A niche model to predict *Microcystis* bloom decline in Chaohu Lake, China*

WANG Zhicong (汪志聪)[1, 2], LI Zhongjie (李钟杰)[1], LI Dunhai (李敦海)[1, **]

[1] *Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China*

[2] *Graduate University of Chinese Academy of Sciences, Beijing 100049, China*

Abstract   Cyanobacterial blooms occur frequently in lakes due to eutrophication. Although a number of models have been proposed to forecast algal blooms, a good and applicable method is still lacking. This study explored a simple and effective mathematical-ecological model to evaluate the growth status and predict the population dynamics of *Microcystis* blooms. In this study, phytoplankton were collected and identified from 8 sampling sites in Chaohu Lake every month from July to October, 2010. The niche breadth and niche overlap of common species were calculated using standard equations, and the potential relative growth rates of *Microcystis* were calculated as a weighted-value of niche overlap. In July, the potential relative growth rate was 2.79 (a.u., arbitrary units) but then rapidly declined in the following months to -3.99 a.u. in September. A significant correlation (R=0.998, P<0.01) was found in the model between the net-increase in biomass of *Microcystis* in the field and the predicted values calculated by the niche model, we concluded that the niche model is suitable for forecasting the dynamics of *Microcystis* blooms. Redundancy analysis indicated that decreases in water temperature, dissolved oxygen and total dissolved phosphorus might be major factors underlying bloom decline. Based on the theory of community succession being caused by resource competition, the growth and decline of blooms can be predicted from a community structure. This may provide a basis for early warning and control of algal blooms.

Keyword: *Microcystis* bloom; niche breadth; niche overlap; predictive model; Chaohu Lake

1 INTRODUCTION

In recent decades, lake eutrophication has become increasingly serious in the middle and lower reaches of the Changjiang (Yangtze) River Plain, causing cyanobacterial blooms in most of the large shallow lakes (Yang et al., 2006; Chen et al., 2007; Xing et al., 2007). Various physicochemical factors, biotic effects and hydro-meteorological characteristics have been assumed to be main reasons for cyanobacterial blooms (Paerl et al., 2001; Jin and Wang, 2006; Jiang et al., 2008; Goleski et al., 2010; Wang et al., 2011a). Many models have been developed to predict the dynamics of cyanobacterial blooms. Statistical methods, such as regression analysis and correlation analysis have commonly been used to fit curves of algal biomass to environmental factors to forecast the growth and decline of blooms (Chen et al., 2001; Lane et al., 2009). However, these analyses require a large number of samples and may lead to erroneous results because of the time lag between algal community development and changes in environmental status. Therefore, due to slow model training speed, and complicated calculations required for artificial neural networks (ANN model) (Li et al., 2007; Wang et al., 2010a), these predictive models have been abandoned by most researchers.

A good model should include two important

characteristics: simplicity and reliability. Such a simple and reliable model is required for bloom prediction. Niche models, which have been commonly applied to higher plant populations (Thompson et al., 1999; Shi et al., 2007), may be a suitable choice for bloom prediction. Although there have been some applications of niche models in aquatic system to calculate niche breadth and niche overlap (Ludwig and Reynolds, 1988), niche models have not been used to predict phytoplankton community succession or in particular cyanobacterial blooms.

Niche is a basic concept in modern biology (Leibold, 1995). Studies on niche are fundamental for understanding species relationships, species diversity, community structures and community succession (Zhang, 2004). For a phytoplankton community structure, niche breadth and niche overlap are two important variables that can be calculated using mathematical equations. These two variables are generally considered as decisive factors for community structure and sometimes reflect the structural stability of a community. They may also reveal the ability of resource utilization and functional status of some species. In this paper, the use of ecological niche models to forecast cyanobacterial bloom is examined. Growth and decline of blooms were predicted from community structure, based on the theory of community succession due to resource competition. The principles, construction, and parameterization of the ecological niche model applied in Chaohu Lake are presented. This study may provide a basis for early warning systems and control methods for algal blooms.

2 MATERIAL AND METHOD

2.1 Study site and sampling method

The Chaohu Lake (31°25′28″–31°43′28″N, 117°16′54″–117°51′46″E) is located in the delta region of the Changjiang River in eastern China. It has a mean surface area of 770 km², a mean depth of 2.7 m, and a storage capacity of 2.1 billion m³. Before the 1950s, it was well known for its scenic beauty and richness of aquatic life. However, the lake is currently facing a threat of serious eutrophication (Zhang et al., 2008). Every year during warm season, dense cyanobacterial blooms (mainly composed of genus *Microcystis* and genus *Anabaena*) are observed in the lake (Xu et al., 2007). Based on geographical features and pollution status, 8 sampling sites were chosen

(Fig.1). Samples were collected, measured and analyzed using the following methods.

2.2 Physicochemical parameter measurement

Dissolved oxygen (DO) and water temperature (WT) were measured using a portable dissolved-oxygen meter (YSI 550A). pH was recorded using a portable pH meter (YSI 63). Total nitrogen (TN), ammonia (NH_4^+-N) and total phosphorus (TP) were analyzed according to Wang et al. (2010b). Total dissolved phosphorus (TDP) was measured in the same way as TP after water filtration through cellulose acetate membranes (Kenker, USA) of 0.45 μm. Chlorophyll *a* was extracted and measured spectrophotometrically as described by Parsons and Strickland (1963). Transparency (SD) was determined using a secchi disc.

2.3 Phytoplankton identification and niche variables analysis

Samples (500 mL) were collected vertically in every station from surface layer (10 cm below water surface) monthly July to October, 2010. Samples were fixed immediately with Lugol's solution and then concentrated by using a siphon pipe, to 60 mL after standing for 48 h. Subsequently, 0.1 mL from each concentrated sample was assayed for numbers and types of phytoplankton using a microscope. Calculations of niche breadth and niche overlap were made using the most common species observed in July, August, September, and October. Niche breadth analysis followed Eqs.1 and 2 of Levins (1968), and niche overlap was calculated using Eqs.2 and 3 proposed by Petraitis (1979).
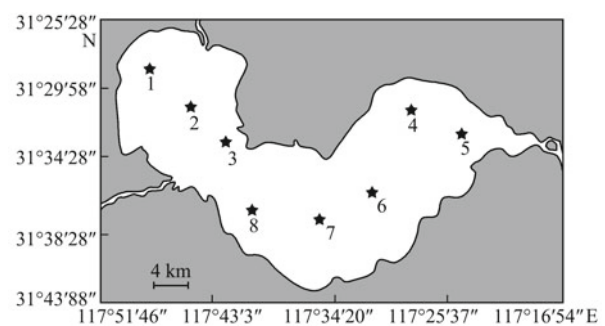
$$B_i = \frac{1}{\sum_{j=1}^{r} P_{ij}^2} \quad (1)$$

Fig.1 Sampling sites in Chaohu Lake

$$P_{ij} = n_{ij} \big/ N_{i+} \qquad\qquad (2)$$

$$\mathrm{SO}_{ik} = e^{E_{ik}} \qquad\qquad (3)$$

$$E_{ik} = \sum_{j=1}^{r}(P_{ij}\ln P_{kj}) - \sum_{j=1}^{r}(P_{ij}\ln P_{ij}) \qquad (4)$$

where, B_i denotes the niche breadth; P_{ij} is the resource occupied by species i (n_{ij}) in comparison with the total resource (N_{i+}) in site j; SO_{ik} is niche overlap of species i versus species k; E_{ik} is exponent of niche overlap of species i versus species k; i and k are species of phytoplankton; r is total number of sampling sites; j is a specific sampling site.

2.4 Correlation analyses

Redundancy analysis (RDA) (Canoco for Windows 4.5 software) was used to examine the correlations between the environmental factors and phytoplankton species. The species chosen to perform RDA should satisfy two conditions: the first condition is that the frequency of the chosen species at all sampling sites should be greater than 12.5%; and the second is that the relative population density of this species in at least one sampling site should exceed 1%.

3 RESULT

3.1 Dominant species of phytoplankton during the bloom period in Chaohu Lake

Five phyla, 49 genera and 78 species were observed in the phytoplankton community from July to October, 2010. The main phyla were Cyanophyta and Chlorophyta, and *Microcystis* was the absolute dominant genus during the investigation period. Based on species frequencies, 35 species that appeared in all months were chosen to calculate niche variables (Table 1).

3.2 Changes in the niche breadth of phytoplankton during the bloom period

The niche breadth of *Microcystis* was 8.37 in July, the highest value during the entire study period. It then decreased significantly in August, September, and October (Fig.2). However, with the niche breadth decrease of *Microcystis* in August, the niche breadth of other species, such as *Anabaena* increased slightly, suggesting a succession between *Microcystis* and other cyanobacteria had occurred within the Cyanophyta. Similarly, the niche breadth of

Table 1 Index of dominant phytoplankton in Chaohu Lake from July to October, 2010

| Index	Species	Index	Species
Cyanophyta		18	*Kirchneria subcapitata*
1*	*Microcystis*	19	*Scenedesmus quadricauda*
2	*Dactylococcopsis*	20	*Scenedesmus platydiscus*
3	*Aphanizomenon*	21	*Scenedesmus denticulatus* Lag.
4	*Chroococcus*	22	*Schroederia nitzschioides*
5	*Merismopedia punctata*	23	*Scenedesmus cavinatus*
6	*Phormidium tenue*	24	*Crucigenia quadrata*
7	*Anabaena flos-aquae*	25	*Chlamydomonas*
Cryptophyta		26	*Ankistrodesmus spiralis*
8	*Chroomonas acuta*	27	*Closterium parvulum*
9	*Cryptomonas erosa*	28	*Tetrastrum staurogeniaeforme*
10	*Cryptomonas ovata*	29	*Staurastrum manfeldtii*
Chlorophyta		Bacillariophyta	
11	*Chlorella vulgaris*	30	*Cyclotella*
12	*Palmellococcus* sp.	31	*Stephanodiscus astraea*
13	*Eudorina elegans*	32	*Melosira granulata var. angustissima*
14	*Tetraedron triangulare*	33	*Melosira granulata*
15	*Tetraedron minimum*	34	*Melosira* sp.
16	*Pediastrum simplex var. duodenarium*	Pyrrophyta	
17	*Pediastrum biradiatum*	35	*Ceratium hirundinella*

* Given number for each species.
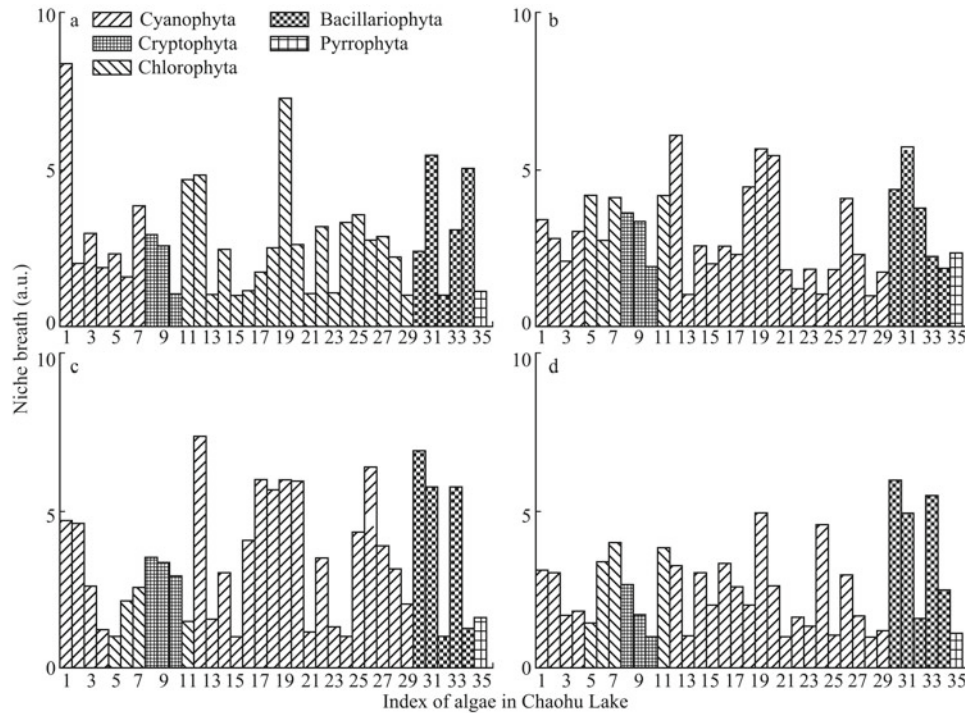
Fig.2 Niche breadth of phytoplankton in Chaohu Lake in July (a), August (b), September (c), and December (d), 2010

Numbers in the *x* axis correspond to those in Table 1 (N° is the species identification), and a.u. = arbitrary units.

Cryptophyta, Chlorophyta, Bacillariophyta and Pyrrhophyta also increased (Table 2) in August. In September, not only *Microcystis* but also all other cyanobacteria declined in niche breadth, while the niche breadths of other algae gradually expanded. The phytoplankton community dominated by Cyanophyta became a community characterized by Chlorophyta. All algae, except Bacillariophyta, exhibited a marked decrease in niche breadth in October, especially Cryptophyta and Chlorophyta (Table 2).

3.3 Resource availability and niche overlap of phytoplankton in Chaohu Lake

The weighted-value of niche overlap ($\sum_{i=1}^{n}SO_{ij}$ or $\sum_{i=1}^{m}SO_{ij}$) and species potential growth rate ($\Delta SO_{ij}=\sum_{i=1}^{n}SO_{ij}-\sum_{i=1}^{m}SO_{ij}$) are shown in Table 3. The negative values of ΔSO_{ij} suggested that some species were declining even though they occupied a high resource status as shown by $\sum_{i=1}^{n}SO_{ij}$. In July, the ΔSO_{ij} of *Microcystis* was positive (3.81 a.u.), suggesting that *Microcystis* was growing and a more serious bloom might result. Then, it sharply decreased to -6.09 a.u., -12.00 a.u. and -2.68

Table 2 Average niche breadth of different phyla of phytoplankton in Chaohu Lake

Category of phytoplankton	July	August	September	October
Cyanophyta	3.30±2.37	3.20±0.76	2.68±1.46	2.63±0.97
Cryptophyta	2.20±1.01	2.97±0.93	3.28±0.31	1.78±0.84
Chlorophyta	2.65±1.64	2.80±1.66	3.62±2.10	2.37±1.23
Bacillariophyta	3.42±1.85	3.60±1.58	4.14±2.79	4.10±1.94
Pyrrophyta	1.14±0.00	2.36±0.00	1.60±0.00	1.10±0.00

a.u. in August, September and October, respectively, indicating that 1) the bloom began to decline in August and 2) the most significant decline was occurred in September (Table 3). The weighted-values of niche overlap ($\sum_{i=1}^{n}SO_{ij}$ or $\sum_{i=1}^{m}SO_{ij}$) in October (4.92 a.u. and 5.92 a.u. respectively) were significantly lower than those in September (9.12 a.u. and 11.52 a.u. respectively) (Table 3).

The average ΔSO_{ij} of all species in Cyanophyta was as low as -0.14 a.u. in July, and decreased to a lower value (-2.38 a.u.) in August (Table 4), closely related to the decline of cyanobacteria, especially *Microcystis*. In this *Microcystis* decline period, an increase and decline

Table 3 Resource availability and niche overlap of phytoplankton in Chaohu Lake

Species number	July			August			September			October		
	$\sum_{i=1}^{n} SO_{ij}$	$\sum_{i=1}^{m} SO_{ij}$	ΔSO_{ij}	$\sum_{i=1}^{n} SO_{ij}$	$\sum_{i=1}^{m} SO_{ij}$	ΔSO_{ij}	$\sum_{i=1}^{n} SO_{ij}$	$\sum_{i=1}^{m} SO_{ij}$	ΔSO_{ij}	$\sum_{i=1}^{n} SO_{ij}$	$\sum_{i=1}^{m} SO_{ij}$	ΔSO_{ij}
1	7.37	4.57	3.81	4.14	10.23	-6.09	10.09	22.09	-12.00	4.47	7.15	-2.68
2	5.50	5.18	0.33	6.66	6.19	0.48	8.98	9.34	-0.36	3.96	7.43	-3.46
3	4.24	6.02	-1.78	6.62	3.64	2.98	9.33	16.38	-7.05	7.38	8.94	-1.56
4	7.65	5.14	2.51	7.20	8.84	-1.64	8.59	5.72	2.87	5.07	4.81	0.26
5	5.47	5.76	-0.29	6.90	12.28	-5.38	12.45	4.88	7.58	6.49	4.58	1.90
6	4.46	4.29	0.17	4.99	3.87	1.12	8.00	5.62	2.38	4.33	6.23	-1.90
7	4.55	9.29	-4.74	5.85	13.97	-8.12	6.70	6.65	0.05	4.86	11.22	-6.36
8	7.44	7.54	-0.10	7.46	9.38	-1.92	9.35	13.49	-4.15	4.60	3.44	1.16
9	3.98	3.02	0.96	7.99	7.99	-0.01	7.09	6.27	0.81	3.76	3.55	0.21
10	4.96	2.12	2.84	7.62	5.91	1.71	8.45	9.24	-0.79	4.60	1.64	2.96
11	5.12	8.68	-3.56	8.22	11.55	-3.33	6.00	2.73	3.27	3.58	3.85	-0.27
12	6.22	13.40	-7.18	7.09	21.19	-14.10	10.40	25.20	-14.80	3.74	10.14	-6.40
13	7.74	3.14	4.60	8.76	3.10	5.67	9.99	7.59	2.40	5.19	1.07	4.12
14	5.31	6.15	-0.83	7.88	6.43	1.45	6.80	4.71	2.09	2.98	3.35	-0.38
15	5.05	2.22	2.83	5.56	3.49	2.08	5.75	1.17	4.58	5.13	3.36	1.77
16	5.98	3.92	2.05	5.00	8.93	-3.94	10.12	20.31	-10.19	4.13	7.32	-3.18
17	4.97	6.90	-1.92	7.97	8.14	-0.17	9.86	13.42	-3.57	3.84	5.34	-1.50
18	6.10	4.26	1.84	5.86	6.93	-1.07	8.68	10.20	-1.51	3.97	2.73	1.24
19	4.71	16.57	-11.86	7.37	15.25	-7.88	10.40	23.06	-12.66	4.16	9.59	-5.43
20	5.71	6.81	-1.11	7.51	18.62	-11.11	9.24	20.61	-11.37	3.92	4.08	-0.16
21	11.10	5.21	5.88	7.55	4.14	3.42	5.58	2.50	3.08	3.84	5.50	-1.66
22	4.52	2.92	1.60	9.06	4.22	4.84	8.16	9.42	-1.26	6.34	5.50	0.85
23	9.94	4.97	4.97	3.71	2.82	0.90	10.50	6.69	3.82	6.60	4.96	1.65
24	4.55	3.58	0.98	4.57	2.01	2.56	12.41	4.92	7.49	3.51	7.41	-3.91
25	4.92	8.12	-3.20	8.23	8.18	0.04	7.65	8.03	-0.38	11.29	7.88	3.42
26	6.69	3.25	3.44	7.20	11.95	-4.76	9.48	21.74	-12.26	3.41	5.53	-2.12
27	5.35	13.76	-8.41	6.27	6.30	-0.03	9.03	17.38	-8.35	6.97	8.85	-1.88
28	4.37	4.23	0.14	10.30	3.88	6.43	8.49	7.05	1.44	4.80	3.03	1.77
29	4.76	2.63	2.13	8.09	6.79	1.30	8.89	8.35	0.54	4.49	2.31	2.17
30	5.14	12.30	-7.16	7.16	17.56	-10.40	9.84	21.51	-11.66	3.43	14.08	-10.65
31	5.39	12.67	-7.29	6.40	18.87	-12.47	10.92	23.31	-12.39	4.66	11.14	-6.48
32	6.34	2.93	3.42	7.80	11.61	-3.81	12.45	6.50	5.95	3.91	3.16	0.75
33	4.14	5.56	-1.41	7.88	14.45	-6.57	10.69	23.85	-13.16	4.81	8.31	-3.50
34	5.14	11.81	-6.67	8.17	5.02	3.15	9.44	5.14	4.30	3.58	3.77	-0.19
35	9.89	6.29	3.60	7.28	6.50	0.78	9.43	8.08	1.35	10.37	5.99	4.38
Average	5.85 (1.71)	6.43 (3.73)	-0.58 (4.27)	7.04 (1.42)	8.86 (5.10)	-1.83 (5.22)	9.12 (1.74)	11.52 (7.37)	-2.40 (6.80)	4.92 (1.82)	5.92 (3.03)	-1.00 (3.37)

Note: $\sum_{i=1}^{n} SO_{ij}$: the resource status that species i occupies in comparison to other algae; $\sum_{i=1}^{m} SO_{ij}$: the resource status of species i which is occupied by other algae; ΔSO_{ij}: species potential growth rate; m and n are line number and column number of niche overlap matrix, respectively.

process of Chlorophyta occurred, suggested by a positive ΔSO_{ij} (1.23 a.u.) in July and a high negative ΔSO_{ij} (-1.38 a.u.) in September, respectively. In October (Table 4) the ΔSO_{ij} of Chlorophyta gradually increased to a positive value (1.44 a.u.).

3.4 Major driving forces of *Microcystis* bloom decline

The correlation between environmental factors and phytoplankton variation, as shown in Fig.3, revealed the effects of environmental factors on algae, especially on the dominant species in the community, *Microcystis*. The analysis results were considered reliable as the correlation coefficient between first and second RDA axis was very low (almost zero). It can be concluded from RDA analysis that WT, DO and TDP were significantly positively correlated with *Microcystis* biomass, while SD had a negative, but insignificant correlation with *Microcystis* biomass.

3.5 Predictive validity of the ecological niche model for *Microcystis* bloom decline

The net-increase in biomass of *Microcystis* was expressed by the difference in biomass between two consecutive months. The pattern of net-increase in biomass was recorded in the field was very similar with the predicted trend calculated using the niche model. The correlation between actual biomass and the predicted potential growth rate (ΔSO_{ij}) was significant ($R=0.988$, $P<0.01$) (Fig.4). The ΔSO_{ij} of *Microcystis* was 3.81 in July, suggesting *Microcystis* would grow. The field data in August showed a *Microcystis* biomass increase from 4.04×10^7 to 6.82×10^7.

4 DISCUSSION

Niche breadth of species is a summation of all the resources utilized by that species (Van Valen, 1965) and is sometimes referred to as the migration "length"

Table 4 Average niche overlap of different categories of phytoplankton in Chaohu Lake

Category of phytoplankton	July	August	September	October
Cyanophyta	-0.14±2.58	-2.38±4.19	-0.93±6.57	-1.97±2.65
Cryptophyta	1.23±1.49	-0.07±1.82	-1.38±2.53	1.44±1.40
Chlorophyta	-0.40±4.47	-0.93±5.49	-2.51±6.89	-0.52±2.87
Bacillariophyta	-3.82±4.73	-6.02±6.13	-5.39±9.63	-4.01±4.68
Pyrrophyta	3.60±0.00	0.78±0.00	1.35±0.00	4.38±0.00

Fig.3 RDA analysis of phytoplankton species and environmental variables in Chaohu Lake

Mic.: *Microcystis*; *Aph.*: *Aphanizomenon*; *Ana.*: *Anabaena flos-aquae*; *Pal.*: *Palmellococcus* sp.; *Sce.*: *Scenedesmus quadricauda*; *Cyc.*: *Cyclotella*; *Mel.*: *Melosira granulata* var. *angustissima*; *Cer.*: *Ceratium hirundinella*.
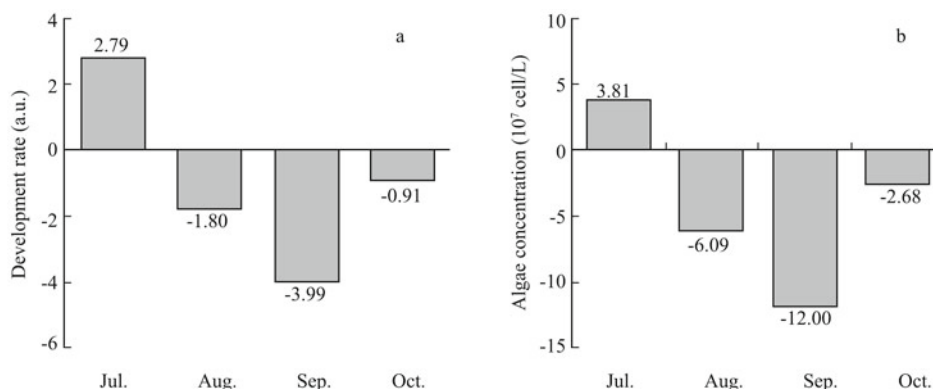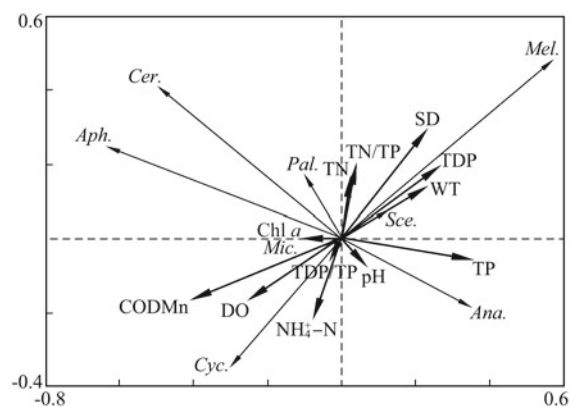

Fig.4 Algal development rate predicted by the niche model (a) and net increase in algal concentration in the lake (b) for various months

a.u. = arbitrary units.

along a certain directional line in niche space (Levins, 1968). Species with a bigger niche breadth have a greater capacity to compete for resources than those with a smaller niche breadth (Pianka, 1976; Thompson et al., 1999). Such a species is usually called a cosmopolitan or generalist species. Another aspect of niche measurement is niche overlap, which determines whether two similar species can live together stably when there is some resource competition (Petraitis, 1979). Therefore, niche overlap is defined as the utilization ability of a common and limited resource by two species (Colwell and Futuyma, 1971; Abrams, 1980; Sylvain et al., 2000). In the matrix of niche overlap, the developing status of a species i can be shown by potential growth rate $(\Delta SO_{ij} = \sum_{i=1}^{n} SO_{ij} - \sum_{i=1}^{m} SO_{ij})$. A growth status of a species is indicated by a positive ΔSO_{ij} whilst a decline status corresponds to a negative ΔSO_{ij}, and a neutral status is usually given as a null ΔSO_{ij}.

Under suitable environmental conditions in July, the niche breadth and niche overlap of *Microcystis* was bigger than that of other species, reflecting that the *Microcystis* population was growing and its dominance within the community was potentially increasing. This predicted that a potentially more serious bloom would occur in late July or August. Subsequently, the niche breadth and niche overlap of *Microcystis* decreased in August, suggesting a decline. According to RDA analysis, the *Microcystis* bloom decline was closely related to WT, DO, and TDP. This result was consistent with our previous findings (Wang et al., 2010c), where low concentrations of inorganic phosphorus in the culture medium could significantly limit the fluidity of the thylakoid membrane, and finally result in a marked decrease in photosynthetic activity and primary productivity.

Other previous research has also observed that photo-inhibition and/or photo-damage commonly occurs in serious bloom areas (Wang et al., 2011b). However, *Microcystis* can grow well under low light conditions (Zevenboom and Mur, 1984; Thomas and Walsby, 1985), suggesting that light is not a significant limiting factor. Here transparency (SD) rather than light intensity was investigated as one of factors affecting bloom dynamics. The result that SD had an insignificant negative correlation with *Microcystis* biomass corroborates the suggestion that light does not have a significant effect on bloom growth. With no significant difference among the temperatures in July, August and September (data not shown), the main

factors leading to the rapid decline of the *Microcystis* bloom from August to September could be attributed to decreasing DO and nutrient concentration.

The decline rate of the bloom in September, indicated by a ΔSO_{ij} was higher than that in August, suggesting that environmental stress became more intense in September. In October, it was not only the decline rate of *Microcystis* that increased but also the average decline rate of all phytoplankton decreased, as the temperature significantly decreased. This result indicted that resource competition is not always the major factor leading to bloom decline; the sudden drop in temperature was the major factor in the rapid decline of the *Microcystis* bloom in autumn.

Our previous study found a decline in *Microcystis* blooms occurred between July and August in Meiliang Bay of Lake Taihu, China (Wang et al., 2012). Certain decline processes and mechanisms were determined from this study. With the decline of the bloom in August, interspecific succession occurred but there were no significant changes in niche breadth and niche overlap in the community. This confirmed that resource competition was the main cause for bloom decline in August. However, a typical seasonal succession occurred among species and categories of bloom organisms with decreasing temperature, leading to a further decline in the *Microcystis* bloom.

A niche model was proposed based on community structure which could forecast species potential growth rate (ΔSO_{ij}) using measurements of niche breadth and niche overlap. Environmental factors were not considered as parameters in this niche model, effectively removing human error caused by the time difference between sample collection and data analysis and avoiding the effects of this time-lag on model construction. The *Microcystis* bloom was observed to decline in autumn (Wang et al., 2012). However, from field data, the exact timing of this decline and the decline rate was unknown. The ability of the model to solve this problem was tested and was found to provide good predictions for *Microcystis* bloom decline, when net-increase in biomass in algal samples were compared with the predicted values of species potential growth rate (ΔSO_{ij}). Thus the population dynamics of cyanobacterial growth and decline and particularly bloom biomass may be predicted if the structural characteristics and distribution patterns of the phytoplankton community are available. Such forecasting could provide bloom early warning allowing suitable methods for controlling bloom-formation to be activated immediately.

References

Abrams P A. 1980. Some comments on measuring niche overlap. *Ecology*, **61**: 44-49.

Chen Y, Qin B, Gao X. 2001. Prediction of blue-green algae bloom using stepwise multiple regression between algae and related environmental factors in Meiliang Bay, Lake Taihu. *J. Lake Sci.*, **13**: 63-71.

Chen Y, Yin F, Lu G. 2007. A Catastrophe model for water bloom prediction: a case study of China's Chaohu Lake. *Hum. Ecol. Risk Assess.*, **13**(4): 914-921.

Colwell R K, Futuyma D J. 1971. On the measurement of niche breadth and overlap. *Ecology*, **52**: 567-576.

Dolédec S, Chessel D, Gimaret-Carpentier C. 2000. Niche separation in community analysis: a new method. *Ecology*, **81**: 2 914-2 927.

Goleski J A, Koch F, Marcoval M A, Wall C C, Jochem F J, Peterson B J, Gobler C J. 2010. The role of zooplankton grazing and nutrient loading in the occurrence of harmful cyanobacterial blooms in Florida Bay, USA. *Estuar. Coast.*, **33**: 1 202-1 215.

Jiang Y, Ji B, Wong R N S, Wong M H. 2008. Statistical study on the effects of environmental factors on the growth and microcystins production of bloom-forming cyanobacterium—*Microcystis aeruginosa*. *Harmful Algae*, **7**: 127-136.

Jin X C, Wang S R, Pang Y, Wu F C. 2006. Phosphorus fractions and the effect of pH on the phosphorus release of the sediments from different trophic areas in Taihu Lake, China. *Environ. Pollut.*, **139**: 288-295.

Lane J Q, Raimondi P T, Kudela R M. 2009. Development of a logistic regression model for the prediction of toxigenic *Pseudo-nitzschia* blooms in Monterey Bay, California. *Mar. Eco. Prog. Ser.*, **383**: 37-51.

Leibold M A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology*, **76**: 1 371-1 382.

Levins R. 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, USA. p.132.

Li H, Hou G, Song L, Liu Y. 2007. Modelling algal blooms in lake Dianchi, China using neural networks. *Fresen. Environ. Bullet.*, **16**: 798-803.

Ludwig J A, Reynolds J F. 1988. Statistical Ecology: A Primer on Methods And Computing. John Wiley & Sons, New York. p.341.

Paerl H W, Fulton R S 3rd, Moisander P H, Dyble J. 2001. Harmful freshwater algal blooms, with an emphasis on cyanobacteria. *Sci. World*, **1**: 76-113.

Parsons T R, Strickland J D H. 1963. Discussion of spectrophotometric determination of marine plant pigment, with revised equations for ascertaining chlorophylls and carotenoids. *J. Mar. Res.*, **21**: 155-163.

Petraitis P S. 1979. Likelihood measures of niche breadth and overlap. *Ecology*, **60**: 703-710.

Pianka E R. 1976. Competition and niche theory. *In*: May R M ed. Theoretical Ecology: Principles And Applications. Blackwell Scientific Publications. p.114-141.

Shi H W, Jiang M X, Hu L L. 2007. Niche characteristics of *Berchemiella wilsoni var. pubipetiolata*, an endangered species in China. *J. Wuhan Bot. Res.*, **25**: 163-168.

Thomas R H, Walsby A E. 1985. Buoyancy regulation in a strain of *Microcystis*. *J. Gen. Microbiol.*, **131**: 799-809.

Thompson K, Gaston K J, Band S R. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *J. Ecol.*, **87**: 150-155.

Van Valen L. 1965. Morphological variation and the width of the ecological niche. *Am. Nat.*, **100**: 377-389.

Wang M, Xu Q, Che Y, Yang K. 2011a. Research on the meteorological and hydrological factors of cyanobacteria bloom in Lake Dianshan. *J. East China Norm. Univ.* (*Nat. Sci.*), (1): 21-31.

Wang Z, Huang K, Zhou P, Guo H C. 2010a. A hybrid neural network model for cyanobacteria bloom in Dianchi Lake. *Procedia Environ. Sci.*, **2**: 67-75.

Wang Y, Wang Z, Wu W, Hu M, Wang Z, Xu A, Li G, Liu Y. 2010b. Seasonal regime shift of an alternative-state Lake Xingyun, China. *Fresen. Environ. Bullet.*, **19**: 1 474-1 485.

Wang Z C, Li D H, Li G W, Liu Y D. 2010c. Mechanism of photosynthetic response in *Microcystis aeruginosa* PCC7806 to low inorganic phosphorus. *Harmful Algae*, **9**: 613-619.

Wang Z C, Zuo M, Wang Y C, Liu Y D, Li D H. 2011b. Dynamics of chlorophyll fluorescence and eco-morphological properties of *Microcystis* bloom in Meiliang Bay of Lake Taihu, China. *Fresen. Environ. Bullet.*, **20**: 2 295-2 305.

Wang Z C, Li G W, Li G B, Li D H. 2012. The decline process and major pathways of *Microcystis* bloom in Lake Taihu, China. *Chin. J. Oceanol. Limnol.*, **30**(1): 37-46.

Xing W, Huang W M, Liu Y D, Li D H, Shen Y W, Li G B. 2007. Environmental mechanism of change in cyanobacterial species composition in the northeastern part of Lake Dianchi (China). *Fresen. Environ. Bullet.*, **17**: 82-90.

Xu J, Zhang M, Xie P. 2007. Stable carbon isotope variations in surface bloom scum and subsurface seston among shallow eutrophic lakes. *Harmful Algae*, **6**: 679-685.

Yang D T, Pan D L, Zhang X Y, Zhang X F, He X Q, Li SJ. 2006. Retrieval of chlorophyll *a* and suspended solid concentration by hyperspectral remote sensing in Taihu Lake, China. *Chin. J. Oceanol. Limnol.*, **24**: 428-434.

Zhang J T. 2004. Quantitative Eclogy. Science Press, Beijing. p.120-240.

Zhang M, Xu J, Xie P. 2008. Nitrogen dynamics in large shallow eutrophic Chaohu Lake, China. *Environ. Geol.*, **55**: 1-8.

Zevenboom W, Mur L R. 1984. Growth and photosynthetic response of the cyanobacterium *Microcystis aeruginosa* in relation to photoperiodicity and irradiance. *Arch. Microbiol.*, **139**: 232-239.