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Empirical modelling of submersed macrophytes in Yangtze lakes

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Abstract

Submersed macrophytes in Yangtze lakes have experienced large-scale declines due to the increasing human activities during past decades. To seek the key factor that affects their growth, monthly investigations of submersed macrophytes were conducted in 20 regions of four Yangtze lakes during December, 2001–March, 2003. Analyses based on annual values show that the ratio of Secchi depth to mean depth is the key factor (50% of macrophyte biomass variability among these lakes is statistically explained). Further analyses also demonstrate that the months from March to June are not only the actively growing season for most macrophytes, but the key time the factor acts. Five key-time models yielding higher predictive power (r^2 reaches 0.75, 0.76, 0.77, 0.69 and 0.81) are generated. A comparison between key-time models and traditional synchronic ones indicates that key-time models have higher predictive power. Analyses of transparency thresholds during macrophyte growing season and the limitations of the models are presented. The models and other results may benefit the work concerning submersed macrophyte recovery in Yangtze lakes.

Keywords: Key-time models; Submersed macrophytes; Yangtze shallow lakes; Biomass; Transparency thresholds

1. Background and purpose

Situated in the warm, humid Yangtze basins in China, there are hundreds of shallow lakes with a total area exceeding 20,000 km^2 (Liu, 1984), where the submersed macrophytes are remarkably abundant. Macrophytes provide food and shelters for aquatic animals, regulate nutrient dynamics within the system and prevent resuspension of the sediments (Scheffer, 1998). Hence, they are important for normal lake ecosystems. However, on account of the increasing human activities for decades, deterioration of submersed macrophytes has widely occurred (Ni, 1999). It eventually turned the macrophyte-dominated, clear-water lakes into

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algae-dominated, turbid waters. Realizing their importance, the recovery of submersed macrophytes has become an increasing public concern. In addition to many practical works ought to be done for that purpose, the creation of certain models to predict growing tendency of vegetation under different conditions is also necessary.

Modelling referring to submersed vegetation may be categorized into distribution models and biomass models. Distribution models focus mainly on analyzing plant occurrence probability, maximum colonizing depth and cover rate (Chambers and Kalff, 1985; Duarte et al., 1986; Håkanson and Boulion, 2002; Scheffer et al., 1992), but neglect plant quantity. On the other hand, biomass models, including growth simulation and holistic empirical ones, are developed for quantitative purpose. Simulation models are advantageous to predict daily growth or seasonal trends of macrophyte biomass (Best et al., 2001; Collins and Wlosinski, 1989; Scheffer et al., 1993; Van Nes et al., 2002, 2003), but their generation requires a large number of detailed physiological and daily environmental data. Comparatively, holistic empirical models enable us to pay less attention to growing details and use fewer independent variables. Holistic models consist of empirical and dynamic models. In practice, empirical models have the advantage of using fewer parameters. A number of empirical models were established and have successfully predicted submersed macrophyte biomass or production (Canfield and Duarte, 1985; Duarte and Kalff, 1986, 1990; Duarte et al., 1986; Håkanson and Boulion, 2002; Janse et al., 1998; Squires et al., 2002). Among them, the comprehensive research on North Temperate lakes by Håkanson and Boulion (2002) was the most impressive. They used several parameters including ratio of Secchi depth to water depth, latitude, maximum water depth, and lake area above 1 m to predict submersed macrophyte production and achieved great success ($r^2 = 0.68$, slope = 1.5, intercept = −23.8). Unfortunately, their model did not work well in Yangtze lakes ($r^2 = 0.59$, slope = 16.79, intercept = -3.54×10^4) owing to the differences in latitudes, depths and plant components.

A similar empirical model in China has been reported by Liang et al. (1995) from Baoan Lake (a Yangtze lake). They pointed out that the ratio of Secchi depth (Z_{SD}, m) to mean depth (Z_M, m) was the key factor influencing submersed macrophyte biomass (B_{Mac}, g/m^2) and described an empirical relationship as:

$$B_{Mac} = -811.3 + 3596.91 \frac{Z_{SD}}{Z_M},$$
$$r = 0.42, \quad p = 0.004 \qquad (1)$$

However, their work was more or less preliminary, especially it was confined to a single lake.

The present study was conducted in 20 regions of four lakes. Its purpose is fourfold. First, to determine the key factors that affect the growth of submersed macrophytes; secondly, to generate key-time models by analyzing the annual effective intensity of key factors; thirdly, to compare the predictive power between key-time models and synchronic ones (using paired variates obtained at same time); and, lastly, to analyze briefly the thresholds of the key factor and the limitation of models in application.

2. Lakes and methods

Studies were carried out in four fluvial lakes (114°08′–48′ E, 30°07′–23′ N), with areas ranging from 29 to 67 km^2 and average depths within 2–4 m. Nets or dikes were presented inside the lakes and, thus subdivided the waters into 20 regions in total (Fig. 1).

The macrophyte communities in the lakes are quite similar, mainly consisting of *Potamogeton crispus* Linn., *P. maackianus* A. Benn., *Najas major* Linn., *Vallisneria* spp., *Hydrilla verticillata* (Linn. f.), *Ceratophyllum oryzetorum* Kom., *Myriophyllum spictum* Linn. All species are treated as the same functioning group.

Quantitative work was conducted during December, 2001–March, 2003, in which submersed macrophyte biomass (B_{Mac}), water depth (Z_M) and transparency (Z_{SD}) were determined monthly, while water temperature (T), conductivity (Cond), pH, concentration of total nitrogen (TN), ammonium (NH_3-N), total phosphorus (TP) and chlorophyll-a in phytoplankton (Chl *a*) were determined seasonally.

In terms of the methods, submersed macrophytes were sampled by scythes 2–4 times at each site, then cleaned, removed superfluous water and weighed for wet biomass. The dry weight biomass of macrophyte

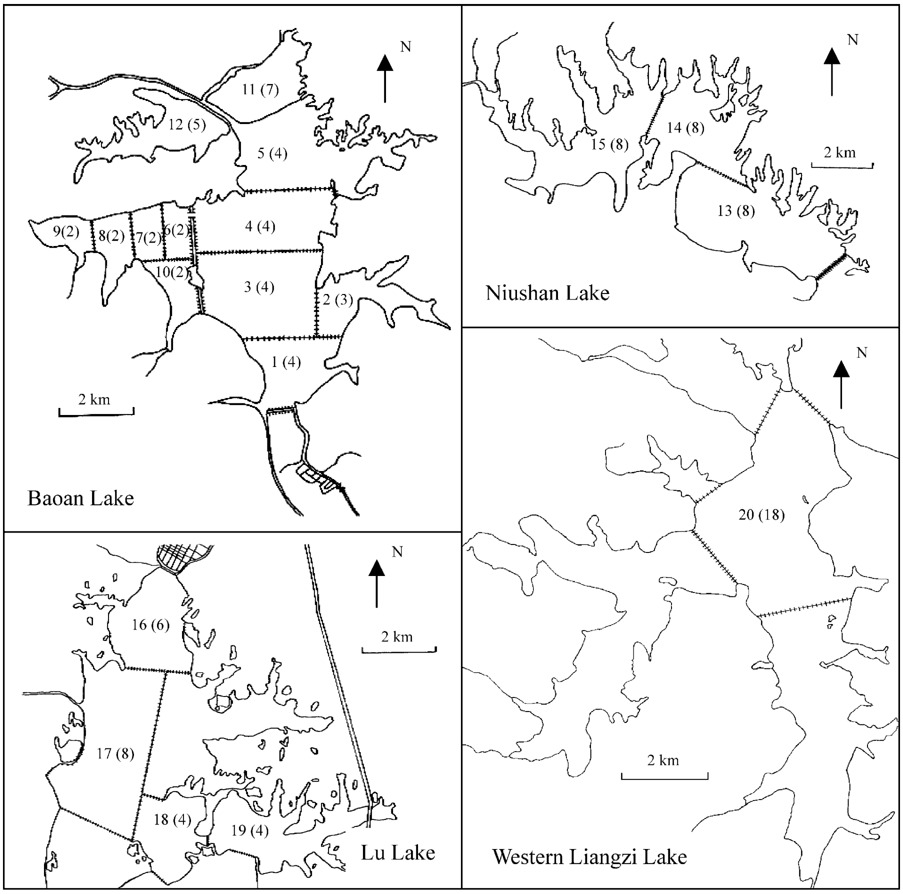

Fig. 1. Regions in four lakes. The anterior number is region-code and the posterior one in parenthesis denotes the number of sampling sites.

material can be calculated by multiplying the wet biomass by 0.08, a factor that represents the average percent dry weight of submersed macrophytes (Chen and Ho, 1975). Z_M and Z_{SD} were measured by sounding lead and Secchi Disc respectively. T, Cond and pH were measured in the field with YSI Environmental Monitoring Systems 6600. TN, NH_3-N, TP and Chl *a* were determined according to Chinese Water Analysis Methods Standards (Huang et al., 1999).

STATISTICA6.0 was used for ANOVA, correlation and regression analyses. When analyzing, region-specific data were used instead of site-specific data for two reasons: (1) our aim is to predict regional biomass level rather than site-specific values; (2) sampling errors caused by clumped distribution of plants can be reduced.

3. Results and discussions

3.1. Annual mean data

Data from 105 sites of 20 regions in four lakes were taken into account. One-way ANOVA analyses showed that the differences of macrophytic biomass and other parameters from separate regions were significantly greater than those among sites within a region ($P < 0.005$). It means that most region-specific data are independent enough and the communications between regions, if any, can be neglected. Table 1 presents the annual means of B_{Mac} and environmental factors of all investigated regions.

It should be pointed out that the datum $Z_{SD}/Z_M = 1$ derived from the method so far we use can hardly reflect light attenuation, because it means that the trans-

Table 1
Annual mean value of factors in regions studied

Lake	Region	Code	Area (km^2)	B_{Mac} (g/m^2)	Z_M (m)	Z_{SD} (m)	Z_{SD}/Z_M	T (°C)	Cond (mS/cm)	pH	NH_3-N (mg/L)	TN (mg/L)	TP (mg/L)	Chl *a* (μg/L)
Baoan Lake	Baoankou	1	3.63	6415	2.18	1.54	0.71	17.6	0.376	7.92	0.171	0.441	0.011	3.91
	Huangfengkou	2	1.88	3763	1.93	1.87	0.97	17.8	0.885	7.94	0.083	0.257	0.015	1.11
	Changlingzhou	3	8.80	2211	2.50	1.97	0.79	17.3	0.457	8.06	0.136	0.257	0.009	1.49
	Zhuzhou	4	6.45	661	2.55	1.72	0.67	17.3	0.355	8.03	0.141	0.188	0.013	4.28
	Longwangtou	5	6.25	239	2.54	1.65	0.65	17.3	0.374	7.96	0.158	0.230	0.017	4.27
	Lianhuazhou	6	1.57	26	2.64	1.70	0.64	18.2	0.252	8.10	0.177	0.241	0.015	2.47
	Outang	7	1.45	3426	2.53	1.87	0.74	18.3	0.236	8.18	0.143	0.180	0.013	3.99
	Shuimiao	8	1.57	8508	2.33	2.08	0.89	18.3	0.213	8.38	0.137	0.194	0.011	2.22
	Changlingtou	9	1.49	6747	1.86	1.77	0.95	18.8	0.199	8.41	0.154	0.268	0.016	1.98
	Tongshawan	10	1.91	1703	2.21	1.44	0.65	18.6	0.253	8.08	0.219	0.205	0.016	2.04
	Biandantang	11	3.50	307	2.17	1.36	0.63	17.3	0.193	8.07	0.214	0.270	0.018	4.46
	Xiaosihai	12	1.50	914	1.80	1.27	0.71	16.9	0.321	7.90	0.152	0.190	0.032	2.04
Niushan Lake	Dongpian	13	17.5	1052	3.63	2.93	0.81	20.5	0.129	8.17	0.110	0.861	0.008	2.75
	Zhongpian	14	11.8	138	3.61	2.79	0.77	20.7	0.137	7.85	0.107	0.931	0.005	1.80
	Xipian	15	13.3	972	3.46	2.65	0.77	20.9	0.134	8.03	0.115	0.977	0.005	3.30
Lu Lake	Wuqianmu	16	5.71	49	2.36	0.80	0.34	17.9	0.241	7.69	0.330	0.783	0.037	7.05
	Yiwanwu	17	12.1	63	2.48	0.72	0.29	17.6	0.195	7.60	0.263	0.530	0.033	4.24
	Hongqicha	18	4.51	30	1.91	0.98	0.51	17.6	0.168	7.48	0.096	0.254	0.022	5.87
	Caimohu	19	7.12	300	2.07	1.32	0.64	18.0	0.142	7.82	0.107	0.286	0.020	1.85
Western Liangzi Lake		20	66.7	663	3.79	2.48	0.65	21.0	0.110	7.82	0.130	0.438	0.013	2.37
		Mean	8.39	1909	2.53	1.75	0.69	18.4	0.269	7.97	0.157	0.399	0.016	3.17
		CV	160.8	133.7	24.4	35.5	24.8	7.1	64.8	2.9	38.4	67.4	53.5	48.9

parency is actually greater than water depth but Secchi Disc can only work above the bottom. For that matter, correction of the datum was made by comparing the transparencies synchronously measured from deeper but homogeneous habitats.

3.2. The key factor

Table 2 shows the linear correlation coefficients (*r*) computed from absolute data in Table 1.

From Table 2, it is easy to recognize that the most prominent correlation occurs between Z_{SD}/Z_M and B_{Mac} ($r^2 = 0.50$), so that statistically the key factor for macrophyte growth should be Z_{SD}/Z_M. Biologically, it demonstrates that plant growth depends greatly upon light intensity and depth, or, in other words, cleaner and shallower aquatic habitats have greater carrying capacity for submersed vegetation. This result is in agreement with that of Liang et al. (1995). Similar results were also obtained by Håkanson and Boulion (2002), and Squires et al. (2002) from several North Temperate and Arctic lakes. Besides the above-mentioned factors, some authors (Duarte and Kalff, 1986; Duarte et al., 1986) were of the opinion that the change of littoral slope and annual precipitation might successfully explain the variation of submersed macrophyte biomass. It is, however, not the case in Yangtze lakes, mostly because our lakes are shallow and the annual precipitation around lake area is almost the same (1200–1600 mm, according to Changchun Institute of Geography, 1998).

A significant correlation also exists between pH and B_{Mac}, but it is considered to be a result mainly due to plant metabolism.

Stepwise multiple regression analyses were made for both absolute and transformed (according to Håkanson and Lindström, 1997) data. The r^2 reaches maximum when absolute B_{Mac} is selected as *y*-variable and, when *F*-value to enter is set as 4, only Z_{SD}/Z_M works well ($F = 17.95$, $r^2 = 0.50$). It further indicates that Z_{SD}/Z_M is the key factor affecting plant growth. As a driving variable for predictive modelling, it has several advantages: (1) high correlation to B_{Mac} in these areas; (2) lower variability than many other factors (Table 1); (3) easy operation and relatively high precision; (4) involving information of other factors, as indicated by the correlation coefficients in Table 2.

Table 2
Simple correlations (*r*) in non-transformed parameters

	B_{Mac}	Z_M	Z_{SD}	Z_{SD}/Z_M	T	Cond	pH	NH_3-N	TN	TP	Chl *a*
B_{Mac}	1.00	−0.31	0.25	**0.71**	−0.06	0.24	**0.62**	−0.17	−0.27	−0.30	−0.30
Z_M		1.00	**0.70**	0.08	**0.84**	−0.42	0.02	−0.20	**0.69**	**−0.52**	−0.11
Z_{SD}			1.00	**0.64**	**0.77**	−0.09	**0.54**	**−0.62**	0.41	**−0.84**	**−0.55**
Z_{SD}/Z_M				1.00	0.20	0.32	**0.75**	**−0.60**	−0.19	**−0.59**	**−0.66**
T					1.00	**−0.47**	0.14	−0.31	**0.69**	**−0.54**	−0.28
Cond						1.00	0.04	−0.15	−0.36	0.00	−0.24
pH							1.00	−0.19	−0.22	**−0.53**	**−0.47**
NH_3-N								1.00	0.08	**0.66**	**0.55**
TN									1.00	−0.16	0.15
TP										1.00	**0.48**
Chl *a*											1.00

Significant correlation ($p < 0.05$) in bold letters.

Table 3
Simple correlations and probability levels between yearly B_{Mac} and monthly Z_{SD}/Z_M

		Z_{SD}/Z_M												
		December	March	April	May	June	July	August	September	October	November	December	January	March
B_{Mac}	*r*	**0.67**	**0.76**	**0.60**	**0.63**	**0.68**	**0.45**	**0.57**	0.28	**0.77**	**0.69**	0.30	0.41	0.37
	n	20	17	20	20	20	20	19	20	16	20	20	20	20
	p	0.001	<0.001	0.005	0.003	0.001	0.048	0.011	0.23	<0.001	0.001	0.203	0.076	0.108

Significant correlation ($p < 0.05$) in bold letters.

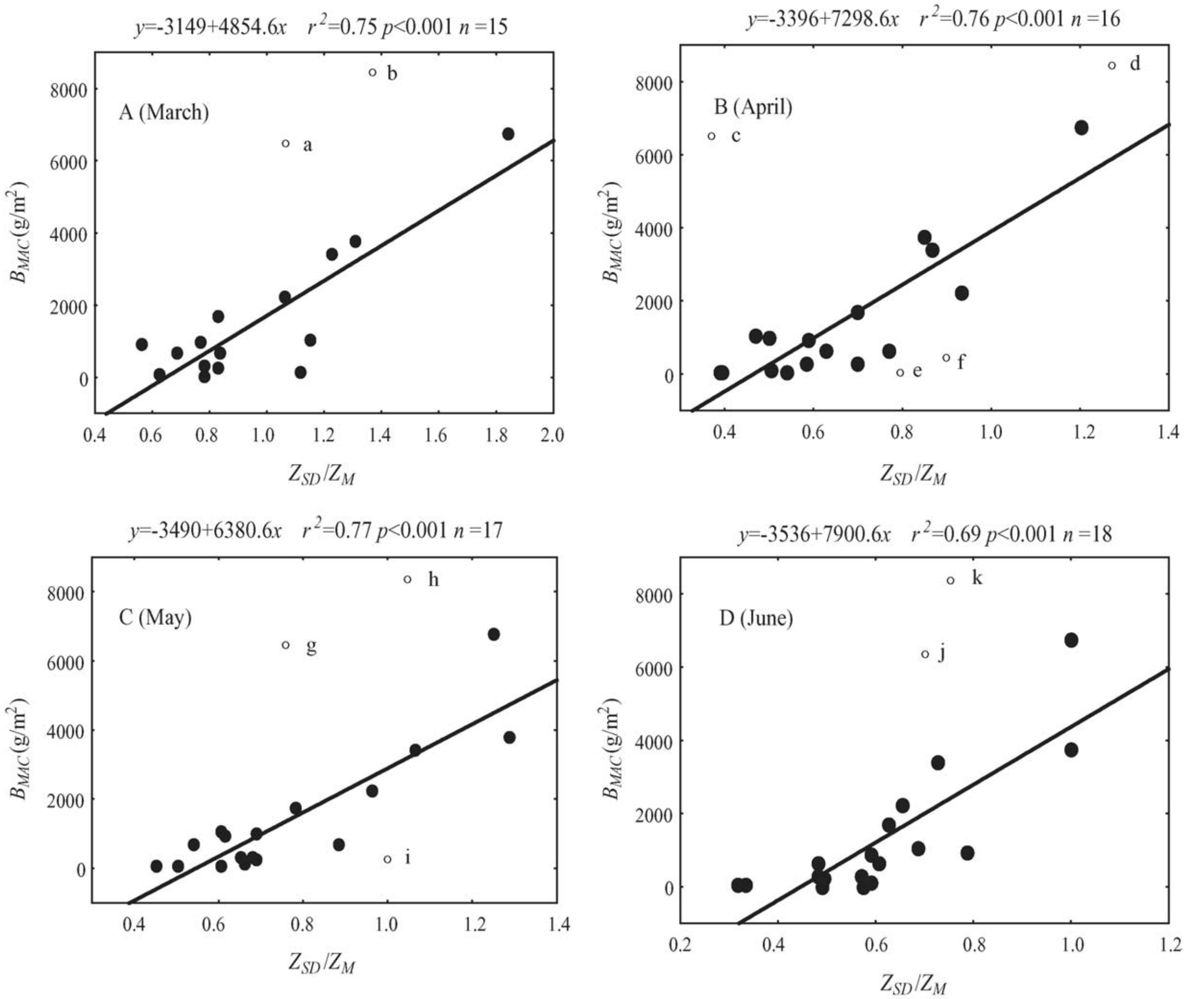

Fig. 2. Relationships between annual mean B_{Mac} and $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ during the critical period after deleting 11 dots (open circles): (A) March, (B) April, (C) May, (D) June.

3.3. Key-time and key-time models

Correlations between annual mean B_{Mac} and monthly $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ are shown in Table 3. Significant correlations occur in most months.

Under natural condition, B_{Mac} changes seasonally like a sigmoid curve. It increases conspicuously in July, reaches maximum around August, then maintains relatively stable until next February or March. During its maximum period, the large vegetation may greatly influence water clarity and so submersed intensity. In that case, the key effective factor is rather B_{Mac} per se than $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$, although their correlations may still be significant. Hence, using $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ obtained after July for prediction purpose seems to have deviated from our original intension. Moreover, the great amount of work in an annual study should also be considered indeed.

No matter what it is, it would be more reasonable to confine our attention to the important or critical period in a year. According to previous studies (Sun, 1992; Chen, 2000) and our observations, we define the months from March to June as the critical period or, as used here, the key-time, for it is the actively growing season of macrophytes on the one hand, and the most critical period also for $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ due to the increasing temperature and precipitation on the other.

Fig. 2A–D gives the regressions between annual mean B_{Mac} and $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ in March–June. Outlier tests were made according to Håkanson and Peters (1995). Eleven dots (open circles) in Fig. 2 should be deleted by following reasons: (1) a, c, g and j, low transparency caused by paper mill effluence; (2) b, d, h and k, too shallow to measure Z_{SD} correctly; (3) f and i, dense fishing nets obstructing waves and temporarily increasing Z_{SD}; (4) e, *P. crispus* abruptly withered.

After deleting those abnormal data, four key-time models are generated:

$$\text{March}: \ B_{\mathrm{Mac}} = -3149 + 4854.6\frac{Z_{\mathrm{SD}}}{Z_{\mathrm{M}}}, \quad r^2 = 0.75, \quad p < 0.001, \quad n = 15 \tag{2}$$

$$\text{April}: \ B_{\mathrm{Mac}} = -3396 + 7298.6\frac{Z_{\mathrm{SD}}}{Z_{\mathrm{M}}}, \quad r^2 = 0.76, \quad p < 0.001, \quad n = 16 \tag{3}$$

$$\text{May}: \ B_{\mathrm{Mac}} = -3490 + 6380.6\frac{Z_{\mathrm{SD}}}{Z_{\mathrm{M}}}, \quad r^2 = 0.77, \quad p < 0.001, \quad n = 17 \tag{4}$$

$$\text{June}: \ B_{\mathrm{Mac}} = -3536 + 7900.6\frac{Z_{\mathrm{SD}}}{Z_{\mathrm{M}}}, \quad r^2 = 0.69, \quad p < 0.001, \quad n = 18 \tag{5}$$

where B_{Mac} (ww, g/m^2) is annual mean biomass of submersed macrophytes; $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ is monthly value in the four months.

Due to the fact that the data in each single month are not stable enough. A comprehensive key-time model based on mean data during the four months is further generated (Fig. 3):

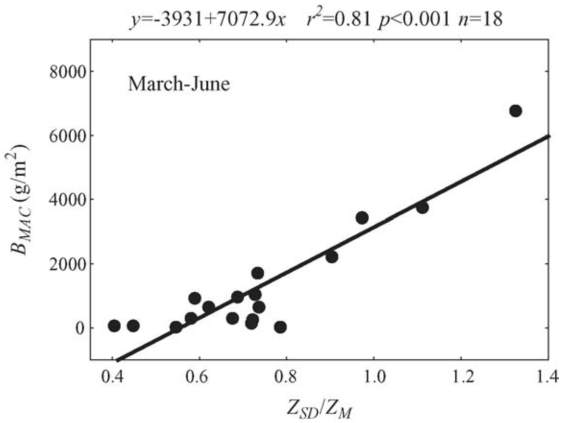

Fig. 3. Relationship between annual mean B_{Mac} and mean $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ of March, April, May and June.

$$B_{\mathrm{Mac}} = -3931 + 7072.9\frac{Z_{\mathrm{SD}}}{Z_{\mathrm{M}}}, \quad r^2 = 0.81, \quad p < 0.001, \quad n = 18 \tag{6}$$

Here, B_{Mac} (ww, g/m^2) is annual mean biomass of submersed macrophytes; $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ is the means for March–June (dots deleted as Fig. 2, not shown in Fig. 3).

3.4. Comparisons of predictive power between key-time and synchronic models

To compare predictive power between key-time and synchronic models, a new synchronic model by using our annual means is generated as follows:

$$B_{\mathrm{Mac}} = -3690 + 6915.1\frac{Z_{\mathrm{SD}}}{Z_{\mathrm{M}}}, \quad r^2 = 0.67, \quad p < 0.001, \quad n = 18 \tag{7}$$

Here, $Z_{\mathrm{SD}}/Z_{\mathrm{M}}$ is annual means.

Table 4
r^2, p and n values corresponding to Eqs. (1)–(7)

Models	Synchronic	Synchronic	Key-time				
Data	Site-specific	Region-specific	Region-specific				
Eq.	(1)	(7)	(2)	(3)	(4)	(5)	(6)
r^2	0.18	0.67	0.75	0.76	0.77	0.69	0.81
p	0.004	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
n	*	18	15	16	17	18	18

* Estimated to be 30–40.

Table 5
Thresholds of transparency during growing season

$B_{Mac} = 0$	Eq. (2) (March)	Eq. (3) (April)	Eq. (4) (May)	Eq. (5) (June)	Eq. (6) (March–June)
Z_{SD}/Z_M	0.66	0.47	0.55	0.45	0.56
Z_M (m)	2.0	2.5	3.0	3.0	2.5
Z_{SD} (m)	1.3	1.2	1.7	1.4	1.4

Table 4 shows the values of r^2, p and n corresponding to Eqs. (1)–(7).

As indicated by the r^2-value in Table 4, the predictive powers of various models are ranked as: key-time models > synchronic model with region-specific data ≫ synchronic model with site-specific data. Obviously, the key-time models with region-specific data are the most effective models we have obtained so far. The lower predictive power of synchronic models is regarded as a result of time-lag effects of environmental factors.

No previously published paper has dealt with the use of key-time element for modelling of submersed vegetation. As an attempt with originality, our key-time models have following advantages: (1) they are based on a solid and reliable data-set. All the year-round macrophytic and environmental data were measured in situ by ourselves. They differed from many other models that only analyzed the month with maximum macrophyte biomass or used a lot of data from different sources with high uncertainties and low time-compatibility (Duarte et al., 1986; Håkanson and Boulion, 2002); (2) they enable us to predict vegetation growing tendency before plant biomass reaching maximum and stability; (3) practically, they are more accurate and easier to be operated in comparison with some other models, because they have higher predictive power and only two operated x-variables are needed.

For actual application of the models, one may use any monthly Z_{SD}/Z_M data in March–June to predict yearly mean macrophyte biomass (models (2)–(5)) or, better, use mean Z_{SD}/Z_M data of four months for (model (6)) that purpose.

3.5. *Thresholds of transparency and limitations in application*

Thresholds of transparency are analyzed in Table 5. Taking Eq. (5) on first line as an example, assume B_{Mac} is 0, and then Z_{SD}/Z_M in June is calculated to be 0.45. The fact that the mean depth of Yangtze lakes in June is generally about 3 m, then the Secchi reading should reach over 1.4 m to enable a normal growth of submersed macrophytes. Therefore, it is necessary to keep a higher transparency for the maintenance or recovery of submersed macrophytes. This is in good agreement with the opinion of Liang et al. (1995).

The models we hitherto obtained are still imperfect. The main concern is Secchi depths. In fact, Secchi Disc is merely a simple tool. Many factors, such as wave action, great reading errors, and even invalidity when light penetrates until bottom, all affect its accuracy. For the determination of transparency, better results may be expected if more advanced method (e.g. with luxmeter) is used. Further, the use of our models is confined to sub-eutrophic and eutrophic lakes. No attempt is made to extend their use to hyper-eutrophic waters where the anaerobic, loose substrate may exert even greater influence on the distribution and abundance of the submersed vegetation (Barko et al., 1986; Scheffer, 1998).

4. Conclusions

In the work, we ascertained that the ratio of Secchi depth to mean depth is the key factor affecting submersed macrophyte growth in shallow lakes. It acts strongly on actively growing plants during key-time from March to June annually. By relating the ratios to annual mean biomass of macrophytes, several corresponding key-time models are generated. Predictive power analyses demonstrate that they are highly effective for predicting possible annual mean biomass of macrophytes. They may benefit the work dealing with the recovery of macrophytes in Yangtze lakes.

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