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PRIMARY RESEARCH PAPER

Responses of phytoplankton diversity to physical disturbance under manual operation in a large reservoir, China

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Abstract In aquatic ecosystems, physical disturbances have been suggested to be one of the main factors influencing phytoplankton structure and diversity. To elucidate whether large-scale artificial operation of a hydroelectric reservoir has potential impacts on phytoplankton diversity, the impact on phytoplankton biodiversity of physical disturbances under artificial operation from May 2007 to April 2008 in tributaries of the Three Gorges Reservoir (TGR), China, was analysed. Two disturbance parameters, i.e. the absolute incremental rates of discharge ($R_{d,i}$) and precipitation ($R_{p,i}$), were created in this study for evaluating physical disturbance intensities during low and high water level periods of the TGR. Results showed that river discharge seemed to be the main factor controlling the phytoplankton diversity in low water level periods (≤151 m), and that precipitation was a potential promoter of the physical disturbance. During the 156-m impoundment process, the species diversity clearly decreased due to the high dilution effect on the phytoplankton communities. At high water level periods (>151 m), the low levels of disturbance eventually allowed the phytoplankton community to approach competitive exclusion in late February 2008. Sharply declining diversity values appeared when the Dinophyta blooms occurred in late March and late April 2008 (*Peridinium* and *Ceratium*, respectively).

Keywords Phytoplankton · Physical disturbance · Intermediate disturbance hypothesis · Species diversity

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Introduction

The ecological impact of large hydroelectric dams on aquatic ecosystems has often been studied (Humborg et al., 1997; Kelly, 2001). The operation of hydroelectric power plants perturbs the integrity of natural rivers and significantly changes the hydrological conditions, including water level, river flow, water velocity, and hydraulic retention times (HRT) (Pringle, 2003; Magilligan & Nislow, 2005). As a result of these hydrological changes, the physical, chemical and biotic characteristics of rivers have been altered, and in many cases, the equilibrium state of the aquatic ecosystem has even been destroyed (Bain et al., 1988; Poff & Ward, 1989). Thus, the ecological assessment of aquatic ecosystems is necessary for the construction and operation of hydroelectric power stations. It is known that phytoplankton are sensitive aquatic organisms, and that their community characteristics are driven by physical environmental variations on a short time scale (Jeong et al., 2007; Cabecinha et al., 2009). The structure, distribution and diversity of phytoplankton communities are often used to assess the impact of large-scale dams on aquatic ecosystems (Bertrand et al., 2001; Nhiwatiwa & Marshall, 2007).

In aquatic ecosystems, physical disturbances have been suggested to be one of the main factors influencing phytoplankton structure and diversity. The Connell's intermediate disturbance hypothesis (IDH) is an influential conceptual theory that attempts to explain the effects of disturbances on species diversity (Connell, 1978). This hypothesis states that high local diversity can be maintained under intermediate levels of physical disturbance. Low and high levels of disturbance are expected to be less effective for maintaining high diversity because the former enables competitive exclusion and the latter directly eliminates many species (Kimbro & Grosholz, 2006). The IDH has been tested in natural aquatic ecosystems such as lakes (Padisák, 1993; Weithoff, 2003), river floodplains (Davis et al., 2007; Paidere et al., 2007), rivers (Descy, 1993) and reservoirs (Barbiero et al., 1999; Lopes et al., 2009). However, these ecosystems were mainly regulated by natural hydro-meteorological conditions without anthropogenic disturbance. The Three Gorges hydroelectric plant in China provided an opportunity to analyse the impacts of anthropogenic disturbances on a phytoplankton community on the basis of the IDH.

The drastic changes in hydrodynamic conditions in the Three Gorges Reservoir (TGR) played a critical role in transforming the aquatic ecosystem from a riverine-type to a nearly lentic-type system (Hart et al., 2002; Magilligan & Nislow, 2005). Previous studies have shown that the dramatic changes in hydrodynamic conditions that occurred as a result of the Three Gorges Project (TGP) induced a series of ecological problems, including eutrophication and algal blooms in tributaries of the Yangtze River in the TGR (Meng & Zhao, 2007; Li et al., 2009a). To assess variations in the hydrodynamic conditions following the completion of the TGP, some researchers have investigated the influence of hydrodynamic parameters on the aquatic environment and on phytoplankton community characteristics in the main stream and tributaries. Evidence from such studies showed that there were significant differences in phytoplankton communities in the TGR before and after the 156-m impoundment (Kuang et al., 2005; Hu & Cai, 2006). It was supposed that seasonal variations in phytoplankton communities were affected by physical disturbances caused by the operation strategies of the TGR. However, an analysis of phytoplankton biodiversity in the tributaries as a response to variations in the hydrodynamic conditions has not been reported. Moreover, it is not currently clear how the physical processes in the TGR impact the observed phytoplankton biodiversity and the subsequent occurrence of algal blooms. In response to these problems, this study aims to compare and analyse the phytoplankton diversity within different time periods in the Pengxi River backwater area in the TGR. The specific aims of this site-specific study are as follows:

(1) to identify seasonal variations in the phytoplankton species diversity and the main physical environmental parameters in the Pengxi River during operation of the TGR;
(2) to interpret the potential impact on phytoplankton species diversity of different physical disturbances during the low and high water level periods in the Pengxi River applying the IDH theory.

Materials and methods

Study area

The Three Gorges Dam (TGD) on the Yangtze River in China is one of the world's largest dams, with a height of 185 m and a length of 2,335 m (Wu et al., 2003). The TGR, with a water surface of up to 1,080 km^2 located in the middle of the Yangzte River, was formed after the construction of the dam (Fig. 1). The TGR is located at 29°16′–31°25′N, 106°–111°10′E and has a catchment of the typical gorge type (Zeng et al., 2006). In 2006, the impoundment of the TGR resulted in a water level increase in the Yangtze River from 145 to 156 m, at which point the TGR began performing its multiple functions. According to the operational strategies of the TGR, the water level in the TGR would be permitted to rise during drought seasons for power generation. Conversely, a

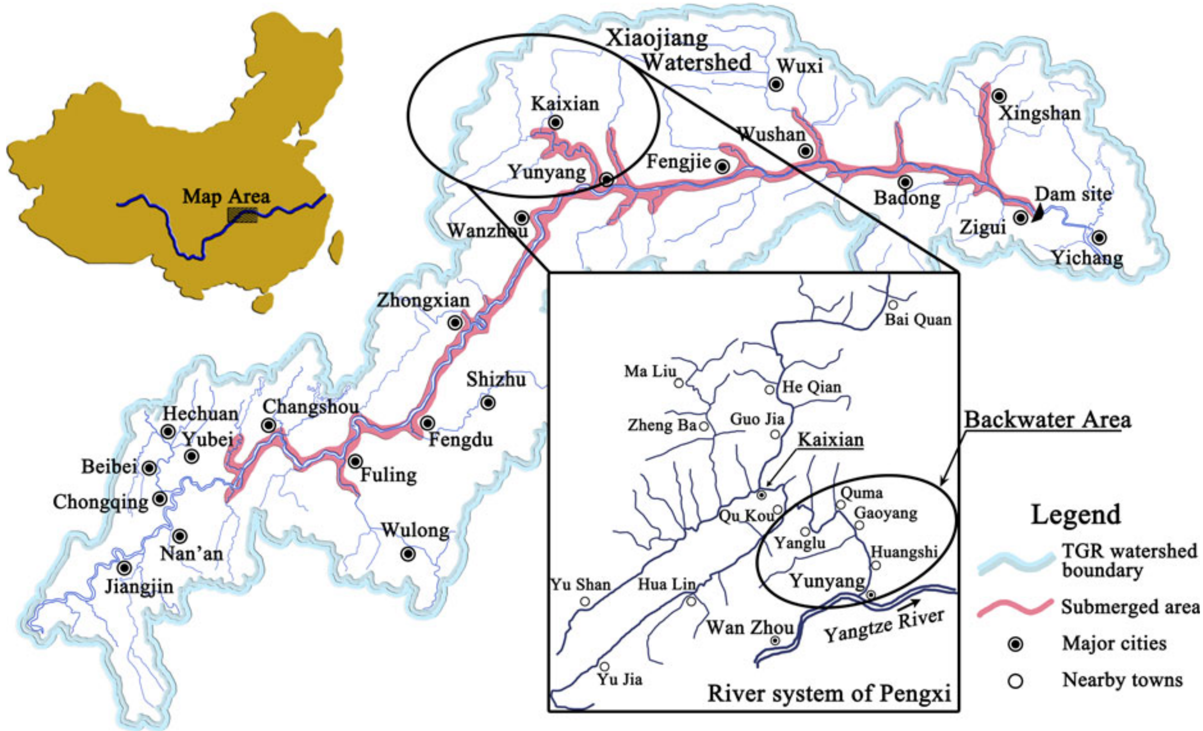

Fig. 1 The river system in the TGR and Pengxi Watershed

low water level would be maintained during the summer flood season to prevent floods downstream.

The Pengxi River is one of the largest tributaries in the central part of the TGR and is located about 247 km upstream from the TGD (Li et al., 2009b). The Pengxi River covers a watershed area of 5,172.5 km^2 located at 30°49′–31°42′N, 107°56′–108°54′E. It has a main stream length of 182 km and an average slope of 1.25‰. The area has warm, humid and subtropical weather conditions. The average annual precipitation in the watershed is 1,100–1,500 mm, and the flood season is from July to September. The average annual flow is 118 $m^3\ s^{-1}$ with a runoff of 3.41 billion m^3.

After the 156-m impoundment, the Pengxi River formed a backwater area approximately 60 km from its confluence with the Yangtze River that extended upstream from Shuangjiang Town to Qukou Town (Fig. 2). In this study, five sampling sites were established in the centre of the main channel of the Pengxi River. The spatial coordinates of the sampling sites (from upstream to downstream) were as follows: Quma (QM, 31°07′50.8″N, 108°37′13.9″E), Gaoyang (GY, 31°07′50.5″N, 108°40′29.5″E), Huangshi (HS, 31°03′38.6″N, 108°41′36.2″E), Shuangjiang (SJ, 30°56′51.1″N, 108°41′37.5″E) and Hekou (HK, at the confluence with the Yangtze River, 30°57′03.8″N, 108°39′30.6″E).

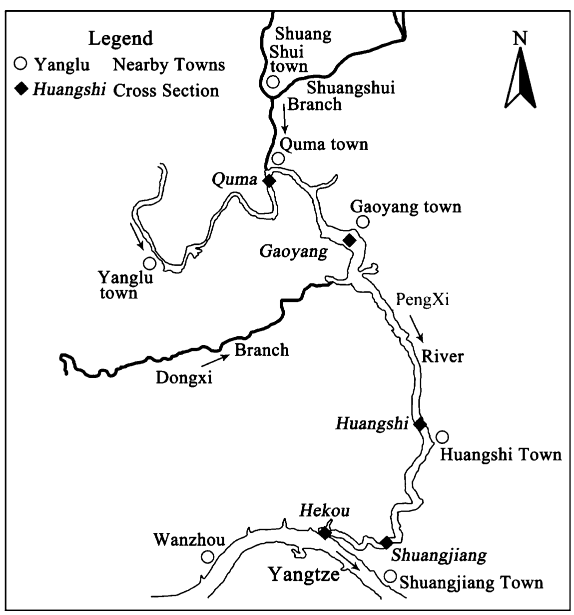

Fig. 2 The Pengxi River backwater area in Yunyang County, Municipality of Chongqing, China

Sampling methods

Phytoplankton samples were collected twice a month at the five sampling sites from May 2007 to April 2008. Sampling was conducted between 9:30 AM and 16:30 PM. Phytoplankton samples for qualitative identification were collected from the surface water with 25-µm phytoplankton nets and immediately preserved with formaldehyde (Heise, 1949; Zeng et al., 2006). Samples for quantitative analysis were collected from each sampling site at different water depths (0.5, 1, 2, 3, 5, and 8 m) using 250-ml polyethylene bottles. The quantitative samples were fixed by adding Lugol's solution (Zhang & Huang, 1991; Donk & Hessen, 1993). After mixing equal amounts of the above six samples, 1,000 ml was set aside for sedimentation for approximately 48 h before counting according to Utermöhl's method (Utermöhl, 1958). Phytoplankton were counted with a standard light microscope (XSP-8CA), and all algal taxa were identified to species level according to the classifications of Hu & Wei (2006). Algal cells were counted across 100-graticule areas with a compound microscope at ×400 magnification. All the algal individuals, including colonial and filamentous algae, were counted and sized according to standard methodology (Hu & Wei, 2006). A maximum counting error of 25% was accepted for the abundance estimates of each major algal group (Venrick, 1978). The biovolume of each species was calculated on the basis of cell size and number and then converted to carbon biomass units of mg ml^{-1} (Strathmann, 1967; Montagnes et al., 1994).

Data processing

Biodiversity depends on two different measures: (1) community structure or richness, i.e., the number of species in the community, and (2) evenness or the degree of similarity in abundance among species (Krebs, 1999; Scrosati & Heaven, 2007). In this study, the Shannon–Weaver diversity index (H index), Margalef richness index (d index) and Pielou evenness index (J index) were applied to comprehensively estimate the characteristics of the phytoplankton community. The formulae are as follows (Shannon & Weaver, 1949; Pielou, 1966; Margalef, 1975):

$$H = -\sum_{i=1}^{s} P_i \log_2 P_i (P_i = N_i/N) \tag{1}$$

$$d = (S - 1) \ln N \tag{2}$$

$$J = H/\log_2 S \tag{3}$$

where S is the number of phytoplankton species, N is the total phytoplankton biomass in the same water sample, and N_i is the biomass of i species.

The daily precipitation in the watershed was downloaded from the China Meteorological Data Sharing System (http://cdc.cma.gov.cn/). The water level at HK in the Pengxi River was estimated according to the water surface gradients between the TGD dam site (http://www.ctgpc.com.cn/) and the Wanxian hydrology monitoring station (http://www.cqwater.gov.cn). The daily water level data from both of those sites can be downloaded online. The daily discharge of the Pengxi River was calculated using a distributed hydrologic model of the Pengxi watershed, which was calibrated and validated by historical measurements of 52 years of monthly discharge (Long et al., 2009; Wu et al., 2010). The HRT was calculated based on the Hydrologic Engineering Centres River Analysis System (HEC-RAS, v.4.1) 1D hydrodynamic model of the Pengxi River (Li et al., 2012).

To discuss the variation of phytoplankton biodiversity in response to different hydrodynamic conditions, the year was divided into two periods: (1) the low water level period (before impoundment) when the water level was less than 151 m, from May to September 2007, and (2) the high water level period (after impoundment) when the water level was higher than 151 m, from October 2007 to April 2008 (Fig. 3). The disturbance intensities during the two different water level periods were calculated from the absolute incremental rates of discharge ($R_{\mathrm{d},i}$) and precipitation ($R_{\mathrm{p},i}$) using the following formulae:

$$R_{\mathrm{d},i} = \frac{|D_i - D_{i-1}|}{\Delta t} \tag{4}$$

$$R_{\mathrm{d},i} = \frac{|P_i - P_{i-1}|}{\Delta t} \tag{5}$$

where D_i is the discharge of the current day ($\text{m}^3\ \text{s}^{-1}$), D_{i-1} is the discharge during the previous day ($\text{m}^3\ \text{s}^{-1}$), P_i is the precipitation of the current day (mm), P_{i-1} is

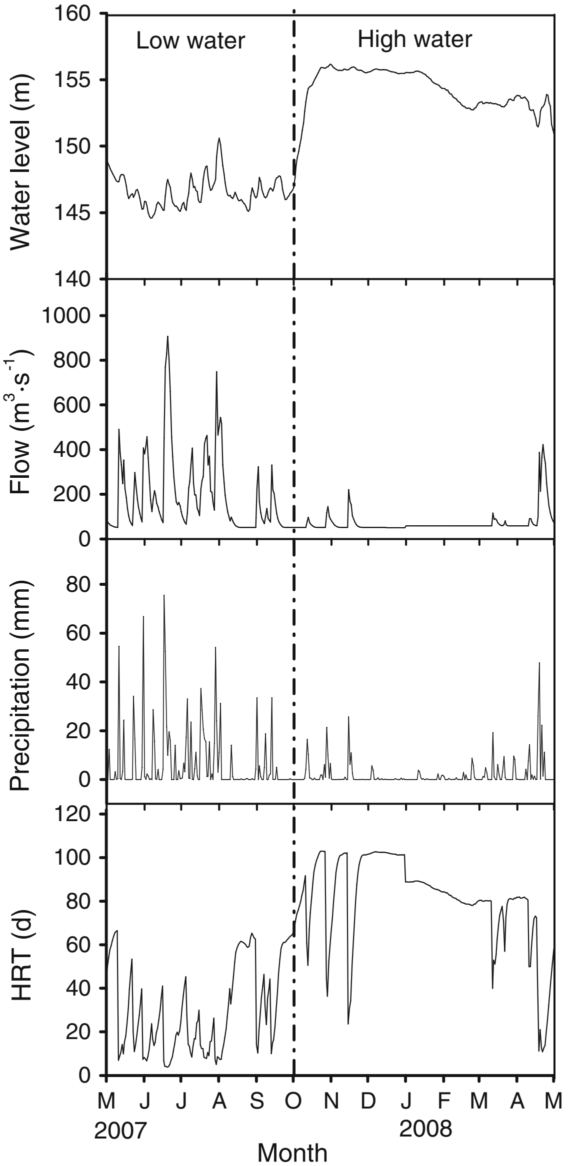

Fig. 3 Variations in the hydrological conditions in the Pengxi River at its confluence with the Yangtze River

the precipitation of the previous day (mm) and Δt is the interval time (1 day).

The rate data were then divided into three groups sorted by incremental size (0–30, 30–70, and 70–100%); these three groups represented low, intermediate and high intensities of disturbance, respectively, and are referred to hereafter as levels 1, 2 and 3, respectively (Table 1). To analyse the relationship between disturbance and diversity, the average rate from all sampling data within every sampling interval was used to express the intensity of disturbance that occurred during every sampling interval.

The statistical analyses in this study were conducted using SPSS® 16.0 and ORIGIN® 8.0. To analyse the differences among the five sampling sites during the two water level periods, both *t* test and one-way ANOVA were performed. Coefficient of variance (CV) was also applied to quantify the level of variance within specific datasets. In addition, Spearman correlation analyses were applied to analyse the relationships between the hydrodynamic conditions during the two different water level stages.

Results

Hydrologic conditions and physical disturbance

There were significant differences in the water level, HRT, discharge and precipitation before and after the 156-m impoundment in the Pengxi River ($P < 0.05$). Before the 156-m impoundment in October, the water level changed from 144.58 to 150.60 m (mean = 146.60 m; CV = 0.77%). The water level varied between 146.44 and 156.10 m (mean = 154.14 m; CV = 1.2%) after impoundment (Fig. 3). The significant difference in the HRT between the two stages was caused by the artificial water scheduling in the TGR. Before the impoundment, the river had a short HRT and was similar to a riverine-type system (mean = 38.07 days; CV = 57.65%); after the 156-m impoundment, it shifted to a near lentic-type system with a prolonged HRT (mean = 83.77 days; CV = 25.72%). During the low water level period, the HRT was significantly negatively correlated with the river flow ($r = -0.950$; $P < 0.01$), while during the high water stage, the HRT was strongly correlated with the water level ($r = 0.851$, $P < 0.05$) and negatively correlated with the river flow ($r = -0.771$, $P < 0.01$). The precipitation data showed characteristic local seasonal patterns in the TGR. The rainy and dry seasons occurred in the low and high water level periods, respectively (mean = 5.05 mm vs. 0.85 mm; CV = 223.52% vs. 273.44%). Before the impoundment, the river flow changed dramatically from 50.90 to 907.09 $m^3 s^{-1}$ (mean = 199.87 $m^3 s^{-1}$; CV = 88.9%); this change was attributed mainly to the variability in precipitation ($r = 0.676$, $P < 0.05$).

Table 1 Classification of the physical disturbance intensity during the two water level stages

Percent	Rate of change		Disturbance	
	Discharge (m^3 s^{-1} day^{-1})	Precipitation (mm day^{-1})	Intensity	Level
0–30	0–0.04	0	Low	1
30–70	0.04–19.46	0–3.27	Intermediate	2
70–100	19.46–440.18	3.27–71.36	High	3

After the impoundment, the river discharge stayed at a relatively stable level between 50.80 and 423.15 m^3 s^{-1} during the drought season.

During the study, river discharge and precipitation regulated the hydrodynamic features of the Pengxi River and acted as the main factors influencing the physical disturbance. Before the impoundment, the daily absolute incremental rate of discharge ($R_{d,i}$) ranged from 0 to 440.18 m^3 s^{-1} day^{-1}, and the daily incremental rate of precipitation ($R_{p,i}$) ranged from 0 to 71.36 mm day^{-1} (Fig. 4). The fluctuations in $R_{d,i}$ and $R_{p,i}$ induced different intensities of disturbances in the river system. The average disturbances of discharge and precipitation were mainly of high intensity, but the disturbances reached an intermediate intensity in early May, late August and late September (Fig. 5). After the impoundment, the variations in $R_{d,i}$ and $R_{p,i}$ ranged from 0 to 288.48 m^3 s^{-1} day^{-1} and 0 to 47.68 mm day^{-1}, respectively, and were much less than the variations during the low water level stage. The average disturbances in the discharge were mainly of low and intermediate intensity with several changes, but the disturbances from precipitation were in the intermediate and high intensity range with few fluctuations. The discharge maintained a low intensity of disturbance from January to February 2008, when the precipitation caused an intermediate intensity of disturbance.

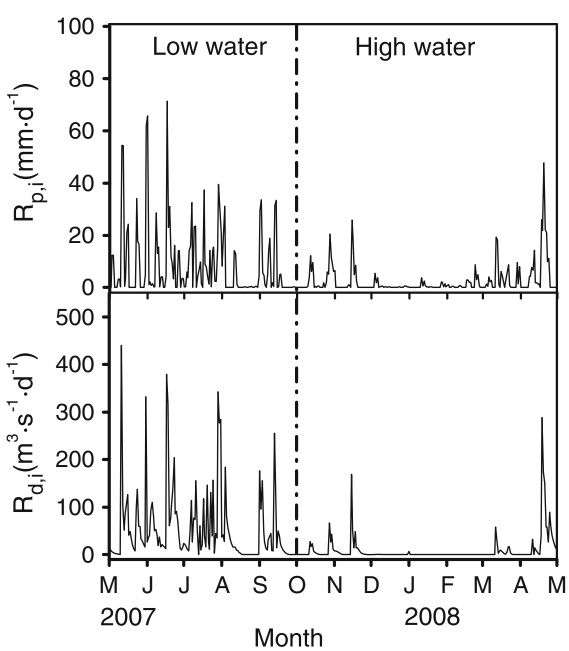

Fig. 4 Variations in the absolute incremental rates of discharge ($R_{d,i}$) and precipitation ($R_{p,i}$) in the Pengxi River

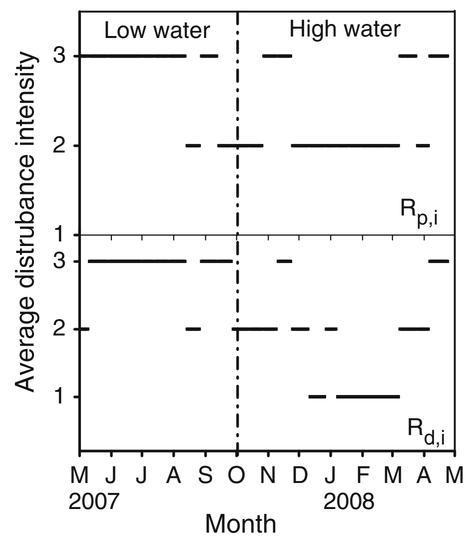

Fig. 5 Average disturbance intensities of the absolute incremental rates of discharge ($R_{d,i}$) and precipitation ($R_{p,i}$) at every sampling interval

Phytoplankton biomass and community composition

Throughout the year, the phytoplankton biomass showed great seasonal variation (Fig. 6). The highest biomass of 16.75 mg l^{-1} occurred in late May, while the lowest value, 0.23 mg l^{-1}, occurred in mid-January 2008. The biomass during spring and summer

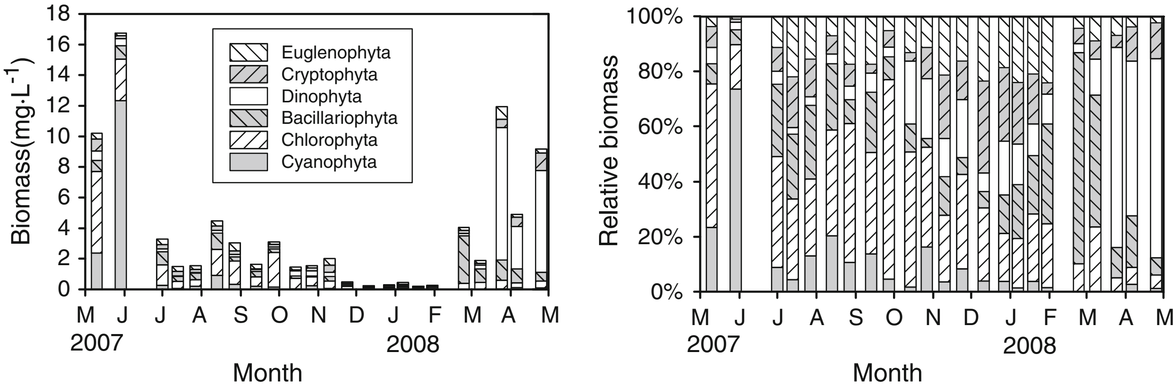

Fig. 6 The phytoplankton biomass and relative biomass of various taxonomic groups in the Pengxi River

Table 2 Phytoplankton blooms in the Pengxi River during the research period

Num.	Beginning time	Duration (days)	Dominant species	Relative abundance (%)
1st	Late May 2007	20	Cyanophyta (*A. flos-aquae*)	69.7 ± 3.1
2nd	Late February 2008	15	Bacillariophyta (*A. formosa*)	59.8 ± 4.4
3rd	Late March 2008	20	Dinophyta (*Peridinium* spp.)	69.4 ± 9.8
4th	Late April 2008	50	Dinophyta (*Ceratium* spp.)	84.3 ± 9.1

Relative abundance is calculated using the phytoplankton biomass

(February–August) was higher than that during the autumn and winter (September–January). This seasonal difference was significant ($P < 0.01$). Throughout the year, Chlorophyta was the dominant group (28.98%) followed by Bacillariophyta (19.28%) and Cyanophyta (17.27%). Chlorophyta dominated from May to November except for the dominance of Cyanophyta (73.68%) in late May, when the first algal bloom occurred before the impoundment. The Cyanophyta bloom, which was dominated by *Anabaena flos-aquae*, lasted for 20 days, and the relative biomass abundance reached 69.7 ± 3.1% in the Pengxi River (Table 2).

During the high water level stage, Cryptophyta dominated in December (33.33 and 26.70% abundance at the two sampled times during the month), but was then replaced by Euglenophyta (24.07%) in early January 2008. Bacillariophyta became the dominant taxonomic group from late January to early March (36.37, 76.75, and 47.75%, respectively). The Bacillariophyta bloom, dominated by *Asterionella formosa*, appeared in late February and lasted for about 15 days. At the end of the high water level stage, Dinophyta dominated from late March to April, and two Dinophyta blooms occurred within that short period. A *Peridinium* spp. bloom occurred in late March, and a *Ceratium* spp. bloom occurred in late April 2008. The *Ceratium* bloom lasted for about 50 days, during which time the relative biomass abundance reached 84.3 ± 9.1%, attaining a steady state (Sommer et al., 1993).

Species diversity, richness and evenness indices

The seasonal variations in phytoplankton species indicated by the three diversity indices are shown in Fig. 7. There were no significant differences in any of the diversity indices among the five sites ($P > 0.05$). The maximum and minimum Shannon–Weaver indices appeared in the low and high water level periods, with 3.77 ± 0.06 (mean ± SE) in July and 1.58 ± 0.26 in March, respectively. Both the Margalef and Pielou indices reached their maximum and minimum values during the high water level stage. The maximum of the Margalef index was attained in November with a value of 3.31 ± 0.17, and the minimum occurred in January (1.79 ± 0.17). The maximum Pielou index was 1.23 ± 0.08 in January, and its minimum value of 0.51 ± 0.18 occurred in March. However, *t* tests showed that there were no

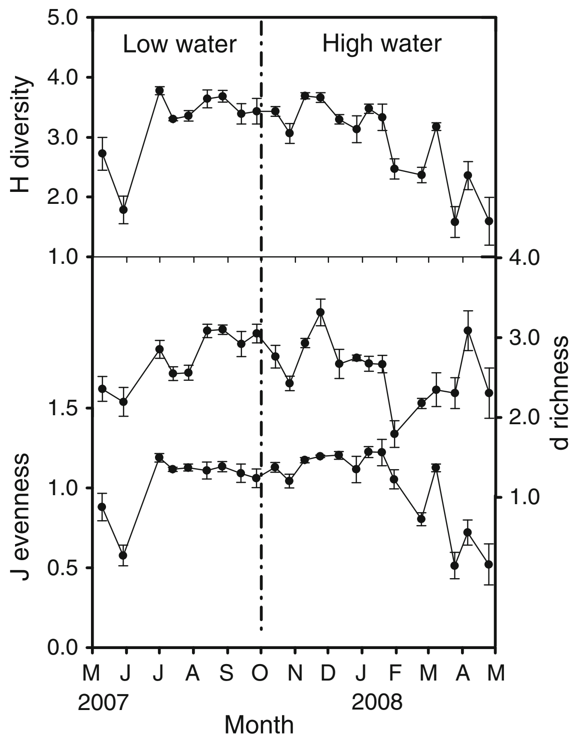

Fig. 7 The annual Shannon–Weaver (*H*), Margalef (*d*) and Pielou (*J*) indices (mean ± SE) in the backwaters of the Pengxi River

significant differences for the three diversity indices between the low and high water level periods ($P > 0.05$).

Before the impoundment, the only dramatic drop in the three indices occurred in May when the Cyanophyta bloom appeared. During the bloom, the Shannon–Weaver index declined from 2.72 ± 0.27 to 1.79 ± 0.23, and the Pielou index dropped from 0.88 ± 0.19 to 0.58 ± 0.15. After the bloom, the three indices continued to increase and maintained high values during the rest of the low water level period.

At the beginning of the impoundment, the three indices all declined in October, when the water level rose from 145 to 156 m within 1 month. The Shannon–Weaver index decreased from 3.43 ± 0.08 to 3.06 ± 0.17. The Margalef index decreased from 2.76 ± 0.14 to 2.43 ± 0.09. After the impoundment, the biodiversity indices decreased dramatically when the algal blooms occurred. During the Bacillariophyta bloom, the Shannon–Weaver index declined to 2.37 ± 0.13, and Margalef index dropped to its minimum in February. During the *Peridinium* bloom, the Shannon–Weaver and Pielou indices both reached their minimum values in March. Moreover, during the last *Ceratium* bloom, the Shannon–Weaver and Pielou indices decreased to 1.60 ± 0.40 and 0.52 ± 0.28 respectively in late April.

Discussion

According to the IDH, species diversity should reach its maximum at intermediate intensities and frequencies of disturbance within certain time scales (Sommer et al., 1993). Because disturbances are random events in natural ecosystems, the principal difficulty in the application of IDH is the recognition and measurement of disturbances (Reynolds et al., 1993). Many events can induce physical disturbances, including wind, precipitation and discharge (Muylaert et al., 1999). In this study, river flow and precipitation with strong fluctuations appeared to be the major factors influencing physical disturbance and phytoplankton community dynamics (Jones & Barrington, 1985; Paidere et al., 2007). Qualitative analyses of the response of phytoplankton biodiversity to physical disturbances were undertaken during two water level periods.

Low water level stage

At the low water level period in the Pengxi River, the river flow appeared to be a major factor regulating the phytoplankton biomass in the river system because water movement determined the turbulence in the system (Becker et al., 2009; Centis et al., 2010). Ács & Kiss (1993) found that the numbers of individuals and phytoplankton diversity in the Danube River at Göd reached a maximum when the flow was in the range of 100–400 $m^3\ s^{-1}$ under an intermediate level of disturbance. In the Moselle River, the maximum phytoplankton diversity also occurred when the fluctuations in the discharge were within 100–400 $m^3\ s^{-1}$, and large discharge variations resulted in low diversity (Descy, 1993). Our analysis failed to confirm the range of water discharge during the intermediate disturbance. Nevertheless, the $R_{d,i}$ range between 0.04 and 19.46 $m^3\ s^{-1}\ day^{-1}$ was considered to be an intermediate disturbance by reference to the statistical analyses.

It should be noted that a late spring bloom occurred in the Pengxi River during late May 2007. The bloom, with abundant Cyanophyta, especially *A. flos-aquae*, resulted in a sharp decrease in the three diversity indices (Li et al., 2009a). It is frequently mentioned in the literature that diversity indices decline rapidly when algal blooms develop (Jacobsen & Simonsen, 1993; Figueredo & Giani, 2001). The steep decline in the biodiversity indices in the Pengxi River during 2007 coincided with a sharp increase in disturbance intensity; during this period, the disturbance transformed from an intermediate level with an average $R_{d,i}$ to a high intensity disturbance, and the average $R_{p,i}$ thereafter maintained a high intensity. The bloom occurred 1 week after the last major rainfall in mid-May, and this rainfall event was considered to be a potential promoter of the physical disturbance (Beyruth, 2000). During this week, the $R_{d,i}$ increased and the discharge declined from 296.62 to 92.46 $m^3\ s^{-1}$. The Cyanophyta bloom occurred immediately after the decline in discharge. In addition, the irradiance and temperature were increasing, and both factors favoured the dominance of *A. flos-aquae* through interspecific competition (Guo et al., 2008; Li et al., 2010). Similar results were reported in the Nakdong River, South Korea, and the Meuse River, Belgium; in each case, a sharp drop in discharge and an increase in water temperature triggered the bloom (Gosselain et al., 1994; Ha et al., 1998).

The process of impoundment

The 156-m impoundment was the main characteristic feature of the TGR under artificial operation. In October, the water level of the Pengxi River increased rapidly to a maximum of 156 m. It is worth noting that the Shannon–Weaver and Margalef indices clearly decreased during that month. The impoundment process was similar to the “flood pulse” in river-floodplain systems; the increase in the water level that occurs due to this pulse can impact the phytoplankton composition and diversity and can therefore be considered a disturbance factor (Huszar & Reynolds, 1997). In river-floodplain systems, the quantitative relationship between water level changes and turbulence has been established effectively from the long-term annual flooding frequency (Gruberts et al., 2007), but could not be established using the rate of water level change (Paidere et al., 2007). An quantitative relationship between the water level variation and phytoplankton diversity was not obvious in the Pengxi River because the diversity index was not sensitive to physical forcing on a daily time scale in the river reservoirs (Pannard et al., 2008). In addition, the sharp rise in the dilution induced by the water level affected the river phytoplankton communities (Ha et al., 1998; Mihaljević et al., 2009). The high dilution forced a decline in the phytoplankton density, which occurred in parallel with a decline in diversity values (Carvajal-Chitty, 1993).

High water level period

The Pengxi River resembled a lentic-type system after the winter impoundment, after which the water level, flow and HRT were maintained at stable values. From January to February, the average $R_{d,i}$ consistently maintained the lowest intensities of disturbance, and the $R_{d,i}$ was at an intermediate disturbance intensity without any fluctuations. The IDH states that the lowest biodiversity appears at the lowest levels of disturbance because only the best competitors can persist under these conditions (Sommer et al., 1993). However, in the Pengxi River, the diversity indices did not decline in January immediately after the winter impoundment; instead, they decreased in February in response to the low disturbance intensity. Despite this delay, it is evident that low levels of disturbance eventually create a tendency toward competitive exclusion (Padisák, 1994). It was found in earlier studies that competitive exclusion in phytoplankton community occurs when conditions of ecosystem stability persist for about 20 generations (Harris, 1986; Train & Rodrigues, 1997). As suggested by Reynolds, the succession process may well require 12–16 generations and may therefore require periods of 35–60 days (Reynolds et al., 1993; Padisák, 1994). In this study, the time required for succession was approximately 45 days, from January to late February 2008, at which time the dominant phytoplankton species appeared. *A. formosa*, a eurythermal species, became the dominant species under the low levels of hydrodynamic disturbance (low variability in hydrologic conditions and long retention times) that prevailed during the cold season (Suzuki & Takahashi, 1995; Bertrand et al., 2003). In later February 2008, after the 45-day succession time, the winter Bacillariophyta bloom of *Asterionella* occurred in the backwater area of the Pengxi River, with a concomitant decrease in the biodiversity values.

At the end of the high water level stage, a clear decline in phytoplankton diversity occurred in late March and late April 2008, when two Dinophyta blooms occurred sequentially (*Peridinium* spp. and *Ceratium* spp.). *Peridinium* dominated in the lentic water system under warmer conditions, determined by the hydrological features and the eutrophic state of the system (Kishimoto et al., 2001; Canion & Ochs, 2005). *Ceratium* was able to undertake significant diel vertical migrations (DVM), apparently for its optimal exploitation of light and nutrients in temperate conditions (Hart & Wragg, 2009). *Ceratium* blooms frequently appear in lakes and reservoirs during late summer across the trophic status range (Padisák & Reynolds, 1998). During the two Dinophyta blooms, the tremendous precipitation and flow resulted in high levels of disturbance. The average $R_{p,i}$ maintained a high disturbance intensity during March, while the $R_{d,i}$ switched from a low to intermediate disturbance intensity before the blooms. The high levels of disturbance were the major reason that the biodiversity decreased and the Dinophyta blooms occurred. Moreover, the water transparency was lower during the spring rainy season as a result of the higher influx of sawdust particles into the Pengxi River (Fang et al., 2010; Zhang et al., 2010). The water transparency was correlated with daily photosynthetic rates, available nutrients and growth rate, and ultimately impacted the variations in phytoplankton density and species composition, and may be completely responsible for the decrease in phytoplankton diversity (Figueredo & Giani, 2001).

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