Pol. J. Environ. Stud. Vol. 23, No. 5 (2014), 1609-1616

Original Research

Interspecies Competition between *Microcystis aeruginosa* and *Scenedesmus obliquus* under Phenanthrene Stress

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Received: 11 May 2013
Accepted: 6 March 2014

Abstract

Interspecies competition is considered an important effector of community structure in ecosystems. Interspecies interactions may change due to changing environmental factors, including exogenous organic pollutants. In this paper, we measured the change in population density, based on the logistical growth model, of *Microcystis aeruginosa* and *Scenedesmus obliquus* when they were cultivated in single-species and mixed-species cultures, under the stress of the polycyclic aromatic hydrocarbon (PAH) phenanthrene. The single-species culture experiment showed that *S. obliquus* could tolerate greater phenanthrene stress than could *M. aeruginosa*, and exhibited hormesis when the concentration of phenanthrene was 0.0625 mg/l. In the mixed-species culture experiment, the toxicity of phenanthrene on the two algae changed. In the 0.0625 mg/l and 0.25 mg/l treatments, the population density of *S. obliquus* increased, whereas the population density of *M. aeruginosa* in each group decreased. Finally, the influence of different phenanthrene concentrations on the interspecies competition was evaluated.

Keywords: algal, ecology, phenanthrene pollution, population density

Introduction

As ecological and environmental problems intensify, the biological and ecological effects of toxic organic pollution are increasingly being considered and tested. Human interference and pollution have negatively impacted the number and distribution of biological populations. Polycyclic aromatic hydrocarbons (PAHs) are a type of organic pollutant that can result in cancer, deformity, and mutation [1]. PAHs easily accumulate in organisms and the food chain, affecting not only population growth, but also the interspecies balance in ecosystems and, thus, the diversity and the stability of the whole community structure. PAHs have different effects on the growth of aquatic organisms [2-4] due to the differing adsorptionor toxicity responses of aquatic organisms faced with pollutant degradation. However, there are few reports concerning interspecies relationships in ecosystems under the stress of PAH pollution, and most of the studies on interspecies competition focus on the optimum conditions of population coexistence, such as nutrients [5-7], illumination [8], and temperature [9, 10]. Under the stress of exogenous pollutants, the interspecies competition is likely to change, and this change will further influence the composition and structure of communities and may affect ecosystem services. Therefore, the study of the interspecies response mechanism under pollu-

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tant stress is a very important scientific problem and is indispensable for the analysis and evaluation of the hazard of various types of pollutants to the environment.

Population dynamics are the essence of population ecology. The basic model of population dynamics is the logistic equation, which describes density-dependent population growth. This model is widely applied to the dynamics of interspecies competition and coexistence. The present study investigated the population dynamics of two typical types of algae in fresh water under the stress of phenanthrene and the response mechanism of the two algae's interspecies competition under the stress based on the logistic growth model. By revealing the populations' dynamic laws and regulatory mechanisms, this study will provide evidence for protecting endangered species and forecasting eco-catastrophe.

Materials and Methods

Cultures

M. aeruginosa (FACHB-912) and *S. obliquus* (FACHB-39) were both obtained from the Freshwater Algae Culture Collection, held at the Institute of Hydrobiology (FACHB- Collection). Under sterile conditions, *M. aeruginosa* and *S. obliquus* were transferred to BG medium and expanded culture when growing during the logarithmic phase. When co-cultured, the two algae were also in the BG medium [11]. The incubation conditions were as follows: the temperature was set at 24±1°C, pH value was 7.2±0.2, light illumination was controlled as 4,000 lux with a light and dark cycle of 14 hr:10 hr, and the culture was a stewing culture that was manually stirred three times a day.

Experimental Chemicals and Design

Phenanthrene is analytically pure and was purchased from the Sigma Corporation.

We used 4 treatments: 1) 0.0625 mg/l, 2) 0.25 mg/l, 3) 1 mg/l, and 4) control. In consideration of the volume ratio of the two algae and the results of the prior experiment, the concentration ratio of the two algae was set at 2:1 when co-cultured, and the total number of cells was 1×10^4 cells/ml. Meanwhile, single-species cultures of *M. aeruginosa* and *S. obliquus* were grown. Each treatment group was replicated three times. Because of the culture conditions for the algae, exposure only occurred once during the whole process. After exposure, the sample was measured periodically until 20 days after culture.

Measurement of Population Growth

Population densities were measured using the linear relationship between population density and the light absorption value for single-species algae. From the co-cultured algae, 0.1 ml of sample was taken, and the cell number was counted with a hemocytometer using the vision notation method.

Fitting of the Growth Curve

Algal growth of the algae was fitted to the logistic equation:

$$N(t)=K/(1+e^{a-rt})$$

...where K value was estimated using the three-point method, and a and r values were estimated using a regression analysis (least square fitting). The time of the inflection of the logistic fitting curve was calculated as $t_p=a/r$.

Calculation of the Inhibition Parameter of Interspecies Competition

All the competition inhibition parameters in each unit time after inflection were calculated based on the Lotka-Volterra competition model, taking the average value as the estimated value of the algae's competition inhibition parameter.

Statistical Analysis

Statistical analyses were conducted by SPSS 11.5 software. Algal population density on Day 20 was analyzed by one-way Analysis of Variance (ANOVA) and Dunnett's adjustment was also made between the different concentrations. During the whole growth period, the t-test was used to examine whether growth significantly differed between cultures exposed to phenanthrene stress and those not exposed to phenanthrene. Results were plotted using Matlab 7.0 software.

Results and Analysis

Characteristics of Population Growth of Two Algae

During the early stages of the experiment, we obtained the linear correlation between the population density and light absorption value of the two algae as follows:

$$y\ (\times10^4\ \text{cells/ml}) = 1089.60x+2.52,\quad R^2=0.9943\ (\textit{S. obliquus});$$
$$y\ (\times10^4\ \text{cells/ml}) = 1837.35x+1.51,\quad R^2=0.9948\ (\textit{M. aeruginosa}).$$

In the above equation, y is the population density (cells/ml) and x is the light absorption value at 650 mm (1 cm) point.

The changes in the population density of single-species and mixed-species cultured *S. obliquus* and *M. aeruginosa* without stress (0 mg/l) are shown in Figs. 1 and 2. In the single-species culture experiment, the population density of *S. obliquus* was greater than that of *M. aeruginosa* in the first 15 days; after that, the population density of *M. aeruginosa* was greater than that of *S.obliquus*. This indicated that *S. obliquus* could adapt to the environment better and

multiplied faster, while *M. aeruginosa* had a growth advantage in the later period. When mixed species cultured, the population density of *S. obliquus* did not differ from the single-species culture, while the density of *M. aeruginosa* decreased when mixed species cultured. The carrying capacity and population growth rate of *M. aeruginosa* decreased compared to the single-species culture (Tables 1 and 2). The fast growth of *S. obliquus* inhibited the growth of *M. aeruginosa*, which decreased both the living space and reproductive ability. This indicated that the two algae competed for resources in the same environment. Although the growth of *M. aeruginosa* was inhibited, it had greater growth potential in the later period.

Population Growth Trend of Single-Species under the Stress of Phenanthrene

The growth of the two algae when single-species cultured under the stress of phenanthrene is shown in Fig. 1. The curves fitted the values very well, and each parameter in the logistic equation and inflection time are shown in Table 1. The population increase of the two algae differed greatly under the stress of phenanthrene (Fig. 1). Growth of both algal species was altered under phenanthrene stress at the he $p<0.05$ significance level and evaluated the student's t-test. The population density of *S. obliquus* did not change relative to that of the control group (0 mg/l) when the concentration of phenanthrene was 0.0625 mg/l and 0.25 mg/l; the population density of the *S. obliquus* of treated with 1 mg/l group was inhibited. On the 20th day, the population density ($\times 10^4$ cells/ml) was 1,142.2 (control group), 1,082.3 (0.0625 mg/l), 1,084.1 (0.25 mg/l), and 949.0 (1 mg/l). Using a multiple comparison, we found that the population density of the 0.0625 mg/l group and the 0.25 mg/l group was not significantly different from that of the control group, while the population density of the 1 mg/l group was significantly different from that of the control group ($p=0.011$). The carrying capacity decreased gradually with increasing phenanthrene concentration (except the control group) according to the fitting of the logistical equation, but the population growth rate increased gradually with increasing phenanthrene. The population growth rate of the 0.0625 mg/l group was lower than that of the control group, but the time until the inflection point increased, which meant that the longer the time for free growth, the weaker the density-dependenct effect. In other words, a low concentration stimulatory effect existed.

The growth inhibition effect of phenanthrene on *M. aeruginosa* was more obvious than that on *S. obliquus*. On the 20th day, the population density ($\times 10^4$ cells/ml) under

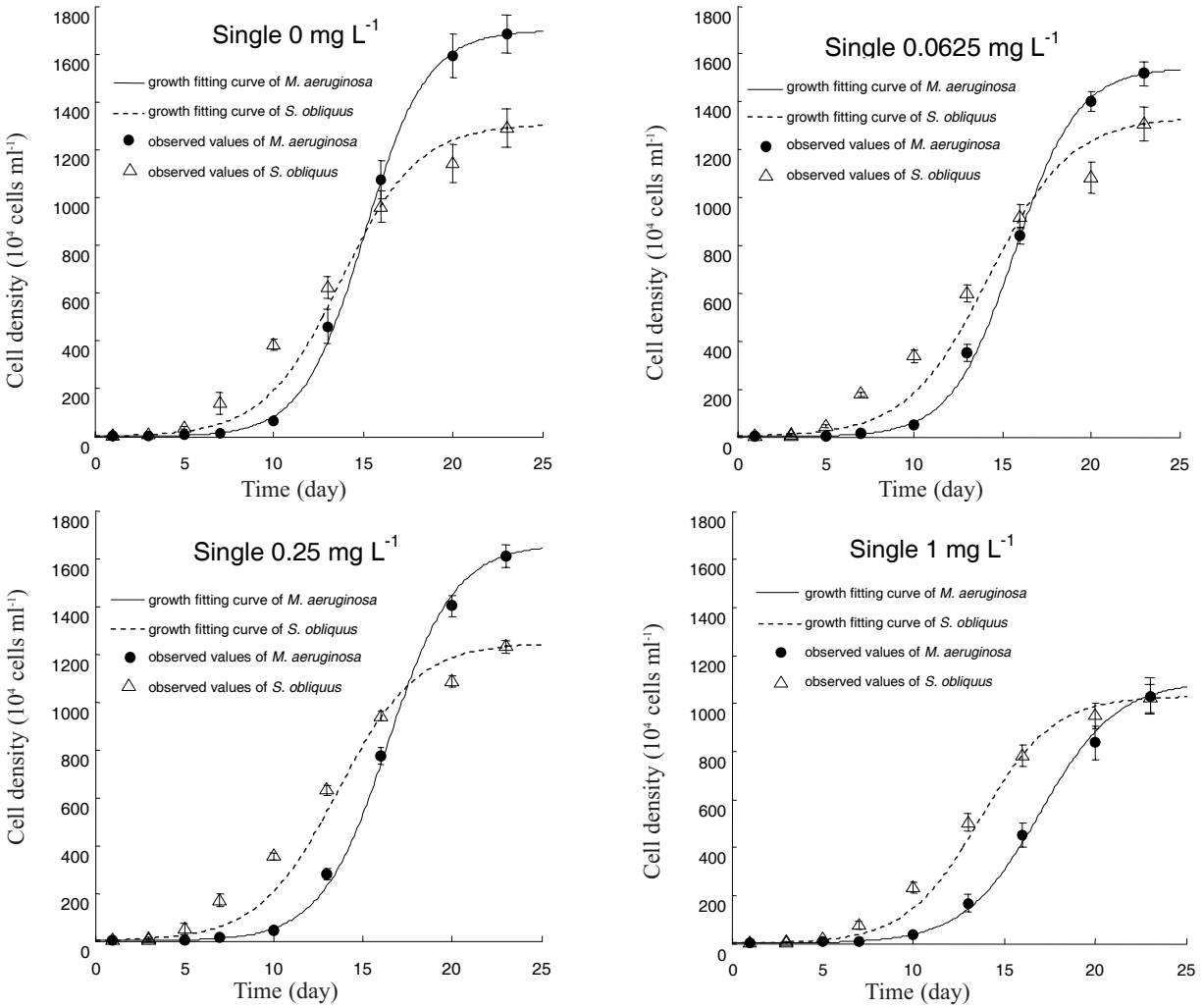

Fig. 1. The logistical growth fitting curve of single-species cultured *S. obliquus* and *M. aeruginosa*, and discrete points with σ error bars.

Table 1. The logistical equation parameters and inflectin time of two single-species cultured algae.

	Single *S. obliquus*				Single *M. aeruginosa*			
	K (10^4 cell/ml)	r	a	t_p (d)	K (10^4 cell/ml)	r	a	t_p (d)
0 mg/l	1,307.46	0.47	6.39	13.72 (13)	1,698.48	0.58	8.72	15.08 (15)
0.0625 mg/l	1,335.89	0.43	6.18	14.20 (14)	1,541.30	0.56	8.81	15.66 (15)
0.25 mg/l	1,248.04	0.45	6.17	13.59 (13)	1,658.61	0.53	8.77	16.47 (16)
1 mg/l	1,031.01	0.50	6.75	13.62 (13)	1,092.06	0.47	8.08	17.03 (17)

phenanthrene stress of *M. aeruginosa* was 1,592.0 (control group), 1,401.5 (0.0625 mg/l), 1,401.5 (0.25 mg/l), and 825.6 (1 mg/l). The population density of each treated group was significantly different from that of the control group. By fitting the logistic growth equation, it was shown that the carrying capacities of other groups of *M. aeruginosa* were slightly higher than those of the *S. obliquus* groups, except in the 1 mg/l group. With an increasing phenanthrene concentration, the population growth rate of *M. aeruginosa* gradually decreased. The time of inflection of *M. aeruginosa* under the treatments was delayed.

S. obliquus could tolerate phenanthrene stress better than *M. aeruginosa* when single-species cultured. The stress of phenanthrene mainly affected the population growth rate of *S. obliquus* but had little influence on its inflection time. However, for *M. aeruginosa* both the population growth rate and the inflection time were greatly affected. The reason for this may be that different cell structures and models of physiology and metabolism bring about different response mechanisms to pollutant stress.

Characteristics of Population Competition Trends of Two Algae under Phenanthrene Stress

S. obliquus and *M. aeruginosa* were co-cultured under the stress of different concentratins of phenanthrene. The

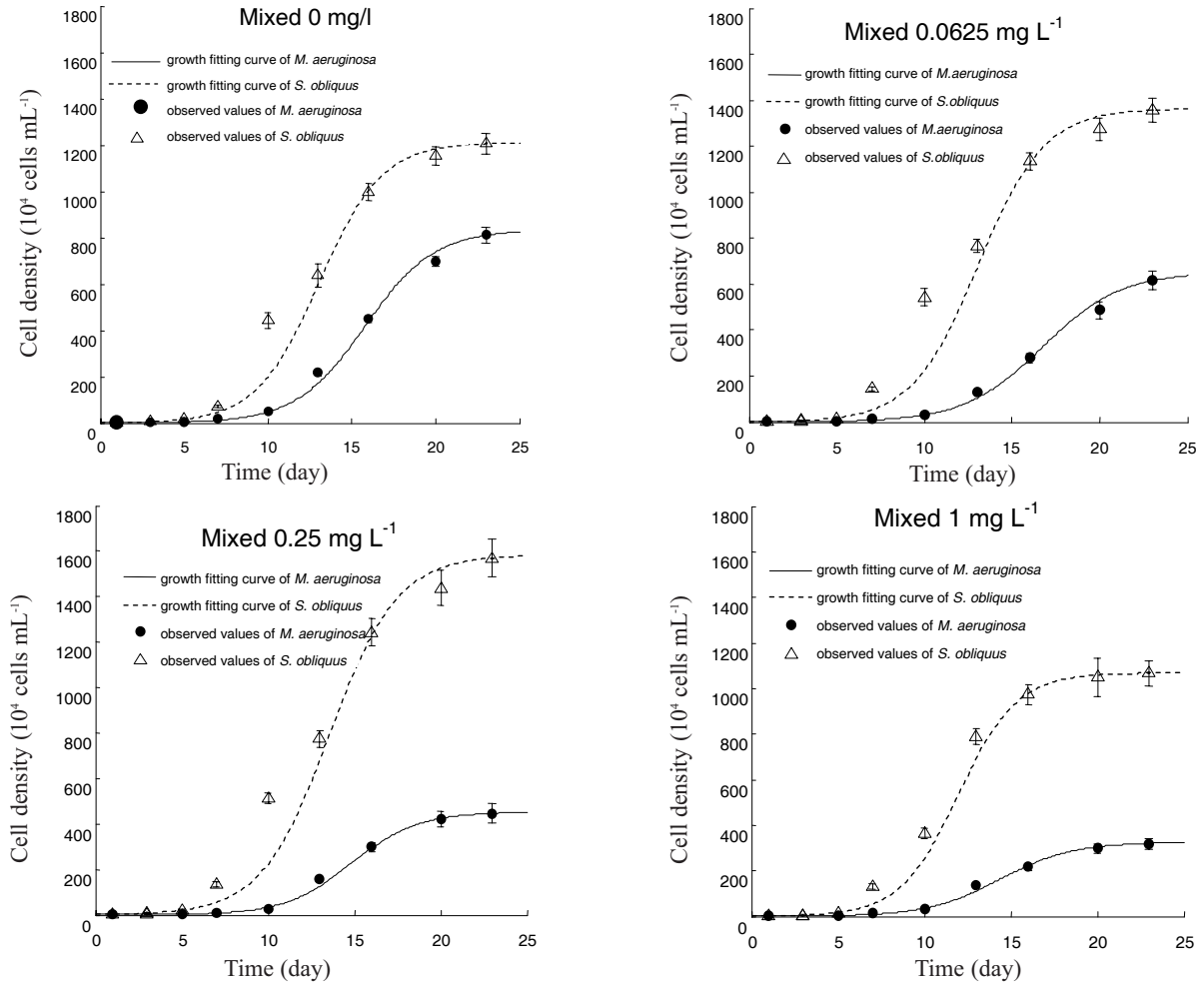

Fig. 2. The logistical growth fitting curve of mixed-species cultured *S. obliquus* and *M. aeruginosa*, and discrete points with σ error bars.

Table 2. The logistical equation parameters and inflection time of two algae mixed species cultured algae.

	Single *S. obliquus*				Single *M. aeruginosa*			
	K (10^4 cell/ml)	r	a	t_p (d)	K (10^4 cell/ml)	r	a	t_p (d)
0 mg/l	1,307.46	0.47	6.39	13.72 (13)	1,698.48	0.58	8.72	15.08 (15)
0.0625 mg/l	1,335.89	0.43	6.18	14.20 (14)	1,541.30	0.56	8.81	15.66 (15)
0.25 mg/l	1,248.04	0.45	6.17	13.59 (13)	1,658.61	0.53	8.77	16.47 (16)
1 mg/l	1,031.01	0.50	6.75	13.62 (13)	1,092.06	0.47	8.08	17.03 (17)

Table 3. Influence of phenanthrene stress on the interspecies competition of *S. obliquus* and *M. aeruginosa*.

	α	β
0 mg/L	1.59	0.89
0.0625 mg/L	2.18	0.53
0.25 mg/L	0.86	1.22
1 mg/L	-1.44	1.10

population density and fitting curve are illustrated in Fig. 2. The observed values fit the logistic growth curve well. The parameters in the logistic equation and the inflection time are shown in Table 2.

In the mixed-species culture experiment, the two algae's responses to the stress of phenanthrene changed greatly compared with the single-species culture experiment. Growth of both algal species was altered under phenanthrene stress at the he $p<0.05$, significance level, evaluated by Student's t-test. On the 20th day, the population densities ($\times 10^4$ cells/ml) of *S. obliquus* were 1,153.3 (control group), 1,273.3 (0.0625 mg/l), 1,437.5 (0.25 mg/l), and 1,050.0 (1 mg/l). Compared with the single-species culture experiment, the population density of the 0.0615 mg/l group and the 0.25 mg/l group both increased. On the 20th day, the population densities ($\times 10^4$ cells/ml) of *M. aeruginosa* were 695.8 (control group), 487.5 (0.0625 mg/l), 420.0 (0.25 mg/l), and 299.1 (1 mg/l). Compared with the result of the single-species culture experiment, the population density of each treatment decreased.

Under phenanthrene stress, the population growth rate of *S. obliquus* in the mixed species culture experiment was greater than in the single-species culture experiment, while for the inflection time, the opposite was true. This indicated that when mixed species cultured, the growth or reproduction of *M. aeruginosa* stimulated the growth of *S. obliquus* to some extent. Under phenanthrene stress, the population growth rate and inflection time of *M. aeruginosa* were both less than those of the control group, which was a concentration-dependent effect. Compared with the single-species culture, the carrying capacity, population growth rate, and inflection time of *M. aeruginosa* all decreased, and its growth also was inhibited.

There are different response mechanisms between the single-species culture and the mixed-species culture for both algae. This indicated that the interspecies competition for the resource between the two algae made their response mechanism to pollutants change, and *M. aeruginosa* decreased the inhibitory effect of phenanthrene on the growth of *S. obliquus*.

Effects of Phenanthrene Stress on Interspecies Competition

We used the difference in the Lotka-Volterra competition model to fit the population growth trend of the two algae when mixed-species cultured and to calculate their population competition inhibition parameters. The equations were as follows:

$$(N_{sn}-N_{sn-1})/(t_n-t_{n-1}) = r_{sn}N_{sn-1}(K_{sn}-N_{sn-1}-\alpha N_{mn-1})/K_{sn} \quad (1)$$

$$(N_{mn}-N_{mn-1})/(t_n-t_{n-1}) = r_{mn}N_{mn-1}(K_{mn}-N_{mn-1}-\beta N_{mn-1})/K_{mn} \quad (2)$$

In the equations, N_{sn} and N_{mn} are the cell numbers of *S. obliquus* and *M. aeruginosa*, respectively, at the time of t_n when mixed-species cultured; N_{sn-1} and N_{mn-1} are the cell numbers at the time of t_{n-1}, respectively; r_{sn} and r_{mn} are the instantaneous growth rate of *S. obliquus* and *M. aeruginosa*, respectively (determined by regression calculation from the single-species culture); K_{sn} and K_{mn} are the maximum carrying capacity of *S. obliquus* and *M. aeruginosa*, respectively (obtained through single-species culture); and α and β are competition inhibition parameters of *M. aeruginosa* to *S. obliquus* and *S. obliquus* to *M. aeruginosa*.

The average values of the competition inhibition parameters after inflection are listed in Table. 4. The competition inhibition parameter of *M. aeruginosa* to *S. obliquus* gradually decreased as the phenanthrene concentration increased. The parameters of the 0.25 mg/l group and the 1 mg/l group, but not the 0.0625 mg/l group, were both lower than that of the control group. The competition inhibition parameter of *S. obliquus* to *M. aeruginosa*, however, did not demonstrate a concentration-dependent effect. The competition inhibition parameters of the 0.25 mg/l group and the 1 mg/l group, but not the 0.0625 mg/l group, were both greater than that of the control group. In the control group, α was twice β; in the 0.0625 mg/l group, α was four times β; in the 0.25 mg/l and 1 mg/l groups, β was larger than α. This indicated that under phenanthrene stress, the interspecies competition of the two algae changed.

Table 4. The parameters in the Lotka-Volterra interspecies competition model.

	$1/K_{sn}$	β/K_{mn}	$1/K_{mn}$	α/K_{sn}	Final
0 mg/l	0.00076	0.00052	0.00059	0.0012	*M. aeruginosa* won
0.0625 mg/l	0.00074	0.00035	0.00065	0.0016	*M. aeruginosa* won
0.25 mg/l	0.00080	0.00074	0.00060	0.00069	*M. aeruginosa* won
1 mg/l	0.00097	0.0010	0.00092	-0.0014	*S. obliquus* won

Using the parameters of the Lotka-Volterra interspecies competition model to estimate the competition result, we found that the 0 mg/l, 0.0625 mg/l, and 0.25 mg/l groups had the same competition result; that is, when $1/K_{sn}>\beta/K_{mn}$ and $1/K_{mn}<\alpha/K_{sn}$, *M. aeruginosa* won and *S. obliquus* was supplanted. In the 1 mg/l group, when $1/K_{sn}<\beta/K_{mn}$ and $1/K_{mn}>\alpha/K_{sn}$, *S. obliquus* won and *M. aeruginosa* was supplanted (Table 4).

Discussion

Difference in the Two Algae's Response to the Stress of Phenanthrene

This study revealed that phenanthrene had a greater inhibitory effect on *M. aeruginosa's* growth than it did on *S. obliquus's* growth when single-species cultured, which indicated that *S. obliquus* tolerated phenanthrene better than *M. aeruginosa*. When the concentration of phenanthrene was low, it had a stimulatory effect on the growth of *S. obliquus* but not on the growth of *M. aeruginosa.* That *S. obliquus* is more tolerant to phenanthrene than *M. aeruginosa* has been previously reported [12, 13]. Stebbing [14] called the stimulating effects of toxicants with low concentration "toxicant hormesis" or "toxicant stimulating effect (hormesis)." In addition, according to the other research results, the low concentrations of exogenous contaminants activate enzymes related to physiological and biochemical cellular processes, thereby promoting algal metabolism and reproduction. At higher concentrations this beneficial effect is reversed; enzyme activity is reduced and metabolism and reproduction are inhibited [15, 16].

The fundamental reason for the different responses of *S. obliquus* and *M. aeruginosa* to phenanthrene stress may be rooted in their different cell structures. The cells of *M. aeruginosa* are nearly spherical, and their diameters were 3-7 micrometers. The cells of *S. obliquus* were fusiform, their lengths were 13-16 micrometers, and their widest parts were 4-6 micrometers. Because the volume of the *M. aeruginosa* cells was small, *M. aeruginosa* cells had a greater contact area with pollutants compared to *S. obliquus. M. aeruginosa* are prokaryotes, their cells consist of a nucleus and cytoplasm, and there are no organelles such as chloroplasts [17]. *S. obliquus* are eukaryotes and have a nucleus and cytoplasm differentiated based on the membrane system. In the cytoplasm, there are many organelles separated based on the membrane system that have more refined structures and more exclusive functions. Observation of the ultrastructure of *S. obliquus* also showed that the outer membrane of the chloroplast was doubled, and inside it were many flaked thylakoids in a parallel arrangement [18]. The complicated structures of the cell and the developed membrane system enabled *S. obliquus* to tolerate pollutant stress better.

According to ecological toxicity studies, PAH pollutants interfere with the algae antioxidant defense system and cause peroxidation of the membrane lipids [2]. Under adverse circumstances, cells produce large numbers of reactive oxide species (ROS), such as O_2^-, ·OH, and H_2O_2, which are cleared by the antioxidant defense system. Many ROS can also cause or aggravate membrane lipid peroxidation, which seriously damages the membrane system. Earlier research results have shown that, under cinnamic acid stress, *M. aeruginosa* produces more active radicals than *S. obliquus*, and that lipid peroxidation is more serious in *M. aeruginosa* [20]. Clearly, the physiological stress mechanisms of *S. obliquus* and *M. aeruginosa* are considerably different.

Some research has indicated that organic pollutants could be degraded by algae to provide a carbon source and a nitrogen source, both of which are necessary for growth [21]. The maximal concentration of a pollutant that algae can degrade was defined as the resistance threshold value of algae to the organic pollutant. Once this value is exceeded, the organic pollutant would harm the algae and inhibit their growth, mainly by affecting photosynthesis, respiration, the biological membrane, and biochemical construction. The free radical damage theory is a modern attempt to explain the mechanism of toxicity in cells. It is widely used to explain the toxic actions of heavy metals, organic pollutants and pesticides [22-25]. As a type of tricyclic polycyclic aromatic hydrocarbons, phenanthrene is capable of photolysis, volatization and biodegradation. The natural loss of phenanthrene would vary with changing environmental conditions. To ensure that all of the experimental conditions were the same, all samples in this study were cultured in the same incubator. The degradation and absorption mechanism of algae to phenanthrene should be studied in the future.

Interspecies Competition between Two Algae and the Influence of Phenanthrene Stress

The results of the pre-experiment in the early period told us the two algae gradually entered into the growth-saturated period and reached the maximum carrying capacity

after 20 days of culture. The growth of *S. obliquus* and *M. aeruginosa* were both in accordance with the typical S curve. Without any stress, the competitive inhibition ability of *M. aeruginosa* to *S. obliquus* was stronger than that of *S. obliquus* to *M. aeruginosa*, which was consistent with the results of other work [30]. *M. aeruginosa* had a larger specific surface area than did *S. obliquus*; therefore, it could absorb more nutrition and illumination to obtain the necessary elements for growth and thus have an advantage in the competition [31, 32]. In addition, *M. aeruginosa* could secrete microcystins that could inhibit the growth of other species in the ecosystem; in particular, when *M. aeruginosa* grew slowly due to poor conditions in terms of resource competition, it would secrete microcystins and other allelochemicals to inhibit its opponents [33]. Under the stress of phenanthrene, the competition inhibition between *S. obliquus* and *M. aeruginosa* changed, which was related to the difference between the carrying capacities and population growth rates of the two algae under the stress of phenanthrene. When the concentration of phenanthrene was 0.0625 mg/l, the competitive inhibition of *M. aeruginosa* to *S. obliquus* was stronger than in the control group. The carrying capacity and population growth rate of *M. aeruginosa* decreased sharply compared with that of the control group, which indicated that the growth of *M. aeruginosa* was inhibited under the stress of phenanthrene, and its dead cells secreted many microcystins [34].

However, the growth of *S. obliquus* was stimulated because of hormesis, and its population density thus increased; this also increased the survival pressure of *M. aeruginosa*, so its competitive inhibition was greater than that of the control group. When the concentration of phenanthrene was 0.25 mg/l, the competitive inhibition of *M. aeruginosa* to *S. obliquus* decreased to half that of the control group, and the carrying capacity of *M. aeruginosa* was also reduced to almost half that of the control group. Although its population growth rate increased and had great potential for growth, the growth of *M. aeruginosa* suffered great toxic stress in the initial stage of growth, and the secretion of microcystins was also affected. On the contrary, as a result of less competitive inhibition and the stimulation of phenanthrene, the growth of *S. obliquus* was unaffected. Phenanthrene at 1 mg/L strongly inhibited *M. aeruginosa* growth, reducing its ability to outcompete *S. obliquus* via resource competition and microcystin secretion. Furthermore, as reported in previous studies, *M. aeruginosa* can absorb and biodegrade organic pollutants such as DBP, DEHP, and phenol [35, 36]. In this way, *M. aeruginosa* can effectively decrease the local phenanthrene concentration, detoxifying the co-culture environment and facilitating growth of *S. obliquus*.

Conclusions

From the above results, it can be observed that there was a difference in the toxic effect of phenanthrene on *S. obliquus* and *M. aeruginosa*. The PAH phenanthrene stimulated the growth of these species when its concentration was low and inhibited the growth when its concentration was high. Different concentrations of phenanthrene had different effects on the interspecies competition between the two algae. The competitive inhibition of *M. aeruginosa* to *S. obliquus* gradually decreased with increasing concentrations of phenanthrene, while the competitive inhibition of *S. obliquus* to *M. aeruginosa* was independent of the concentration of phenanthrene. Futhermore, co-exposure to a pollutant could alter the interspecies competition relationship of the two species and influence the final competitive result. This article only studied the variation of interspecies relationships (population structure) under phenanthrene stress in a simple aquatic ecosystem composed of two types of common algae. However, further research would be required to understand the more integrated response mechanism of algal population structures to the stress of exogenous pollutants.

Acknowledgements

This research was partially supported by the Environmental Public Welfare Industry Research Special Project (grant No. 2011467032) .

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