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Variation of Diatoms and Silicon in a Tributary of the Three Gorges Reservoir: Evidence of Interaction

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Abstract: To gain insight into the variation of diatoms and silicon and their interaction in a tributary of the Three Gorges Reservoir (TGR), the Xiangxi River was chosen as a representative tributary, and dissolved silicon (DSi) and biogenic silicon (BSi) were investigated monthly from February 2015 to December 2016, accompanied by diatom species composition and cell density analyses. The results showed that the diatom population and its relationship with silicon concentration were significantly different between the lacustrine zone and riverine zone ($P < 0.05$). The cell density in the lacustrine zone ($6.20 \times 10^5 \sim 9.97 \times 10^7$ cells/L) was significantly higher than that in the riverine zone ($7.90 \times 10^4 \sim 1.81 \times 10^7$ cells/L) ($P < 0.01$). Water velocity was a key factor in determining the diatom species composition. Centric diatoms were the dominant species in the lacustrine zone, and pennate diatoms were the primary species in the riverine zone, which indicated that centric diatoms outcompete pennate diatoms under the influence of the TGR's operation. BSi showed a significant linear relationship with the cell density. DSi had a significant negative relationship with the cell density in the lacustrine zone, while no significant relationship was found in the riverine zone. This meant that the main contributor to BSi was diatoms, but DSi was primarily affected by water discharge, not diatom uptake. It could be deduced that the spatiotemporal heterogeneity of diatom communities was influenced by the TGR's operation. Silicon cycling in the tributary was significantly affected by diatoms, and the current concentration of DSi was sufficient for diatom growth and showed no significant effects on the diatom community.

Keywords: diatom; cell density; dissolved silicon; biogenic silicon

1. Introduction

Silicon originates from rock weathering and is transported from land to the ocean mainly by rivers. It was estimated that 371 million tons of dissolved silicon (DSi) and 8835 million tons of particulate silicon (PSi) drain into the ocean every year from the continental surfaces in the world [1]. DSi and biogenic silicon (BSi) are considered bioavailable silicon in natural waters. DSi can be directly assimilated by algae and hydrophytes. BSi can contribute to DSi because of its regeneration in the water and sediment. The recycling of BSi provides the major source of soluble reactive silicon required for diatom proliferation [2]. Silicon is a key nutrient for diatom growth because it is a kind of necessary element to form the diatom's rigid cell wall [3]. BSi is generated when diatoms, plants and other organisms uptake DSi during photosynthesis, and it is an important source of DSi due to its typically amorphous form; it plays an important role in the earth's Si cycle. DSi mainly originates from weathering, and anthropogenic activities can scarcely compensate for the loss of DSi from this

source. Dsi and Bsi are not two independent variations in the water. With plenty of time, DSi can be converted to biological available silicon (BSi). When water velocity is high, the hydraulic retention time is short and can't meet the need of converting procedure. Thus, in the lacustrine area, diatom could deplete DSi and produce BSi in a stable environment. Decreased silicon has been observed in many rivers and lakes worldwide [4–6]. Diatom growth is related to silicate and other nutrient availability. Under conditions in which the silicate concentration was higher than 2 $\mu\text{mol/L}$ and other nutrients were sufficient, diatoms were observed to dominate the phytoplankton community, accounting for more than 70% of the total cell density in the community [7]. The distribution patterns of epipelagic and epipsammic diatoms were related to nutrient availability, especially of silicate and ammonium [8]. It was observed that silicate availability by river supply and strong tidal mixing of the water column seemed to determine the year-round dominance of diatoms over dinoflagellates in a Spanish estuary [9]. Studies also found that the ratio between silicates and other nutrients, such as carbon, nitrogen, or phosphorus, affected diatom growth in the phytoplankton succession. *Skeletonema costatum* is influenced by silicate availability and by changes in dissolved inorganic carbon (DIC) pool [10]. Species succession from diatom to blue-green algae was controlled by carbon and silicate in karst cascade reservoirs in Southwest China [11]. It has been proven that decreasing silicon and increasing nitrogen and phosphorus in the Yangtze River estuary resulted in eutrophication, decreased diatom composition in the algal community and frequent harmful algal blooms in coastal waters [12]. Therefore, there was a direct causal relationship between diatom growth and silicate availability.

In addition to silicate availability, algal growth is primarily related to changes in environmental factors, such as the water stability, water renewal rate and water retention time. In reservoirs with considerable hydraulic dynamics, the water renewal rate explained the selection of secondary species, and dominant species adapted to a broad range of environmental conditions [13]. Fast growth was the response of diatoms to changes in physical environmental factors, especially the daily variations in river discharge, which continuously modify the suspended particulate matter concentrations and water retention time [14], while low flow conditions lead to a progressive depletion of dissolved silicon [15]. On the other hand, diatom species varied depending on the environmental conditions. In comparison with pennate diatoms, centric diatoms favour relatively lower temperatures and photoperiods. Pennate diatoms depend more on light and grazer abundance [16]. Therefore, the relationship between diatoms and environmental factors is complex and requires further research.

Three Gorges Reservoir (TGR) is the largest deep river-type reservoir in the world. Large amounts of nutrients and pollutants from headwaters and tributaries drained into the reservoir after Three Gorges Dam began operation, causing severe problems such as eutrophication [17] and algal bloom [18]. Many studies have been conducted to elucidate algal succession [19] and nutrient distribution under TGR's operation [20–24]. It was observed that the frequency and duration of algal blooms has risen in recent years [25]. Furthermore, water intrusion from the main channel of the Yangtze River to the tributaries has worsened eutrophication in tributaries such as the Daning River [26] and the Xiangxi River [27]. Consequently, biogeochemical cycling of some nutrients, such as nitrogen, phosphorus, and silicon, has changed. Previous studies have demonstrated silicon retention in the TGR due to dam construction and its impact on the silicon efflux to the eastern sea through the Yangtze River [5,28,29]. These studies mainly focused on silicon dynamics and its fluxes. Other studies have emphasized algal succession and its relationship with nitrogen and phosphorus in the TGR [30]. However, the relationship between diatoms and silicon in the TGR has not yet been investigated in detail. After the impoundment of the TGR, silicon retention in the reservoir was increased, and the discharge amount of biogenic silicon was gradually reduced. Lower water velocity and higher water transparency accelerated the growth of diatoms and led to frequent diatom blooms in the tributaries of the TGR. In this study, the Xiangxi River was selected as a representative of the tributaries in the TGR, and silicon and diatoms were screened in two distinct zones: The riverine zone and the lacustrine zone. This study aims to understand (i) the diatom community in different water areas of the TGR and (ii) the interactive relationship between the available silicate or hydrodynamics and the diatom

community in the TGR. A monthly investigation was conducted, including diatom species, cell density, silicon concentration, and environmental parameters. This study will help us to gain insight into the interaction between silicon concentration and diatom communities in the TGR and the variation of silicon and changes in the diatom community.

2. Materials and Methods

2.1. Study Site

The water level of the TGR was artificially regulated according to the dam operation strategy. In summer, the water level was low for power generation and flood prevention, and in winter, the water level was high for drought relief and navigation improvement. A typical hydrological year of the TGR was divided into four periods according to a series of specific operations. The impounding period was in autumn from September to October, and the water level increased from 145 m to 175 m. The next three months (November to January) were the high water level period, with the water level maintained at approximately 175 m. Then, in the discharge period (February to June), the water level was decreased from 175 m to 145 m. The last period (July to August) was the low water level period, with the water level remaining at 145 m. The water discharge and sand transport rate displayed opposite trends against the water level in the TGR, which was caused by seasonal variations in precipitation [31].

The source of the Xiangxi River is in the Shennongjia Forest in Western Hubei Province. Its location is 30°57' N–31°34' N, 110°25' E–111°06' E, the length is 94 km, and the watershed is approximately 3100 km². The Xiangxi River contains three main tributaries: the Shendu River, the Baisha River and Gaolan Bay. The TGR does not affect the upstream area of the Xiangxi River; so, this zone is still highly canopied by riparian vegetation and remains the riverine type. In contrast, the canopy of the middle and downstream regions is not well developed due to the wider riverway and inconspicuous riparian zone. Therefore, this zone has changed to the lacustrine type.

Twelve sample zones were set along the Xiangxi River (Figure 1). Sample stations XX01~XX08 were located in the main channel from the estuary to the upstream region (Figure 1). There was one sample site in each of the two tributaries, the Baisha River (Site BSH), and the Shendu River (Site SDH). Two sample zones, GL01 and GL02, were set in Gaolan Bay. Water samples were not collected in XX08 in summer because of the usage of cascade hydropower stations. These sample zones were classified into the lacustrine zone (XX01~XX08 and GL01, GL02) and the riverine zone (BSH and SDH). They were selected to represent a wide range of environmental gradients under the influence of the Three Gorges Dam.

Figure 1. Sketch map of sampling stations in the Xiangxi River.

2.2. Sampling and Testing

Monthly samples were collected from February 2015 to December 2016. Surface water samples (0.5 m) were collected with Van Dorn sampler at each site for three times. Samples for quantitative phytoplankton analyses were fixed with neutral Lugol's solution and concentrated after 48 h of sedimentation. Transparency (SD) was measured with a Secchi disk. Surface water velocity (Fv) was detected by SVRTM (Decatur Electronics Inc.: San Diego, California, USA), a hand held electronic wave water velocity detector. Dissolved oxygen (DO), pH, water temperature (WT), turbidity (Turb), oxidation-reduction potential (ORP), and conductivity (Cond) were measured by a Eureka Manta 2 multiparameter probe (Eureka, Austin, TX, USA).

Before collecting samples, the bottles were pre-rinsed with 10% HCl and distilled water three times. To determine DSi, samples were filtered through 0.45 µm cellulose membrane filters. Using the silicomolybdc blue method, the filtrates were analyzed by a Skalar San++ autoanalyzer (Skalar Corporation, Breda, the Netherlands) with a precision of 2%. The BSi was measured by the double wet-alkaline digestion method. The filter sample was submitted to a first digestion (NaOH, 0.2 M, 4 mL; pH: 13.3) at 100°C for 40 minutes, and all BSi and a portion of the lithogenic silica were converted into Si(OH)₄. Therefore, we can analyse the concentrations of Si and Al ([Si]₁ and [Al]₁) in the supernatant. Then, after rinsing and drying (freeze drying at −60°C), the filter sample was digested again under the same conditions as in the first digestion. In this way, we can determine the (Si:Al)₂ ratio, which is the silicate minerals present in the sample. The exact biogenic silica concentration is calculated by the equation below:

$$[\text{BSi}] = [\text{Si}]_1 - [\text{Al}]_1(\text{Si:Al})_2 \quad (1)$$

where the [Si]₁ and (Si:Al)₂ have been measured. The concentration of Al was determined by ICP-OES [32]. Water samples used for the Chl *a* measurement were filtered with a Whatman GF/C filter, and the residuals were extracted using 90% acetone solution in the dark for 24 h at 4°C. Chl *a* was analyzed spectrophotometrically according to American public health association (APHA, 1995) [33]. Chemical oxygen demand (COD) was analyzed according to APHA (1995) [33].

Phytoplankton samples were preserved by adding 1 mL Lugol's solution to 100 mL sample and then stored in the dark. Samples settled for 48 h and were then siphoned and concentrated to 30 mL. After complete mixing, 0.1 mL of the concentrated sample was counted directly in a counting chamber at 400× magnification with a light microscope (Olympus BX41). The identification of phytoplankton species was performed according to Hu and Wei [34].

2.3. Statistical Analysis

Origin 9.1 (OriginLab Corporation, Northampton, MA, USA) was used for mapping the concentration patterns [35]. Statistical analysis was carried out with SPSS 19.0 (International Business Machines Corporation, Armonk, NY, USA) [36]. A t-test was used to compare the means of silicon concentration and diatom cell density between the lacustrine zone and the riverine zone [37]. Spearman analyses were performed to determine the relationships among diatom cell density and environmental factors [38]. A linear regression model was performed to determine the effect of diatom cell density on the silicon concentration. Prior to analysis, a dataset that did not fulfill the normality and homoscedasticity requirements was logarithmically transformed by log₁₀(x + 1). Redundancy analysis (RDA) was performed to explore the relationship between the diatom community composition and environmental data using CANOCO version 4.5 (Wageningen University & Research, Wageningen, the Netherlands) [39]. Diatoms were used as categorical environmental variables, and the other selected environmental variables were standardized by zero-mean normalization. The minimum number of measured environmental variables that could account for most of the variance in the species data was determined by forward selection with a permutation test at *P* < 0.05.

3. Results

Overall, sites in the upper river exhibited higher pH, DO and turbidity but lower water temperature and SD values than sites in the lower river. Specifically, the riverine zone (BSH and SDH) exhibited higher water velocity than the lacustrine zone (XX01~XX08). The conditions were more homogenous during the dry season than during the wet season when the water level was high (Table 1).

Table 1. Environmental conditions (pH, water temperature (WT), dissolved oxygen (DO), flow velocity (Fv), oxidation-reduction potential (ORP), transparency (SD), and turbidity (Turb)) at each site.

Site	pH	WT (°C)	DO (mg/L)	Fv (m/s)	ORP (mV)	SD (cm)	Turb (NTU)
XX01	8.48 ± 0.37	20.98 ± 5.34	9.09 ± 1.45	0.42 ± 0.14	166.91 ± 51.20	233.91 ± 84.30	1.71 ± 0.99
XX02	8.54 ± 0.37	21.2 ± 5.39	9.32 ± 1.27	0.45 ± 0.14	162.74 ± 50.16	227.83 ± 91.65	1.49 ± 0.80
XX03	8.39 ± 0.35	20.97 ± 5.06	8.88 ± 1.41	0.43 ± 0.11	159.80 ± 50.18	234.13 ± 91.73	1.71 ± 0.95
XX04	8.40 ± 0.39	20.80 ± 5.16	9.01 ± 2.30	0.47 ± 0.21	173.83 ± 57.46	243.48 ± 92.32	1.66 ± 0.86
GL01	8.43 ± 0.39	21.01 ± 5.05	9.20 ± 2.52	0.47 ± 0.17	176.93 ± 59.30	232.17 ± 93.17	2.50 ± 2.96
GL02	8.55 ± 0.46	21.02 ± 5.05	9.80 ± 3.26	0.33 ± 0.11	174.64 ± 63.73	253.70 ± 119.57	2.47 ± 2.97
XX05	8.49 ± 0.42	21.09 ± 5.30	9.32 ± 1.96	0.44 ± 0.13	144.57 ± 56.22	250 ± 102.11	1.50 ± 0.98
XX06	8.58 ± 0.46	20.63 ± 5.23	9.62 ± 2.50	0.36 ± 0.09	138.32 ± 57.41	217.83 ± 122.13	2.32 ± 2.43
XX07	8.61 ± 0.48	20.48 ± 4.92	10.00 ± 2.92	0.30 ± 0.11	140.60 ± 53.88	201.09 ± 127.30	5.12 ± 5.20
XX08	8.57 ± 0.5	18.40 ± 4.04	10.77 ± 4.19	0.42 ± 0.15	156.46 ± 49.58	259.29 ± 114.79	1.94 ± 1.92
BSH	8.6 ± 0.61	18.31 ± 3.70	10.32 ± 3.02	0.61 ± 0.28	164.55 ± 53.96	156.74 ± 125.51	7.14 ± 7.32
SDH	8.63 ± 0.4	18.96 ± 4.08	9.93 ± 2.55	0.93 ± 0.56	168.89 ± 53.58	163.57 ± 123.36	7.00 ± 7.14

The value was expressed as the average value ± SD.

3.1. Variation of Silicon Availability and Diatom Cell Density

The concentration of DSi fluctuated more in the riverine zone (varying from 48.03 $\mu\text{mol/L}$ to 105 $\mu\text{mol/L}$, with an average value of $77.00 \pm 16.85 \mu\text{mol/L}$) than that in the lacustrine zone (ranging from 59.58 $\mu\text{mol/L}$ to 102.85 $\mu\text{mol/L}$, with an average value of $83.23 \pm 12.59 \mu\text{mol/L}$) (Figure 1). DSi in the lacustrine zone was significantly higher than that in the riverine zone ($t = 2.312$, $P = 0.024$). The DSi concentration was higher in the winter and spring seasons, but decreased to a low level in the summer and autumn seasons (Figure 2).

Figure 2. DSi and BSi concentrations at each site (mean value, $N = 23$ at each site).

Spatially, DSi was high in the middle of the Xiangxi River and exhibited a decreasing trend upstream. DSi was lower at BSH and SDH than at other sites. The BSi concentration showed an increasing trend from downstream to upstream (Figure 2).

The peak BSi concentration was observed in the spring and autumn seasons, and its maximum concentration in the riverine zone was higher than that in the lacustrine zone. The BSi concentration ranged from below the detection limit to 4.51 $\mu\text{mol/L}$ in the lacustrine zone, and it reached its peak concentration (10.89 $\mu\text{mol/L}$) in the riverine zone. Furthermore, the lacustrine zone exhibited a high

BSi concentration in summer 2016. During the same period, BSi in the riverine zone was lower than in the lacustrine zone ($t = -2.181$, $P = 0.052$) (Figure 3).

Figure 3. Monthly DSi (A) and BSi (B) variation (mean value, $n = 21$ for lacustrine site, $n = 6$ for riverine site in each month) from February 2015 to December 2016. Spring: March ~ May; Summer: June ~ August; Autumn: September ~ November; Winter: December ~ February.

There were mainly 15 kinds of diatoms detected from the Xiangxi River, *Cyclotella*, *Melosira*, *Amphiprora* and *Synedra* were the most frequent genus. The diatom cell density showed a decreasing trend from downstream to upstream (Figure 4A). Pennate diatoms exhibited an increasing trend (Figure 4B), among them, the increase of *Synedra* and *Amphiprora* was rather obvious. The total cell density of diatoms in the lacustrine zone ranged from 6.20×10^5 cells/L to 9.97×10^7 cells/L, which was significantly higher than that in the riverine zone ($7.90 \times 10^4 \sim 1.81 \times 10^7$ cells/L) ($t = 2.13$, $P = 0.05$). Seasonal trends of BSi showed that in winter, cell density in both zones was low, but it increased dramatically in spring and autumn. However, in addition to spring and winter, summer was also a growth season for diatoms in the lacustrine zone because the peak diatom cell density was observed in summer (Figure 4C). Spearman correlation analysis showed that the diatom cell density had a significant positive relationship with BSi, Chl a, and COD ($P < 0.01$) and a negative relationship with water velocity ($P < 0.01$) in both zones (Table 2). DSi was negatively correlated with the cell density in the lacustrine zone ($P < 0.01$), but no correlation was found in the riverine zone (Table 2).

Table 2. Spearman correlation between cell density and environmental parameters (dissolved silicon (DSi), biogenic silicon (BSi), chlorophyll a (Chl a), pH, water temperature (WT), dissolved oxygen (DO), chemical oxygen demand (COD), conductivity (Cond), and water velocity) in the lacustrine zone (L-CD) and riverine zone (R-CD).

Site	DSi	BSi	Chla	pH	WT	DO	COD	Cond	Water Velocity
L-CD	−0.513 **	0.639 **	0.722 **	0.625 **	0.164	0.506 *	0.522 *	−0.024	−0.549 *
R-CD	0.017	0.830 **	0.755 **	0.258	−0.071	0.265	0.415 *	0.497 *	−0.745 **

* Correlation was significant at the 0.05 level; ** Correlation was significant at the 0.01 level.

DSi showed a linear decrease as a function of diatom cell density in the lacustrine zone, but it was not obvious in the riverine zone (Figure 5). BSi was linearly correlated with diatom cell density in both zones. The regression model showed that cell density explained 48% of the BSi concentration variation ($R^2 = 0.48$), while the slope in the riverine zone was significantly higher than that in the lacustrine zone ($P < 0.001$). The intercept of the riverine zone was significantly lower than that of the lacustrine zone ($P = 0.003$). From the model, it could be speculated that the BSi concentration in the riverine zone was an order of magnitude lower than that in the lacustrine zone (Figure 6).

Figure 4. The diatom cell density (A) and proportion of pennate diatom cell density (B) at different sites. Monthly diatom cell density from February 2015 to December 2016 (C).

Figure 5. Relationships between diatom cell density and DSi in the lacustrine zone (A) and riverine zone (B).

Figure 6. Relationships between diatom cell density and BSi in the lacustrine zone (A) and riverine zone (B).

3.2. Effects of Environmental Variables on Diatom Composition

Different dominant diatom species were identified from the two zones. In summer, there was a significantly higher proportion of pennate diatoms in the riverine zone than in the lacustrine zone ($t = 8.205$, $P < 0.01$). In the riverine zone, pennate diatoms occupied over 30% of the total diatom cell density. However, this proportion never exceeded 10% in the lacustrine zone. In winter and spring, there was no significant difference in the diatom community structure at both zones, and centric diatoms were the dominant species (Figure 7).

Figure 7. Monthly variation of pennate diatoms in the lacustrine zone and the riverine zone.

In Figure 8, environmental variables were standardised by normalisation, and diatom species samples were centered. A forward-selected RDA of the diatom species data set revealed water velocity ($F = 52.34$, $P = 0.002$), DSi ($F = 20.15$, $P = 0.002$), COD ($F = 3.85$, $P = 0.044$), and DO ($F = 10.62$, $P = 0.002$) as the minimum set of significant environmental variables that could describe the greatest variation in the data set; a total 77.3% of the variation in taxonomic compositions was explained. Pennate diatoms showed a significant positive correlation with water velocity, while centric diatoms were negatively correlated with water velocity ($P < 0.05$). A negative correlation between pennate diatoms and DSi was observed, but this relationship was not evident between centric diatoms and DSi.

Figure 8. Biplot diagrams for the RDA of the relationship between diatom composition and environmental variables.

4. Discussion

4.1. Variation in the Diatom Community

The cell density and species composition of diatoms showed significant differences between the lacustrine zone and the riverine zone ($P < 0.05$), which represented the effects of the TGR's operation. Higher cell density in the lacustrine zone than in the riverine zone was first attributed to the relatively stable physical conditions (Table 1). However, the negative coefficient between diatom cell density and water velocity was higher in the riverine zone ($r = -0.745$) than in the lacustrine zone ($r = -0.549$) (Table 2), indicating a stronger influence of water flow on the diatom cell density in the riverine zone than in the lacustrine zone. The TGR's operation changed the hydrodynamics markedly, and the lacustrine zone showed relatively stable physical conditions. It is well known that the riverine zone showed an obvious flow rhythm, which means there was high flow discharge and water velocity in the summer and autumn seasons and low flow discharge and water velocity in the winter and spring seasons. The lacustrine zone, which is also known as the backwater area, exhibited a sharp slowdown of water velocity that significantly enhanced sedimentation, light penetration and water transparency. The decrease in the nutrient exchange rate accelerated the process of eutrophication. Such physical and chemical environmental conditions favoured the growth of diatoms. In contrast, the riverine zone maintained a natural river status with a low water level, characterised by a higher water velocity and nutrient exchange rate than the lacustrine zone. Diatom growth showed that it was more likely to be influenced by hydrodynamics [15]. This strong influence was particularly evident in the summer and autumn seasons when precipitation and water discharge increased significantly, disturbing the diatom growth and reducing its density dramatically in the riverine zone. Therefore, the TGR's operation enhanced the diatom cell density and prolonged the diatom growth period in the lacustrine zone of the tributary.

While centric diatoms were the dominant species in the lacustrine zone, a high proportion of pennate diatoms were found in the riverine zone in the summer and autumn seasons (Figure 7). They were mainly dominated by pennate diatoms from the genera of *Synedra* and *Navicula*. In the winter

and spring seasons, the proportion of pennate diatoms in both zones was similarly low. This finding was consistent with previous studies showing that centric diatoms were dominant in a lacustrine zone, while pennate diatom growth was favored in a fluvial zone [40]. RDA analysis showed that pennate diatoms had a significant positive correlation with water velocity, while centric diatoms had a negative relationship with water velocity (Figure 8). The deep and slow flowing lacustrine zone provided beneficial growth conditions for the growth of *Melosira* and *Cyclotella*, indicating that water velocity was a key factor for the diatom composition. Both lotic and lentic diatoms had different strategies to adapt to distinct physical environments. For example, the increase of small single-celled centric diatoms could resist sinking due to their morphological properties in a stable environment [41]. Moreover, it has been suggested that fluvial algal species such as pennate diatoms have a higher growth rate than lacustrine species [42]. The time to absorb nutrients was limited for fluvial phytoplankton, as these nutrients were transported downstream by the flow. Consequently, the fluvial phytoplankton had to acquire and absorb nutrients faster and more efficiently. Previous studies found that pennate diatoms had a significant increase in affinity for phosphorus compared with centric diatoms. Lotic diatoms also had higher growth rates and photosynthetic efficiencies with small-scale turbulence than those with standing water conditions [43]. These studies demonstrated that pennate diatoms had physiological and morphological advantages over centric diatoms in a turbulent environment. As a result, stable environmental conditions helped centric diatoms outcompete pennate diatoms under the influence of the TGR's operation. This further verified the significant influence of the TGR's operation on the diatom community.

4.2. Effects of Diatom on Silicon Cycling in the TGR

It was reported that the silicon content of diatoms varied among species and sizes [44]. In general, pennate diatoms had a larger size than centric diatoms; consequently, a higher BSi per cell could be found in comparison with that for centric diatoms. In this study, a low cell density with high BSi was found in the riverine zone; cell density had a synchronous trend with BSi in the two zones in winter and spring because centric diatoms were the dominant species due to their high growth rates at low water velocity [45]. From the above, it could be concluded that BSi in the water column showed a significant relationship with diatoms.

There was a significant correlation between diatom cell density and BSi in both zones (Table 2), which indicated that BSi originating from watershed terrestrial phytoliths made little contribution to the BSi pool and that the diatom population was the main contributor to BSi. These results were different from some other regions, such as the Scheldt estuary, where BSi did not follow the dynamics of the living diatoms but rather that of suspended particulate matter [46]. Different regions might show different relationships between diatoms and BSi. Furthermore, diatom cell density was linearly positively related to BSi and had the same explanation coefficients for BSi variation in both zones. The slope in the riverine zone was significantly higher than in the lacustrine zone (Figure 6). It was estimated that BSi increased by 3.24 $\mu\text{mol/L}$ when diatom cell density increased by an order of magnitude in the lacustrine zone; whereas it increased by 5.25 $\mu\text{mol/L}$ when diatom cell density expanded an order of magnitude in the riverine zone. Therefore, diatoms in the riverine zone contained more silicon per cell than those in the lacustrine zone. This phenomenon might be attributed to the distinct diatom composition and provides further evidence that the diatom population was the main contributor to BSi in the tributary of the TGR.

While DSi concentration was sensitive to rapidly changing hydrological conditions [47], some studies have shown diatom blooms were the cause of an intense seasonal decline of DSi concentrations in eutrophic rivers [48]. Our results showed that DSi was negatively correlated with the diatom cell density in the lacustrine zone (Table 2). The regression model indicated that diatom assimilation was the primary reason for DSi decline in the lacustrine zone (Figure 5A). It could be speculated that when the cell density increased by an order of magnitude, the DSi concentration decreased by 6.45 $\mu\text{mol/L}$. However, no correlation was found between DSi and diatom cell density in the riverine

zone (Figure 5B). This was probably due to hydrodynamic disturbance of the DSi assimilation by diatoms, especially in summer when the water velocity and turbidity were high. This phenomenon was consistent with previous studies showing that DSi was primarily affected by discharge, not diatom uptake, in the fluvial system [15]. The DSi concentration was higher than the threshold of 2 $\mu\text{mol/L}$ for diatom growth [7] in both zones, even in the growth period when DSi was assimilated intensively (Figure 3A). Moreover, when diatom cell density was low in both zones, the DSi concentration was relatively high, with no significant difference in the two zones (Figure 3A). If diatoms in the two zones were taken into consideration together, cell density had little correlation with DSi (Figure 8), indicating that the diatoms were not silicon limited. Thus, silicon cycling was more likely to be affected by diatoms, not vice versa.

There are two possible reasons for silicon cycling alterations by diatoms from the above discussions. On the one hand, diatom succession from pennate to centric would reduce BSi in the water despite high centric diatom cell density. On the other hand, centric diatom bloom promotes silicon cycling efficiency in the reservoir, but exerts a negative influence on the downstream river and its adjacent estuary. Sediment and dissolution processes cause silicon accumulation, becoming a silicon source in the reservoir but in the long term acts as a silicon sink [49]. Therefore, the silicon load transported downstream and to the estuary was reduced. Silicon decreased with the anthropogenic enrichment of nitrogen and phosphorus, which changed the algal community, leading to the dominance of non-siliceous algae. Considering that diatoms contribute approximately 40% of the global marine primary productivity [50], silicon retention caused by dams may exert great effects on the structure and function of aquatic ecology.

5. Conclusions

The diatom cell density in the lacustrine zone was higher than that in the riverine zone. Water velocity was a key factor in determining the diatom species composition; centric diatoms were the dominant species in the lacustrine zone, and pennate diatoms were the primary species in the riverine zone, which indicated that centric diatoms outcompete pennate diatoms under the influence of the TGR's operation. The main contributor to BSi in the tributary of the TGR was diatoms, but DSi was primarily affected by water discharge, not diatom uptake. It could be deduced that silicon cycling was significantly affected by diatoms, but the current concentration of dissolved silicon was sufficient for diatom growth, and there were no significant effects on the diatom community.

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