Science of the Total Environment 450-451 (2013) 169–177

Contents lists available at SciVerse ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Responses of phytoplankton functional groups to the hydrologic regime in the Daning River, a tributary of Three Gorges Reservoir, China

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HIGHLIGHTS

► Effects of hydrologic regime on environmental factors were analyzed.
► Dynamics of phytoplankton functional groups were determined by hydrologic regime.
► Water flow regulated the longitudinal difference of phytoplankton functional groups.

ARTICLE INFO

Article history:
Received 20 August 2012
Received in revised form 30 January 2013
Accepted 30 January 2013
Available online 6 March 2013

Keywords:
Functional groups
Hydrologic regime
Mixing regime
Light availability
Longitudinal difference

ABSTRACT

Daning River is a deep tributary of Three Gorges Reservoir (TGR) in China, with water level fluctuations of 30 m annually. It was assumed that the hydrologic regime would be the main driving force in the self-assembling of the phytoplankton community in the river. In order to test this hypothesis, limnological study was performed monthly in the estuary, midstream and upstream of this tributary from May 2008 to April 2009. We identified 17 phytoplankton functional groups among 63 genera. These phytoplankton functional groups varied significantly, both seasonally and longitudinally. During the flood season (March–September), low water level and high inflows caused a marked increase in the turbidity, especially in the estuary and upstream, allowing functional group MP (the meroplanktonic diatoms) to dominate the phytoplankton community. Meanwhile, constant water level and high temperature led to the stability and thermal stratification in the midstream. These conditions resulted in a high phytoplankton biomass and the dominance of phytoplankton functional groups Y (*Cryptomonas* spp.) and Lo (motile *Peridiniopsis niei* and *Peridinium*) that were adapted to water stratification. During the dry season (October–February), although the inflows were low and water retention time was long, the thermal stratification was disrupted by the disturbance due to the impoundment of TGR, and the water column was deeply mixed. The phytoplankton biomass reduced and functional groups changed: group Lo declined, and group C (small diatom *Cyclotella meneghiniana*) increased in the estuary and midstream. Group Y replaced group MP to dominate the phytoplankton community in the upstream with the water becoming clear and stagnant. It could be deduced that the dynamics of phytoplankton in the Daning River were mainly influenced by hydrologic regime.

1. Introduction

Scaling of hydro-morphological stress and its relation to the phytoplankton community are current topics in applied aquatic ecology (Cabecinha et al., 2009). Hydrologic regimes may affect phytoplankton biomass and species composition by influencing photosynthetic active radiation (Naselli-Flores and Barone, 2000) and nutrient dynamics in the water column (Costa et al., 2009). Phytoplankton community assembly is also influenced by water stability and water retention time (Federiche Borges et al., 2008; Huszar et al., 2003; Naselli-Flores and Barone, 1997). In reservoirs, hydrodynamic processes play an active role in determining water quality and bio-productivity. They determine the movement of matter (whether suspended or dissolved) and heat, intensity of circulation, speed of contaminating processes, and the self-purification of the reservoirs; hydrodynamic processes ultimately determine the ecosystem function (Dubnyak and Timchenko, 2000).

Following Grime's (1977) seminal work on classification of terrestrial vegetation based on the adaptive strategy, Reynolds (1997) separated phytoplankton into subdivisions (C-invasive, S-acquisitive, R-attuning) according as species adaptive strategies, and thereby defined several phytoplankton functional groups that may dominate or co-dominate in a given environment (Reynolds et al., 2002). The phytoplankton functional groups were identified using morphological and physiological traits rather than common phylogeny. Within the particular groups, species have similar morphologies, environmental sensitivities and tolerances (Reynolds, 2006). The phytoplankton functional group approach has been used to represent seasonal changes (Kruk et al., 2002; Naselli-Flores et al., 2003), responses to eutrophication (Becker et al.,

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0048-9697/$ – see front matter
http://dx.doi.org/10.1016/j.scitotenv.2013.01.101

2008; Huszar et al., 2003), and the effects of non-seasonal physical forcing (Reynolds, 1993, 2006).

The Three Gorges Reservoir (TGR) in China is a semi-fluvial environment with 30 m fluctuation in the water level, which falls between a river and lake on an aquatic ecosystem continuum. The phytoplankton in TGR has been extensively studied, especially the seasonal variation in phytoplankton species (Zeng et al., 2006; Zhou et al., 2011), algal blooms (Wang et al., 2011b; Ye and Cai, 2011), eutrophication (Zheng, 2007; Zhong et al., 2005), and the relationship between biotic and abiotic factors (Bi et al., 2010; Zhang et al., 2010).

The impoundment of TGR transformed the downstream part of tributary into a typical bay, but the upstream still kept the river property, such as the Daning River (Fig. 1) (Zheng, 2007). Studies of this river have focused on eutrophication (Zhong et al., 2005), the seasonal succession of phytoplankton composition and the mechanism of algal bloom formation (Zhang et al., 2010), and the role of nutrient concentrations on phytoplankton succession (Zhou et al., 2007). Phytoplankton structure in the Daning River was studied in these documents, but little information on function groups and its relationship with hydrologic characters could be obtained. Reynolds (1999) considered that there were the same principles that influence phytoplankton composition in reservoirs and lakes, even though these two types of water body are significantly different from each other limnologically and hydrologically. As to the Daning River after TGR's impoundment, the complex hydrological conditions made it different from the typical reservoir and lake; actually, it also differed from the traditional opinion on river. Up to now, there were few documents on the phytoplankton function group in such a complex water body. We assumed that hydrologic regime would be the main driving force acting on biomass and composition of phytoplankton in the Daning River. Therefore, the intention of this contribution is to survey the dynamics of phytoplankton using the functional group approach, and identify how the hydrologic regime structured the functional groups over temporal and spatial scales.

2. Materials and methods

2.1. Study area

Daning River is a tributary of the Three Gorges Reservoir on the Yangtze River in central China (31°04′–31°18′N, 109°40′–109°53′E)

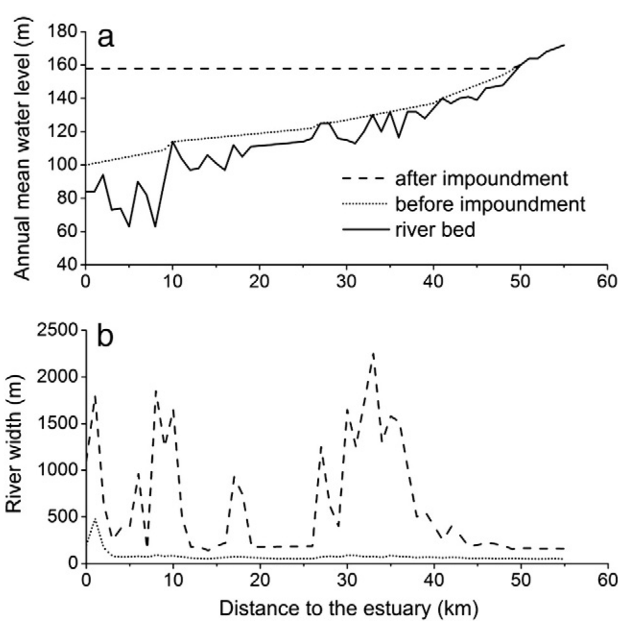

Fig. 1. Longitudinal variation of (a) annual mean water level, and (b) river width before and after the impoundment of TGR.

(Fig. 2). The Daning River is canyon shaped, long and deep (z_{max} = 110 m), and flows from north to south, entering the reservoir 123 km upstream of the Three Gorges Dam; the backwater area is 32 km^2 at 175 m (Table 1). The river is a famous scenic spot, and the source of water supply for many towns along its banks.

In the flood season, hydrologic regulation in the TGR maintained the lowest water level at 145 m, to achieve a flood storage capacity of 22.15 billon m^3. In the early dry season, the water level rose rapidly to 175 m, and this level was maintained until the end of the dry season. Before the next flood season, the water level slowly lowered to 145 m.

This region of China has a humid subtropical climate, with a hot rainy summer. The mean annual temperature was 18.4 °C and the mean annual precipitation was about 1050 mm (Zheng, 2007).

2.2. Sampling and processing

Our study began in 2008, which was the first year of experimental impoundment at 175 m in the TGR. Surface water samples (0.5 m) were taken monthly at nine sampling stations (D1–D9) from May 2008 to November 2008, and then monthly at ten stations (D10 was added) from December 2008 to April 2009. The sampling stations were divided into three regions according to longitude: estuary (D1, near to the Yangtze River), midstream (D2–D7), and upstream (D8–D10, the end of the backwater area).

At each sampling station, six parameters were determined in the field: (i) water temperature (Temp), (ii) dissolved oxygen (DO), (iii) pH, and (iv) conductivity (Cond), all of which were measured with a YSI model Professional Plus multiparameter probe; (v) water transparency, was measured with a Secchi disk; and (vi) turbidity (Turb), measured with a WGZ-B turbidmeter (XinRui, Shanghai). Qualitative plankton samples for identification of algal species were collected from the surface water with a 64-μm pore size net. For quantitative phytoplankton analyses, nutrient analyses, and chlorophyll *a* concentration, surface water (0.5 m) samples were collected with a Van Dorn sampler. Samples for quantitative phytoplankton analyses were fixed with neutral Lugol's solution, and concentrated after 48 h sedimentation (Utermöhl, 1931).

2.3. Sample analysis

Total nitrogen (TN) and total phosphorus (TP) were analyzed using unfiltered water samples, and the dissolved inorganic nutrients such as nitrate ($N–NO_3$), ammonium ($N–NH_4$) and orthophosphate ($P–PO_4$) were analyzed using filtered samples (Whatman GF/C, glass microfiber filters, 0.45 μm). Chlorophyll *a* (Chl *a*) concentration was measured after quantitative concentration with Whatman GF/C filter. The above variables were determined using UV–VIS spectrophotometer (Shimadzu, UV-1601) in accordance with the Standard methods for the examination of water and wastewater (A.P.H.A., 1995).

Phytoplankton was quantified using a light microscope (Olympus BX41) at 400× magnification. The units (cells, colonies, and filaments) were enumerated in random fields, and at least 200 individuals of the most frequent species were counted (Zhang and Huang, 1991), and data from above was used to calculate algal biovolume. Phytoplankton species were identified according to Hu and Wei (2006) and John et al. (2002).

2.4. Calculations

The euphotic zone (Zeu) was calculated as 2.7 times the Secchi depth (Cole, 1994). The mixing zone (Zmix) was estimated from the water temperature, and the ratio between the euphotic zone and mixing zone (Zeu/Zmix) was used as a measure of light availability (Jensen et al., 1994). The dimensionless parameter of relative water column stability (RWCS) was calculated according to Padisák et al. (2003) using the following formula: $RWCS = (D_b - D_s)/(D_4 - D_5)$, where D_b was the density of the bottom waters, D_s was the density of the surface

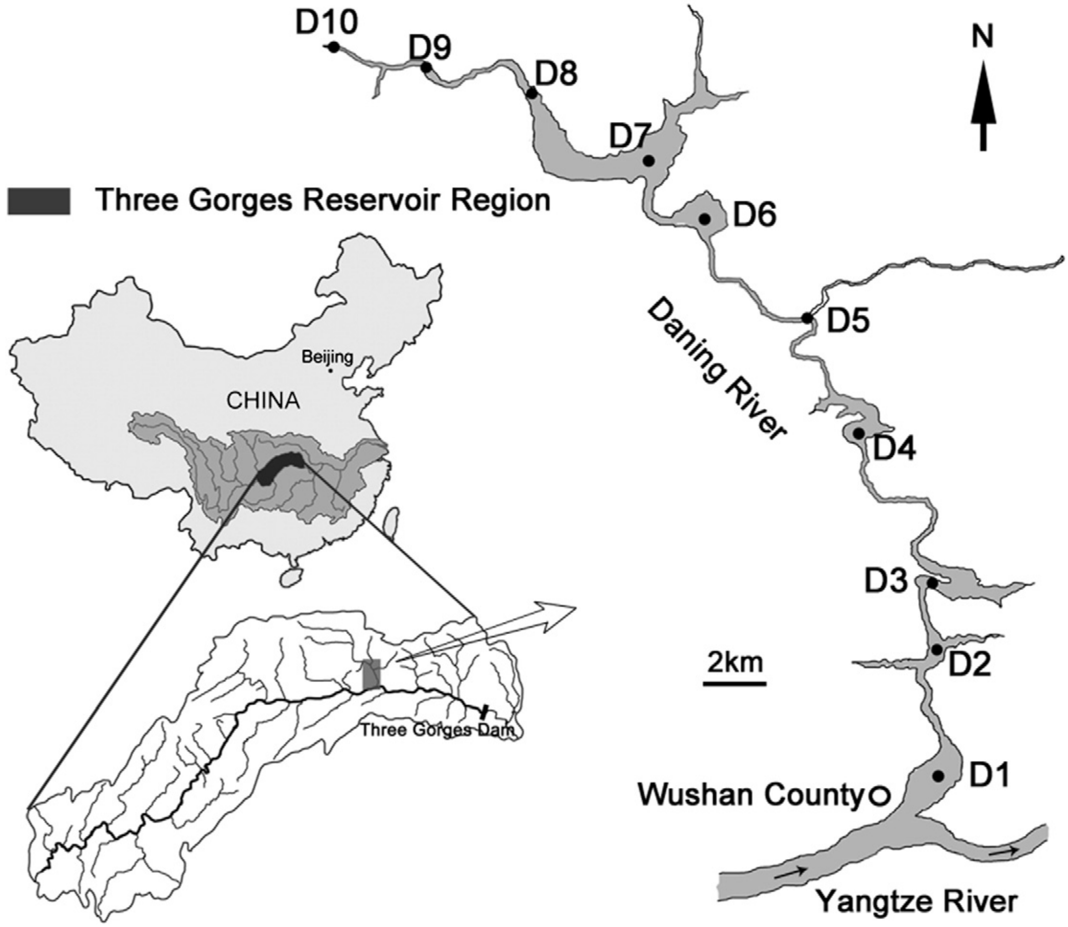

Fig. 2. Maps showing the location of the Three Gorges Reservoir Region, and the sampling sites in the Daning River.

water, and D_4 and D_5 were the densities of pure water at 4 °C and 5 °C, respectively. In the present study, the depth of 15 m was considered as "bottom" because data from deeper strata were not measured, and the depth of 0.5 m was considered as "surface".

Algal biovolume was estimated using formulae for geometric shapes (Hillebrand et al., 1999), and assuming the fresh weight unit as expressed in mass, where 1 mm^3 L^{-1} = 1 mg L^{-1} (Wetzel and Likens, 2000). Species contributing more than 5% to the total biomass were classified into functional groups, using the criteria of Reynolds et al. (2002) and Padisák et al. (2009).

2.5. Statistical analysis

Statistical analysis was carried out using the SPSS 13.0 package. Variance analysis (one-way ANOVA) was employed for comparing means. Non-parametric correlation (Spearman) analyses were used to determine relationships among the biomass of dominant functional groups and the environmental factors. Ordination analysis was performed using CANOCO version 4.5 (Lepš and Šmilauer, 2003) with the abiotic and biological data which were transformed by log(x + 1). Detrended correspondence analysis (DCA) of the species and environmental data was used to determine whether linear or unimodal ordination methods should be applied. Canonical correspondence analysis (CCA) was performed to get an approximate ordering of the phytoplankton functional groups' optima for environmental variables. The biplot scaling type was used with its focus on inter-species distances. The significance of canonical axes and environmental variables to explain the variance of the community was tested using Monte Carlo simulations with 499 permutations.

Table 1
Hydrologic variables at three different water levels in the Daning River (Zheng, 2007).

	Water level (m)		
	145	155	175
Length of backwater area (m)	47,000	49,000	60,000
Mean width (m)	475	495	530
Mean depth (m)	23.0	26.0	36.0
Mean flow (m^3 s^{-1})	113.9	87.6	26.0
Mean velocity (m s^{-1})	0.010	0.007	0.0014
Water retention time (days)	52.1	83.3	488

3. Results

3.1. Hydrodynamics

In 2008, the water level (WL) of the Daning River ranged from 144.69 m to 172.77 m, with higher flow in the flood season than in the dry season (Fig. 3a). At station D4, the relative stability of the water column (RWCS) in the upper (15 m) was strongly associated with the hydrologic regime, reached its maximum of 166 in July 2008, and approximately zero from October 2008 to February 2009 (Fig. 3b). According to variation of the RWCS, mixing regime could be identified: stratification (May–September 2008, March–April 2009) and mixing (October 2008–February 2009).

3.2. Physical and chemical characteristics

The physical and chemical characteristics of the Daning River showed significant spatial differences (estuary, midstream and upstream) and temporal differences (flood season and dry season) (Fig. 4a–h).

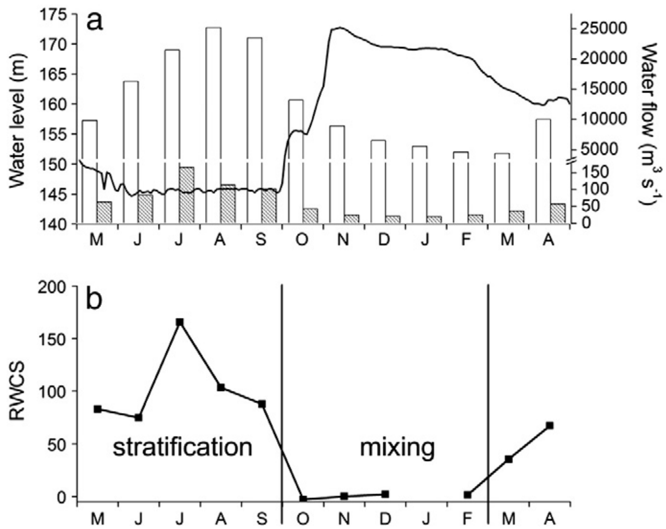

Fig. 3. Seasonal variation in (a) water level in the Daning River (solid line), water flow of the Yangtze River (white bars) and water inflow of the Daning River (gray bars), and (b) relative water column stability (RWCS) in the Daning River.

Although water temperature was significantly lower in the upstream than in the midstream and estuary during the flood season ($p<0.05$), there were no significant spatial differences during the dry season ($p>0.05$) (Fig. 4a). Water temperature was at its highest in August and lowest in February.

Euphotic zone (Zeu) and light availability (Zeu/Zmix) were higher, and turbidity (Turb) was lower, in the midstream than in upstream and estuary during the flood season ($p<0.05$); there were no significant spatial differences during the dry season ($p>0.05$) (Fig. 4b, d, and c respectively).

The annual mean of total phosphorus (TP) was higher in the estuary than in the midstream and upstream ($p<0.05$) (Fig. 4e). There were significant seasonal variations in TP levels only in the estuary, where they were higher during the flood season than in the dry season ($p<0.05$). Dissolved orthophosphate (P–PO_4) was significantly higher in the estuary than in the midstream and upstream during the flood season ($p<0.05$); there were no significant differences among the three sampling regions after the impoundment of the reservoir during the dry season ($p>0.05$) (Fig. 4g). Total nitrogen (TN) and dissolved nitrate (N–NO_3) showed similar changes along the length of the river, with highest concentrations in the estuary and lowest concentrations upstream ($p<0.05$); there were no significant seasonal variations ($p>0.05$) (Fig. 4f and h).

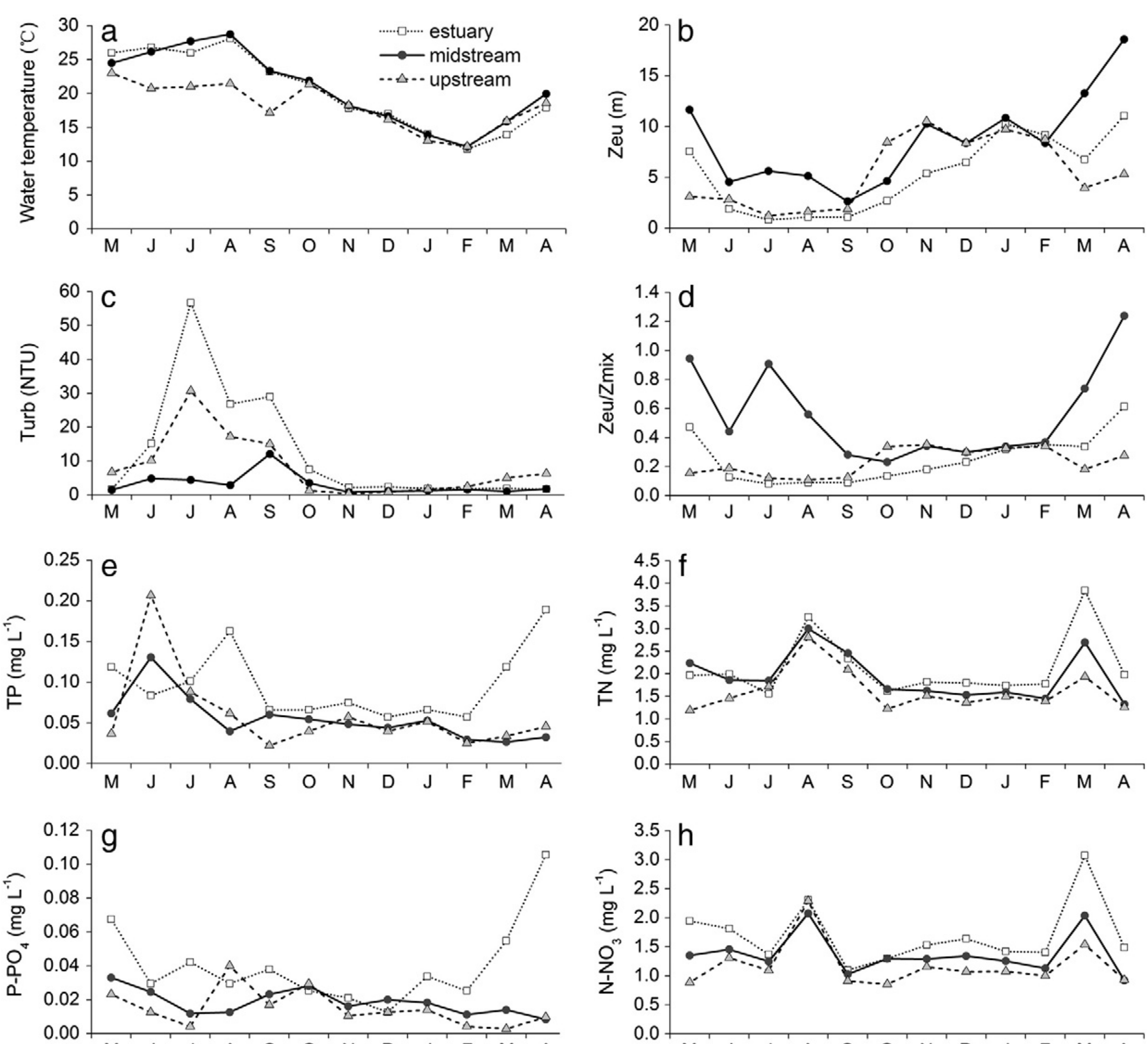

Fig. 4. Seasonal variation of 8 environmental parameters in the estuary, midstream and upstream regions of the Daning River: (a) water temperature, (b) euphotic zone (Zeu), (c) turbidity, (d) light availability (Zeu/Zmix), (e) TP, (f) TN, (g) P–PO4 and (h) N–NO3.

The Spearman correlations among environmental variables and hydrologic variables in estuary, midstream and upstream were presented in Table 2. Water temperature (Temp) was negatively correlated with water level (WL) and positively correlated with water flow in all sampling regions. Relative stability of the water column (RWCS) was negatively correlated with WL too in all sampling regions and positively correlated with water flow in the midstream. Euphotic zone (Zeu) and light availability (Zeu/Zmix) were markedly affected by the flow of the Yangtze River mainstream (Flow-Y) and by the inflow of the Daning River (Flow-D) in the estuary and in the upstream, respectively. Turbidity (Turb) in the midstream and upstream was negatively correlated with WL and positively correlated with water flow.

3.3. Phytoplankton dynamics

We identified 63 algal genera from seven major taxonomic categories, and 17 functional groups were classified including the 32 descriptor taxa (Table 3). The phytoplankton biomass in the upstream reach remained low throughout the year, whereas phytoplankton biomass in both midstream and estuary peaked in June and August (Fig. 5). Furthermore, the phytoplankton biomass in the upstream was lower during the flood season and higher during the dry season, than the biomass in the midstream and estuary (Fig. 5).

There were marked seasonal variations in representation of each of the 11 main functional groups of phytoplankton (>10% of the total biomass) (Fig. 6). The Y, MP, L_O and C functional groups were the main contributors to the biomass in the Daning River, mainly represented by large *Cryptomonas* spp., the meroplanktonic diatoms, the dinoflagellate *Peridiniosis niei*, and the small diatom *Cyclotella meneghiniana*, respectively. Groups B (*Cyclotella* sp. and *Aulacoseira* spp.) and D (*Synedra* spp.) were important contributors to biomass in flood season.

In the estuary, the phytoplankton community during the flood season was dominated by Y, MP, L_O and C; in August biomass peaked and was dominated by group D (60.2%), and during the dry season the community was dominated by group C (mean 44.5%). In the midstream, the flood season was dominated by functional groups Y and Lo, and during the dry season biomass of group L_O decreased while groups C and MP increased. In the upstream, the phytoplankton community during the flood season was dominated by the MP group when the water level was low, at the beginning of the dry season, group L_O was very dominant (95.6%), and then during the dry season, group Y dominated in the upstream with the water bodies becoming clear and stagnant.

The Spearman correlations among chlorophyll *a* concentration (Chl.*a*) of phytoplankton and 11 environmental variables in estuary, midstream and upstream of the Daning River were presented in Table 4. Chl.*a* concentration in the estuary was negatively correlated with WL and positively correlated with water temperature. In the midstream, Chl.*a* concentration was negatively correlated with WL and Zeu, and positively correlated with RWCS, water temperature, Turb, DO, pH and TP. In the upstream, Chl.*a* concentration was negatively correlated with RWCS and Turb, and positively correlated with WL, Zeu/Zmix, Zeu, DO, pH and $N–NO_3$.

The biomass of main functional groups were significantly correlated ($p<0.01$) with most of the environmental factors, such as WL, RWCS, Zeu/Zmix, Temp, Zeu, DO and nutrients (Table 5). The biomass of groups Y and L_O, were negatively correlated with WL and positively correlated with RWCS, and temperature. In contrast, the biomass of groups MP and D were positively correlated with turbidity and negatively correlated with Zeu/Zmix and Zeu.

3.4. Canonical correspondence analysis

Canonical correspondence analysis (CCA) was performed to reveal the relationships between environmental variables and phytoplankton functional groups, and between environmental variables and sample time and location. Automatic forward selection was used for the best

Table 3
Main phytoplankton functional groups and representative species with their taxonomic groups, from the Daning River.

Functional group	Representative species	Taxonomic group
Y	*Cryptomonas* spp.	Cryptophyceae
MP	*Nitzschia* spp.	Bacillariophyceae
MP	*Cymatoplcura* sp.	Bacillariophyceae
MP	*Stauroneis* spp.	Bacillariophyceae
MP	*Cymbella* spp.	Bacillariophyceae
MP	*Gomphonema* spp.	Bacillariophyceae
MP	*Navicula* spp.	Bacillariophyceae
L_O	*Peridiniosis niei*	Dinophyceae
L_O	*Peridinium* sp.	Dinophyceae
L_O	*Ceratium hirundinella*	Dinophyceae
B	*Cyclotella* sp.	Bacillariophyceae
B	*Aulacoseira* spp.	Bacillariophyceae
C	*Cyclotella meneghiniana*	Bacillariophyceae
C	*Asterionella formosa*	Bacillariophyceae
D	*Synedra* spp.	Bacillariophyceae
*X*2	*Chroomonas* sp.	Cryptophyceae
*X*2	*Chlamydomonas* spp.	Chlorophyceae
J	*Pediastrum* spp.	Chlorophyceae
J	*Scenedesmus* spp.	Chlorophyceae
P	*Fragilaria* sp.	Bacillariophyceae
P	*Aulacoseira granulata*	Bacillariophyceae
E	*Mallomonas* sp.	Chrysophyceae
E	*Dinobryon* sp.	Chrysophyceae
G	*Eudorina* sp.	Chlorophyceae
G	*Pandorina* sp.	Chlorophyceae
F	*Oocystis* spp.	Chlorophyceae
F	*Kirchneriella* sp.	Chlorophyceae
H1	*Anabaena flos-aquae*	Cyanophyceae
M	*Microcystis* spp.	Cyanophyceae
N	*Cosmarium* spp.	Zygnemaphyceae
S1	*Pseudanabaena* sp.	Cyanophyceae
W1	*Euglena* sp.	Euglenophyceae

Table 2
Significant Spearman correlations between 3 hydrologic variables (WL, water level; Flow-Y, flow of Yangtze River; and Flow-D, inflow of Daning River) and 7 environmental variables in the estuary, midstream and upstream regions of the Daning River.

Environmental variable	Estuary (n = 12)		Midstream (n = 72)			Upstream (n = 29)	
	WL	Flow-Y	WL	Flow-Y	Flow-D	WL	Flow-D
Temp	−0.75**	0.90***	−0.76***	0.89***	0.89***	−0.56**	0.73***
RWCS	−0.82**		−0.80***	0.62***	0.84***	−0.63***	
Zeu		−0.75**	0.45***	−0.61***	−0.46***	0.76***	−0.77***
Turb			−0.55***	0.52***	0.50***	−0.84***	0.79***
Zeu/Zmix		−0.72**			0.34***	0.59***	−0.58***
TN			−0.41***		0.43***		
TP				0.33**			

** $p<0.01$.
*** $p<0.001$.

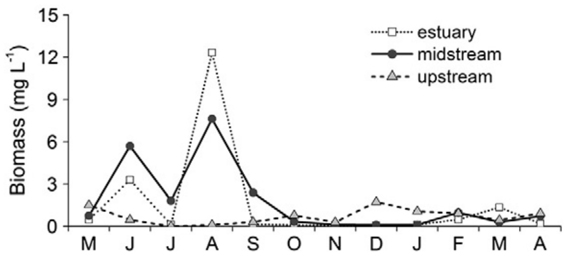

Fig. 5. Seasonal variation of phytoplankton biomass in the estuary, midstream and upstream regions of the Daning River.

9 environmental variables. The ordination diagrams of environmental variables and phytoplankton functional groups, and environmental variables and samples (time and location) for axis 1 and axis 2 were shown in Fig. 7a and b respectively. The Monte Carlo test revealed that the first canonical axis and all canonical axes were significant (F = 13.75, P = 0.002; F = 3.94, P = 0.002; 499 random permutation).

For environmental variables and phytoplankton functional groups, all canonical axes cumulatively explained 84.3% of the variance in species–environment relationships, and the first two canonical axes accounted for 42.7% and 21.9% of the variance separately (Fig. 7a). The forward selection of environmental variables selected four significant variables, Temp (F = 12.23, p = 0.002), Zeu/Zmix (F = 7.04, p = 0.002), DO (F = 3.81, p = 0.002) and WL (F = 3.47, p = 0.002), which together accounted for 74.7% of the total variance. The first CCA species axis was positively correlated with WL (0.59) and negatively correlated with Temp (−0.71), RWCS (−0.57) and Zeu/Zmix (−0.46).

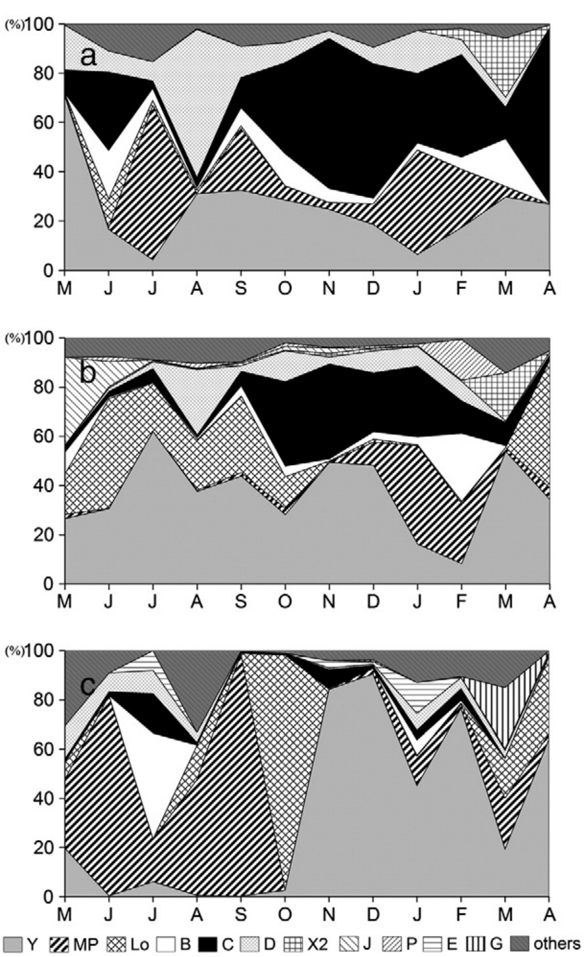

Fig. 6. Seasonal variation in relative biomass (%) of the 12 main phytoplankton functional groups in (a) estuary, (b) midstream and (c) upstream regions of the Daning River.

Table 4
Significant Spearman correlations between phytoplankton chlorophyll *a* concentration (Chl.*a*) and 11 environmental variables in the estuary, midstream and upstream regions of the Daning River.

Environmental variable	Chl.*a*		
	Estuary (n = 12)	Midstream (n = 72)	Upstream (n = 29)
WL	−0.68*	−0.79***	0.59***
RWCS		0.65***	−0.44*
Zeu/Zmix			0.57**
Temp	0.60*	0.73***	
Turb		0.55***	−0.57**
Zeu		−0.58***	0.63***
DO		0.34**	0.45*
pH		0.38***	0.42*
TN			
TP		0.32**	
$N\text{-}NO_3$			−0.51**

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

The second CCA species axis was mainly positively correlated with Turb (0.30) and negatively correlated with Zeu (−0.47), Zeu/Zmix (−0.42) and DO (−0.37).

For the relationship between environmental variables and sampling units, all the samples were primarily ordered by the hydrologic regime (Fig. 7b) and divided into four periods: early flood season (March–April), mid flood season (May–September), early dry season (October–November), and mid dry season (December–February). During the early flood season, high euphotic zone and high light availability were characteristic of the samples when the water level lowered gradually. During the mid flood season, the samples of the estuary and midstream were warm and stratified, while the samples of the upstream were separated since low Zeu/Zmix and RWCS. In contrast, during the early dry season, stratification was broken, and light availability declined markedly with the disturbance of impoundment. During the mid dry seasons, there was thorough mixing in the water column, decreasing temperature, and a high water level.

4. Discussion

The structure of phytoplankton communities is mainly determined by resource availability, especially that of nutrients and light (Reynolds, 2006). In general, long period of stratification could trap nutrients in the hypolimnion, preventing the internal circulation of nutrients. In turn, nutrient availability would decrease and limit the growth of phytoplankton in the euphotic zone (Arfi, 2005; Becker et al., 2010). This phenomenon can happen without any external nutrients entering the euphotic zone. The situation in the Daning River differs from the above. After impoundment of TGR, there has been an increase in water level and water depth in the Daning River, and a long period of stratification. About 80% of the annual precipitation in the Daning River valley falls during the stratification period, bringing external nutrients from the terrestrial ecosystem into the tributary via the surface runoff (Zheng, 2007), increasing nutrient concentration and increasing nutrient availability in the surface water during the stratification period. The dissolved nutrient concentrations in the Daning River ($P\text{–}PO_4$: 0.020 ± 0.015 mg L^{-1}, $N\text{–}NO_3$: 1.4 ± 0.42 mg L^{-1}, $N\text{–}NH_4$: 0.17 ± 0.10 mg L^{-1}) were markedly higher than the threshold for half-saturation for most algal species according to Reynolds (1997). The same scenario was also observed in the Liuxihe reservoir in southern China (Xiao et al, 2011). Considering the correlations between environmental variables and phytoplankton biomass, nutrient availability might affect some functional groups such as J group in the flood season. However, regarding the responses of

Table 5
Significant Spearman rank correlation between the biomass of the 11 main phytoplankton functional groups and 11 environmental variables (n = 113).

Environmental variable	Y	MP	L_O	B	C	D	X2	J	E	G
WL	-0.25^{**}		-0.59^{***}					0.39^{***}		0.43^{***}
RWCS	0.38^{***}		0.55^{***}				0.40^{***}	0.30^{**}		0.49^{***}
Zeu/Zmix	0.25^{**}	-0.33^{***}				-0.33^{***}	0.41^{***}			0.33^{***}
Temp	0.35^{***}		0.63^{***}				0.29^{**}	0.54^{***}		0.43^{***}
Turb		0.26^{**}	0.28^{**}			0.47^{***}				
Zeu		-0.25^{**}				-0.39^{***}				
DO	0.43^{***}		0.28^{**}				0.31^{***}		0.26^{**}	0.25^{**}
pH			0.28^{**}	0.43^{***}	0.27^{**}	0.29^{**}				
TN					0.26^{**}		0.29^{**}	0.29^{**}		0.32^{***}
TP								0.30^{**}		
$N–NO_3$								0.26^{**}		

** $p<0.01$.
*** $p<0.001$).

functional groups, mixing regime and light availability would be more effective than nutrient availability in the Daning River.

Naselli-Flores (2000) showed that in the man-made lakes of Sicily, which were characterized by conspicuous water level fluctuations, the variability in the abundance and composition of phytoplankton may be strongly influenced by the peculiar hydrologic regimes. We demonstrated that the same phenomenon also applies in the Daning River, which has a peculiar hydrologic regime, as shown in Table 1 and Fig. 3, and samples were ordered by the hydrologic regime (CCA results were shown in Fig. 7b). The hydrologic regime in the Daning River significantly affected the mixing regime and light availability, and consequently determined the dynamics of phytoplankton functional groups.

There was an obvious alternation of the stratification (May–September) and mixing (October–February) periods in the Daning River, which was regulated by the fluctuation of water level, variation of water temperature, and change of water inflow. The thermal stratification refers to a change in the water temperature at different depths, and is due to the change in water's density with temperature (Straškraba and Tundisi, 1999). The mixing regime was the main factor determining the temporal dynamics of the phytoplankton functional groups in the Daning River. The CCA result (Fig. 7a) indicated that the main phytoplankton functional groups were regulated by water temperature, RWCS, light availability and the fluctuation of water level, which correlated with axis 1 along the mixing regime.

During the flood season in the Daning River, when the water level was stable, the relative stability of the water column increased, and thermal stratification developed as the water warmed up to 15 °C. Although the inflows in the flood season were relatively higher than in the dry season, the velocity was still very low (0.01 m s^{-1}) and retention time exceeded 50 days. The inflows were insufficient to disturb the development of thermal stratification in the tributary. The stratification and high water temperature led to a high biomass in the epilimnion in the Daning River. The biomass of phytoplankton functional groups Y and Lo increased, especially in the midstream of the river. The Spearman correlation analysis (Table 5) showed that the biomass of these two groups was significantly correlated with WL, RWCS and Temp. Group Y was the most important functional group in the Daning River. The group, characterized by *Cryptomonas* spp., dominated in the midstream and estuary throughout the year. This group is well adapted to live in almost all lentic ecosystems when grazing pressure is low (Padisák et al., 2009; Reynolds et al., 2002). The relatively high surface/volume ratio of cryptomonads facilitates their rapid absorption of nutrients and fast growth (Bovo-Scomparin and Train, 2008). Moreover, the competitiveness of this group is enhanced by the possession of flagella, which allow vertical migration through the water layers to reach optimal light conditions and nutrient concentrations (Bovo-Scomparin and Train, 2008; Jansson et al., 1996). Members of the Lo group, mainly represented by motile *Peridiniopsis niei* and *Peridinium* spp., can obtain nutrients easily from the hypolimnion and grow well in a wide range of nutrient concentration (Liu et al., 2008; Xiao et al., 2011; Yang et al., 2011). Furthermore, high water temperature (20–27 °C) is favorable for reproduction in this genus (Grigorszky et al., 2006).

During the dry season, the water level rose rapidly in the Daning River after the impoundment of TGR. The inflow was low, water retention time was long, and the backwater from the Yangtze River severely disrupted the thermal stratification and there was rapid mixing of water bodies in the Daning River. These conditions led to the decline of group Lo in the midstream, because this group is sensitive to prolonged or deep mixing (Huszar et al., 2003; Reynolds et al., 2002). Meanwhile, groups C and B increased in the midstream and estuary. The CCA biplot diagram (Fig. 7a) showed that groups C and B were well adapted to mixing and low light availability conditions. Although the diatoms of groups B and C have a large volume, their shape contributes to the maintenance of high surface/volume and efficient light harvesting. Population development of groups B and C is often subject to the availability of silicon, and they depend upon turbulence for suspension, thus groups B and C are relatively sensitive to mixed depth and the seasonal onset of near-surface density stratification (Reynolds et al., 2002).

In the Daning River, the longitudinal differences of phytoplankton functional groups were determined by the longitudinal distribution of light availability, which was affected by the hydrologic regime among sampling regions. The same result was also observed in the Xiangxi River, a tributary of TGR (Wang et al., 2011a). In the TGR, water flow was high during the flood season in the mainstream and tributary. As a result, the suspended particulate matter of the mainstream and tributary generated the turbid condition in the estuary and in the upstream in the Daning River, respectively. Species selectivity in the turbid kinetic habitats was likely to favor diatoms, especially those with high surface/volume ratios and which show adaptability to low light, such as species of group MP (Reynolds, 1994). This group, including *Melosira* and pennate diatoms, such as *Navicula*, *Nitzschia* and *Stauroneis*, includes all the meroplanktonic (mostly diatoms) autotrophic organisms which can adapt to frequently mixed, inorganic, turbid habitats (Bovo-Scomparin and Train, 2008; Padisák et al., 2009). We showed that group MP was negatively correlated with Zeu/Zmix and RWCS (Spearman correlation analysis (Table 5), and CCA analysis (Fig. 7a)), showed its tolerance of mixing and low light. In the dry season, water level in the Daning River increased, water flow decreased, and water retention time lengthened. Furthermore, the concentration of suspended particles decreased, and the water column became transparent in the estuary and upstream. The clear and relatively stagnant conditions contributed to the relatively high phytoplankton biomass in the upstream, and the dominance of functional groups Y. In the midstream, throughout the year, the turbidity was almost free from the influence of water level fluctuation.

The degree of horizontal and vertical heterogeneity in a reservoir is decisively influenced by reservoir morphometry, flow and stratification

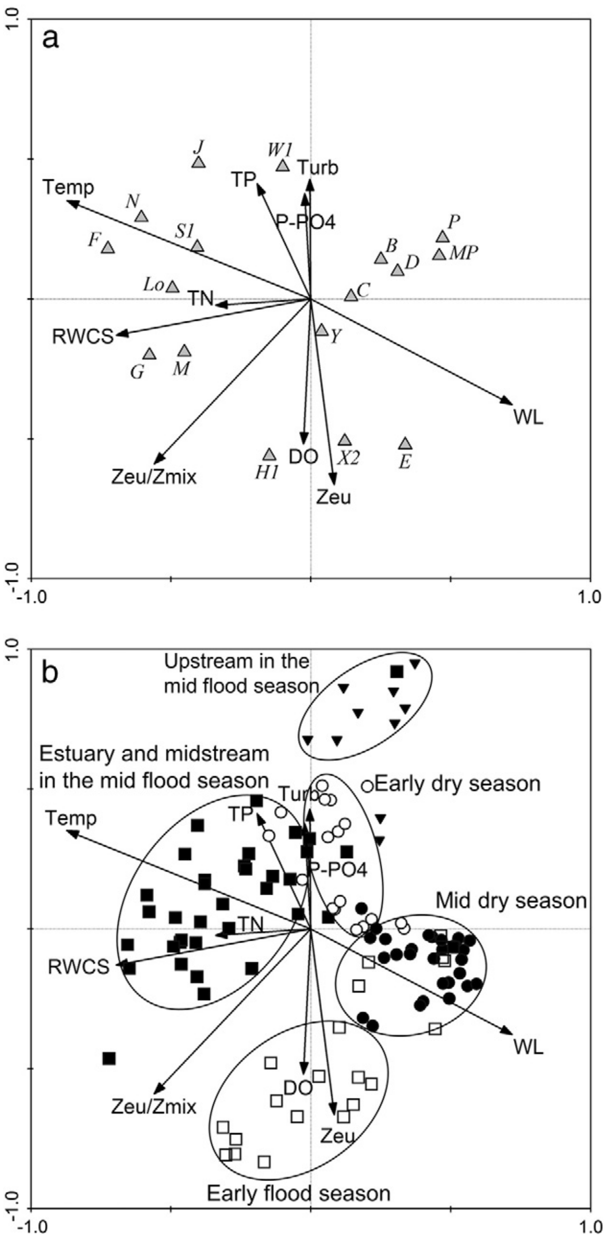

Fig. 7. Biplot diagrams for CCA of the relationship between 10 environmental variables (black lines) and (a) phytoplankton functional groups, and (b) sample time and location. The environmental variables are: DO, dissolved oxygen; P–PO4, orthophosphate; RWCS, relative water column stability; Temp, water temperature; TN, total nitrogen; TP, total phosphorus; Turb, turbidity; WL, water level; Zeu, euphotic zone; Zeu/Zmix, ratio between the euphotic zone and mixing zone. In (a) the functional groups are shown by gray triangles. In (b) the sample times and locations are: □, early flood season; ■ estuary and midstream in the mid flood season; ○ early dry season; ● mid dry season; and ▼ upstream in the mid flood season.

conditions. In a typical reservoir, three major zones can be distinguished: riverine, transitional and lacustrine (Kimmel and Groeger, 1984). Although this zonation theory is applicable to conditions in the mainstream of the TGR, the theory does not apply in the longer tributaries of the TGR such as the Daning River where conditions are rather different. In the Daning River, during the dry season, the riverine zone disappeared and most of the river was lacustrine with a long retention time. During the flood season, while the midstream could be still identified as a lacustrine zone with stratification and high biomass, the upstream region became a riverine zone with turbid kinetic habitats and dominance of group MP. The estuary region was co-impacted by the Daning tributary and the intrusion of mainstream of Yangtze River, which resulted in a flood season characterized by turbidity and high nutrient conditions, leading to a high biomass of phytoplankton and dominance of diatoms.

5. Conclusion

In the Daning River, the variation of water level and water flow played a key role in the stability and turbidity of the water body. The periodic hydrologic regime constrained the mixing regime and light availability in this tributary, and consequently determined the structure of the phytoplankton functional groups. There were marked longitudinal differences of environment and phytoplankton functional groups, consistent with the longitudinal zonation of the Daning River. Furthermore, this study documented the algal sensitivities and tolerances to the hydrologic regime in this deep subtropical reservoir.

Conflict of interest statement

There is no conflict of interest.

Acknowledgments

We are grateful to the associate editor, Prof. Christian E.W. Steinberg, and the anonymous referees for their expert assistance and comments on this manuscript. We are thankful to Boshi Yu, Ying Ai and Qianfu Liu for their assistance with fieldwork. This work was supported by National Natural Science Foundation of China (Grant No. 31123001) and National Basic Research Program of China (Grant No. 2008CB418000).

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.scitotenv.2013.01.101. These data include Google map of the most important areas described in this article.

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