Welssing 1999). Certainly the coexistence of two to three species has been shown in the systems with extrinsic factors. However, coexistence of four or more species is practically impossible due to the extremely sensitive tradeoffs between species. Thus, the coexistence of 10 or 100 species is totally out of question in these systems. Furthermore, such extrinsic factors seem to be not always applicable to aquatic systems. For example, spatial heterogeneity of microhabitats is difficult to imagine in aquatic ecosystems, because aquatic environment is homogeneous and the niches of phytoplankton are almost identical.

We build a lattice explicit model of multi-species competition with local interaction ("lattice Lotka–Volterra model or LLVM"; Tainaka 1988; Matsuda et al. 1992) and global interaction (Lotka–Volterra model, also called mean-field theory; Hofbauer and Sigmund

1988). In our model, competitive exclusion of all but one species is expected at the equilibrium state both in regards to local (Neuhauser 1992) and global interactions (Harris 1974). However, we only focus on the transient temporal dynamics in ecological time scales. We investigate the persistence of population in terms of spatial competition avoidance.

Methods

Lattice model

We consider a competitive ecosystem of ten planktonic algal species ($i=1, ..., N=10$); we apply a two-dimensional lattice (500×500), since phytoplankton distribute near the surface of the body of water and compete for light. Each lattice site is either occupied by i species (X_i) or empty (O). Overall reactions are as follows:

$$X_i + O \rightarrow 2X_i, \quad \text{rate: } b_i \tag{1}$$
$$X_i \rightarrow O, \quad \text{rate: } m_i \tag{2}$$
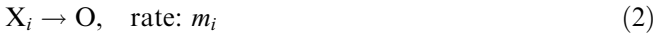
where X_i is an individual (site) of species i of N species. The parameters b_i and m_i denote the rates of birth and death, respectively. The death rate is kept constant ($m_i=0.3$) for all simulation runs. The simulation is carried out according to the contact process where interaction occurs between adjoining lattice sites (Harris 1974; Tainaka 1988; Marro and Dickman 1999).

When interactions are global, the two sites are chosen randomly from the whole lattice. In this case, the population dynamics of our system is given by the mean-field theory. Let x_i be the overall density of species i. Since the probability of finding X_i point becomes equal to overall density of X_i, we have the following dynamics:

$$\frac{dx_i}{dt} = -m_i x_i + b_i x_i e \tag{3}$$

where $i=1, ..., N$, and e is the density of empty site (O). Note that $e = 1 - \sum_i x_i$.

The first and second terms on the right-hand side of Eq. 3 denote death and birth processes, respectively. For example, we consider the cases of $N=1$ and $N=2$. When $N=1$, Eq. 3 becomes the logistic equation:

$$\frac{dx_1}{dt} = -m_1 x_1 + b_1 x_1 (1 - x_1). \tag{4}$$

The non-zero steady-state density for this equation is given by; $x_1 = 1 - m_1/b_1$.

In the two-species system ($N=2$), Eq. 3 can be rewritten as ($i, j = 1$ or 2 and $i \neq j$)

$$\frac{dx_i}{dt} = R_i x_i (K_i - x_i - a_{ij} x_j)/K_i. \tag{5}$$

Here the parameters satisfy the following relations:

$$R_i = b_i - m_i, \quad K_i = \frac{b_i - m_i}{b_i}, \quad a_{ij} = 1. \tag{6}$$

Equation 5 is called the Lotka–Volterra competition model, and its result is well known. Final stationary states are classified into four classes, depending on the values of parameters. Namely, (1) both X and Y coexist, (2) only X survives, (3) only Y survives, and (4) both become extinct. The condition for the coexistence is given by

$$K_1 > a_{12}K_2 \quad \text{and} \quad a_{21}K_1 < K_2. \tag{7}$$

The above relations are not satisfied in our case ($a=b=1$). Hence, at least one species becomes extinct. In general, in the case of $N>2$, we can show that coexistence of two or more species is impossible.

Simulation procedure

The simulation procedures of local interaction are as follows:

1. Algal cells are distributed randomly over some of the square-lattice points in such a way that each point is occupied by only one species, if the point is occupied.
2. Each reaction process is performed in the following two steps.
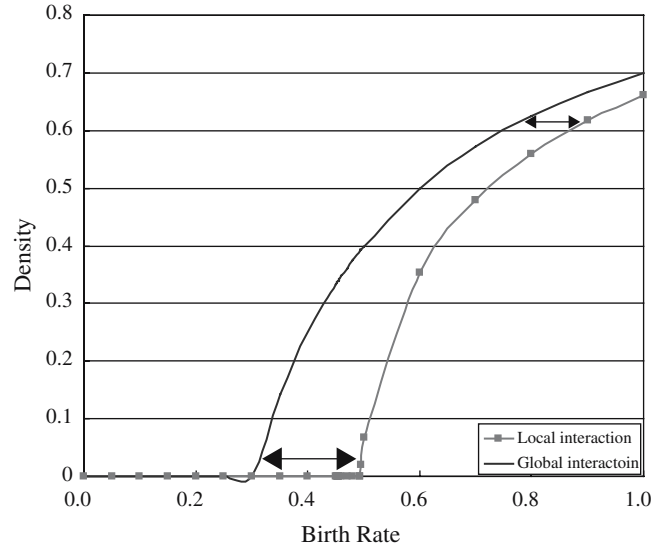
Fig. 1 Steady-state density vs. birth rate (b_i) in a single-species lattice ecosystem with local and global interactions. Death rate is kept at $m=0.3$. For local interaction, the steady-state density is estimated at around 20,000 Monte Carlo steps. The lattice size is 500×500 cells. The threshold value for positive density was $b_1 \approx 0.49$ for local interaction ($b_1=0.3$ for global interaction). Below this value, the population becomes extinct. For global interaction, the density is calculated analytically. The *two horizontal arrows* indicate the comparative parameter conditions between local and global interactions under poor and rich nutritional conditions. When conditions are poor, $b(\text{local})=0.5$, while $b(\text{global})=0.322$. When conditions are rich, $b(\text{local})=0.9$, while $b(\text{global})=0.786$

a. We perform the single body reaction (2). Choose one square-lattice point randomly. Let change the point to O with probability m_i, if it is occupied by the species i.

b. Next, we perform the two-body reaction (1). Select one point randomly and specify one of adjacent points. Here the adjacent site is set as the Neumann neighbors (four sites: up, down, left and right). If the selected pair is X_i and O, then the latter point will become X_i with probability b_i. Here we employ periodic boundary conditions.

3. Repeat step 2 $L \times L$ times, where $L \times L$ is the total number of the square-lattice sites. Here we set $L = 500$. This step is called a Monte Carlo step.

4. Repeat step 3 for a specific length (100,000 Monte Carlo steps).

The simulation procedures of global interaction are almost the same as those of local interaction. However, in the two-body reaction, step b in step 2, we select two lattice points randomly and independently.

Results

We first measure the steady-state density of a single species against birth rate (Fig. 1). For comparison, we determine the values of birth rates so that the steady-state densities (Fig. 1) become equal between local and global interactions.

We simulate both low and high nutrient conditions (Fig. 2). In the low nutrient conditions (near extinction thresholds), the difference in the birth rates is kept small, since algal growth in natural oligotrophic waters is slow and the difference in the growth rates between species is considered small. In the high nutrient concentrations (high productivity), these differences are proportionally increased. In eutrophicated waters, we expect a high variation in species-specific growth rates.

In low nutrient conditions, when interactions are local (Fig. 2a), the two most superior species (S_{10}, S_9) increase their density only slightly more than all of the rest of the species. In contrast, when interactions are global (Fig. 2b), the most superior species (S_{10}) grows out of other species, followed by the second most superior species (S_9). The average density of the surviving species is very low regarding local interaction, while it is relatively higher regarding global interaction (Fig. 2a, b).

Similarly, in high nutrient conditions, species stay together when interactions are local (Fig. 2c). Furthermore, the difference in birth rates is not exactly reflected in the order of species. From the third species, the order in density does not correspond with the order in growth rates. When interactions are global (Fig. 2d), the most superior species (S_{10}) flourishes, reaching nearly 0.5 in

density, while others move toward extinction. Thus the density profiles are almost similar in both high and low nutrient conditions (Fig. 2). When interactions are local, species stay together: none stand out (Fig. 2a, c). In contrast, when interactions are global, one species thrives while the others move toward extinction (Fig. 2b, d).

The extinction process of these dynamics is plotted as the number of species (Fig. 3). Extinction processes show that relatively inferior species become extinct when interactions are global (Fig. 3b, d). In contrast, when interactions are local with high birth rates, all ten species persisted during simulation runs. Even with low birth rates, nine species persisted and only one species became accidentally extinct, because low birth rates are close to the extinction boundary (Fig. 1). Thus, the persistence of species is extremely strengthened by local interactions.

To evaluate the species differences in birth rates, the densities of all ten species at 20,000 time steps are plotted for ten simulation runs under both local and global conditions in low nutrient conditions (Fig. 4). When interactions are local, most species persist with similar densities in all ten runs with slightly higher tendencies with superior species (Fig. 4a). In contrast, the superior species stands out from the others in all ten runs and all inferior species (S_1 to S_7) become extinct (Fig. 4b).

The spatial patterns in regards to local interactions exhibit strong clumping (Fig. 5). In high birth rates, species clumps are almost touching other species' clumps (Fig. 5b), while, in low birth rates, species clumps are isolated/separated by a wide area of open cells (Fig. 5a). No competitive interactions are possible in low birth rates because of spatial separation.

Discussion

The population dynamics in regards to local interaction are different from those when interactions are global (Figs. 2, 3). Regarding global interaction, a superior species "wins out" at the expense of the other species (Figs. 2b, d, 4b). However, when interactions are local, species tends to stay at almost similar densities: no single species stands out among the others (Figs. 2a, c, 4a). This means that the effective time scale is elongated by many orders of magnitude. This condition seems further elongated when the growth rates are lower. The temporal dynamics in regards to local interaction with low growth rates becomes extremely slow. Thus, in the ecological time scale, the coexistence of species is achieved when interactions are local with low growth rate conditions, even though the mathematical expectation (with infinite time horizon) is the exclusion of all but one superior species. With this system, coexistence of hundreds of species is easily achieved by simulation as long as the size of the lattice is large enough. This finite aspect of coexistence is

Fig. 2 Temporal dynamics of ten competitive species in the lattice competition model in ecological timescale under low and high growth rates. Low variable birth rates are assumed ($b_i = b + 0.0001(i\text{-}1)$), where $b = 0.5$ for local interaction and 0.322 for global interaction). High variable birth rates are assumed ($b_i = b + 0.00018(i\text{-}1)$), where $b = 0.9$ for local interaction and 0.786 for global interaction). The death rate is constant at $m_i = 0.3$. The density of each species is plotted for 20,000 Monte Carlo steps. **a** Local interaction with low growth rates. **b** Global interaction with low growth rates. **c** Local interaction with high growth rates. **d** Global interaction with high growth rates

Fig. 3 Temporal changes in the number of persisting species with low and high growth rates in Fig. 2. **a** Local interaction with low growth rates. **b** Global interaction with low growth rates. **c** Local interaction with high growth rates. **d** Global interaction with high growth rates. Below local interaction (**a** and **c**), almost all species persist up to 20,000 time steps. When interactions are global (**b** and **d**), many inferior species become extinct in a short time
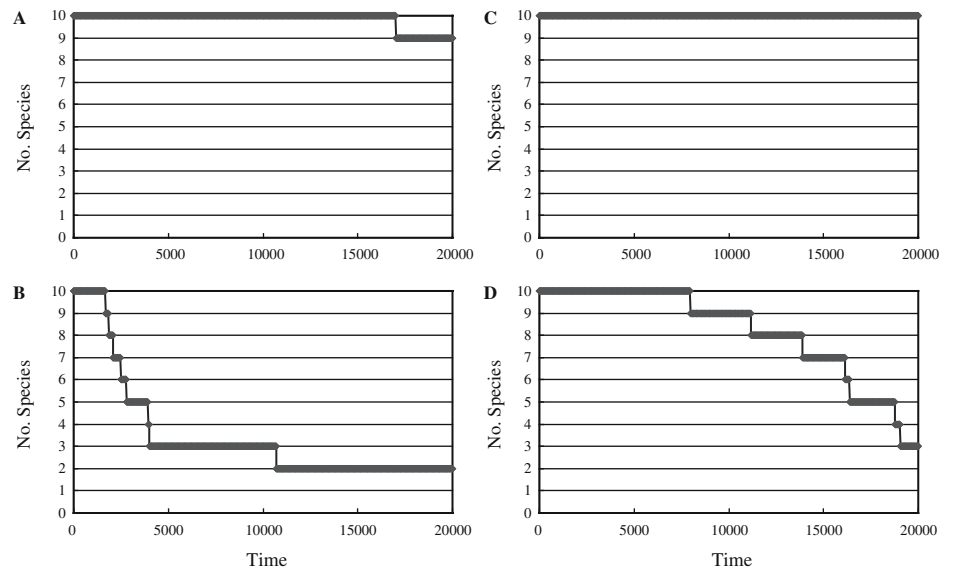
markedly different from the traditional studies of coexistence based on equilibrium analysis (Marro and Dickman 1999).
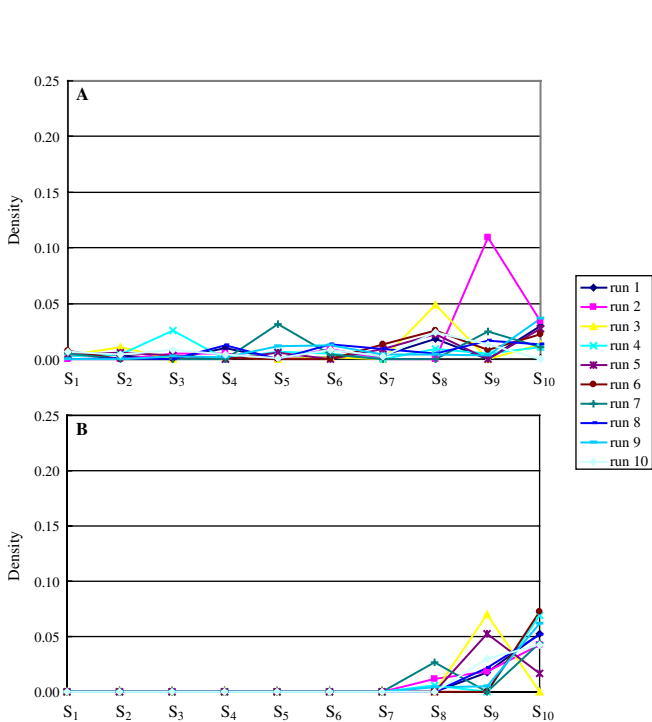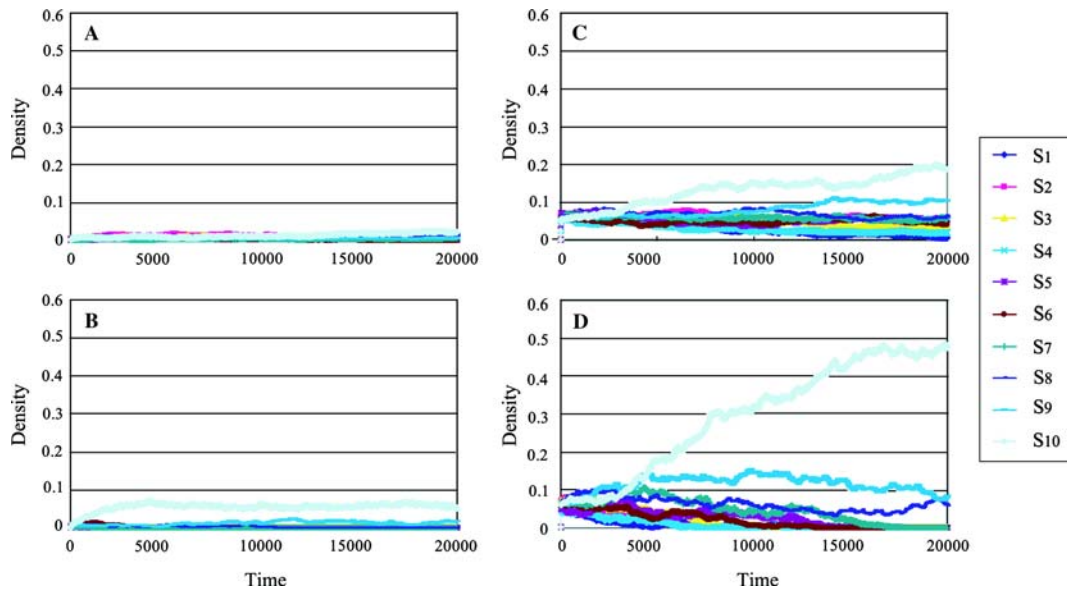
It is well known that it is easy for a low density with a finite lattice to become extinct (Marro and Dickman 1999). However, our results show that extinction seems delayed considerably, due to the lack of actual competition (Fig. 2a). The snapshot of pattern indicates extreme clumping, resulting in a lack of competition (Fig. 5). One of the most important results of LLVM is the "divergence of the clumping degree" in a low density limit (Tainaka and Fukazawa 1992; Tainaka et al. 2004). Namely, the degree of clumping is universally inverse proportional to the density in lattice models.

Many models of coexistence have been suggested since the paradox of plankton was proposed (Hutchinson 1961). The current model is markedly different in terms of the following two points: (1) persistence based on the finite ecological time scale instead of the infinite mathematical equilibrium state, and (2) focus on the local interaction in contrast to global (random) interaction. These two features are very basic to communities and ecosystems. We also do not include specific external factors or a detailed kinetics such as chaotic fluid dynamics. From the natural observation (Ogawa and Ichimura 1984; Ogawa 1988), the biodiversity feature of phytoplankton is common and universal.

Therefore, the mechanism for coexistence should not rely on highly specific factors such as chaotic flows or disturbance patterns. Rather, it is based on very common features which we have missed. In this sense, our model does not have any specific factors, but is based solely on very common features of any organisms. The only main difference is the combination of shifting the viewpoint of coexistence (transient vs. equilibrium states) and the realistic spatial nature of community—local (lattice) vs. global (random) interactions.

We should also note that the current model is also more advantageous than the previous models from the aspect of the number of coexisting species. In previous models, only a few (2–4) species are shown to coexist. It is almost definitely impossible for ten species to coexist in these systems. In our system, however, virtually 100 species can coexist for a long time, depending on the lattice size. Thus, there seems to be almost no limit to the biodiversity of plankton as observed in nature (Hutchinson 1961).
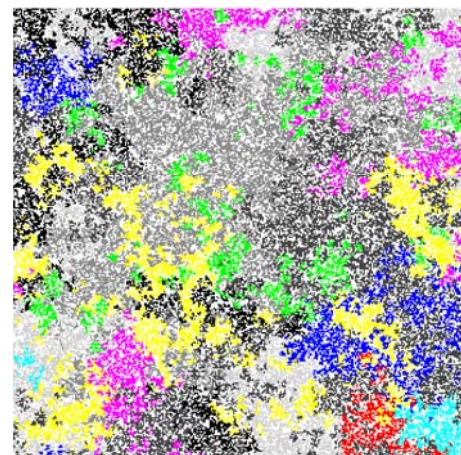
The mechanism of competition avoidance is very simple; the enhancement in the clumping degree originates in the fact that "offspring are located near their mother." Our idea in this paper is based on the divergence behavior. If the nutritional conditions of a system is very poor, or if densities of species are very low, then segregation of habitats may occur. Therefore, in poor

Fig. 4 Densities of ten species at 20,000 Monte Carlo steps in regards to both local (**a**) and global (**b**) interactions. Parameter settings and simulation conditions are the same as in Fig. 2 for all ten simulation runs

conditions, species can coexist for a very long period without actual competitive interactions (Liggett 1999). The poor nutritional condition when interactions are local maintains at least a high species diversity of phytoplankton. It may result in the paradox of enrichment (Rosenzweig 1971). The coexistence of plankton (Hutchinson 1961) thus becomes possible if the interactions are local as is expected in many natural aquatic systems.

Step=20000
S₁=0.000224 S₂=0.054764 S₃=0.017176 S₄=0.009404
S₅=0.033908 S₆=0.016948 S₇=0.008444 S₈=0.000000
S₉=0.009624 S₁₀=0.017220
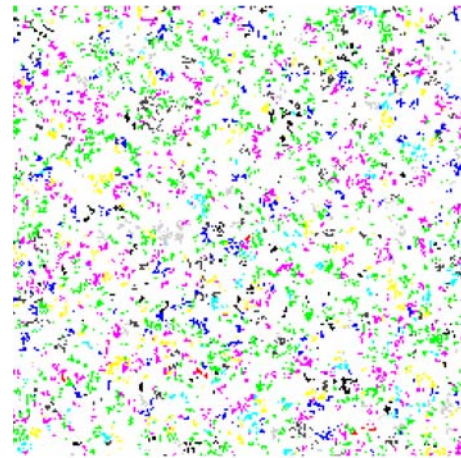
Step=20000
S₁=0.007684 S₂=0.039264 S₃=0.036800 S₄=0.021020
S₅=0.056460 S₆=0.041960 S₇=0.058660 S₈=0.063452
S₉=0.103956 S₁₀=0.189708

Fig. 5 Snapshots of a temporal pattern at 20,000 time steps in Fig. 2. **a** Low growth rates. **b** High growth rates

References

Harris TE (1974) Contact interaction on a lattice. Ann Probab 2:969–988

Hofbauer J, Sigmund K (1988) The theory of evolution and dynamic systems. Cambridge University Press, Cambridge

Huisman J, Welssing FJ (1999) Biodiversity of plankton by species oscillations and chaos. Nature 402:407–410

Hutchinson GE (1961) The paradox of plankton. Am Nat 95: 137–145

Kuwata A, Miyazaki T (2000) Effects of ammonium supply rates on competition between *Microcystis novacekii* (Cyanobacteria) and *Scenedesmus quadricauda* (Chlorophyta): simulation study. Ecol Modell 135:81–87

Levins R (1979) Coexistence in a variable environment. Am Nat 17:765–783

Liggett TM (1999) Stochastic interacting systems: contact, voter, and exclusion processes. Springer, Berlin Heidelberg New York

Marro J, Dickman R (1999) Nonequilibrium phase transition in lattice models. Cambridge University Press, Cambridge

Matsuda H, Ogita N, Sasaki A, Sato K (1992) Statistical mechanics of population: the lattice Lotka–Volterra model. Prog Theor Phys 88:1035–1049

Neuhauser C (1992) Ergodic theorems for the multitype contact process. Probab Theor Relat Fields 91:467–506

Ogawa Y (1988) Net increase rates and dynamics of phytoplankton populations under hypereutrophic and eutrophic conditions. Jpn J Limnol 49:261–268

Ogawa Y, Ichimura S (1984) Phytoplankton diversity in island waters of different trophic status. Jpn J Limnol 45:173–177

Padisák J, Reynolds CS, Sommer U (eds) (1993) The intermediate disturbance hypothesis in phytoplankton ecology. Developments in hydrobiology, vol. 81. Kluwer, Dordrecht, The Netherlands, p 199

Richerson PJ, Armstrong R, Goldman CR (1970) Contemporaneous disequilibrium: a new hypothesis to explain the "Paradox of the Plankton". Proc Natl Acad Sci USA 67:1710–1714

Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171:385–387

Sommer U (1985) Comparison between steady-state and non-steady-state competition: experiments with natural phytoplankton. Limnol Oceanogr 30:335–346

Tainaka K (1988) Stationary pattern of vortices or strings in biological systems: lattice version of the Lotka–Volterra model. J Physical Soc Jpn 57:2588–2590

Tainaka K, Fukazawa S (1992) Spatial pattern in a chemical reaction system: prey and predator in the position-fixed limit. J Physical Soc Jpn 61:1891–1894

Tainaka K, Kushida M, Ito Y, Yoshimura J (2004) Interspecific segregation in a lattice ecosystem with intraspecific competition. J Physical Soc Jpn 73:2914–2915

Takeya K, Kuwata A, Yoshida M, Miyazaki T (2004) Effect of dilution rate on competitive interactions between the cyanobacterium *Microcystis novacekii* and the green alga *Scenedesmus quadricauda* in mixed chemostat cultures. J Plankton Res 26:29–35

Tilman D (1977) Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58:338–348

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton