Predicting the effects of reservoir impoundment on phytoplankton and shoreline vegetation communities using the space-time substitution method
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ABSTRACT

The prediction of the influence of reservoir impoundment on water quality and phytoplankton community is the basis of ecological compensation or restoration. The aim of the current study was to predict the effects of reservoir impoundment on phytoplankton and shoreline vegetation communities using the space-time substitution method. The Huangjinxia Reservoir under construction on the Han River was selected as the research object. The space-time substitution method indicated that the average values of the total phosphorus (TP) and ammonia (NH\textsubscript{4}\textsuperscript{+}-N) increased from 0.049 and 0.279 mg L\textsuperscript{-1} to 0.139 and 1.132 mg L\textsuperscript{-1}, respectively, after reservoir impoundment. The percentage of diatom biomass exceeded 95% before the reservoir impoundment. However, it was gradually decreased to 75% after the reservoir impoundment. Meanwhile, the biomass of Chlorophyta, Cryptophyta and Pyrrophyta increased significantly, accounting for 32, 20 and 13% of the total biomass, respectively, after reservoir impoundment. \textit{Cynodon dactylon} (65.3%), \textit{Polygonum hydropiper} (51.7%) and \textit{Aster subulatus} (50.3%) were the dominant shoreline vegetation before the reservoir impoundment, whereas after the reservoir impoundment, the dominant species shifted to \textit{Alternanthera philoxeroides} (62.3%), \textit{Lobelia chinensis} (55.7%) and \textit{C. dactylon} (53.9%). Our results suggested that the percentage of bloom-forming phytoplankton would gradually increase after the reservoir impoundment. In addition, \textit{A. philoxeroides}, \textit{C. dactylon} and \textit{L. chinensis} would be the plants suitable for living in the shoreline of reservoirs in this area.

Key words | phytoplankton, reservoir impoundment, shoreline vegetation, water quality

HIGHLIGHTS

- A space-time substitution method is used to study effects of damming on algae.
- The Huangjinxia Reservoir under construction on the Han River was studied.
- Reservoir impoundment may increase the concentration of the total phosphorus and ammonia.
- The biomass of Chlorophyta, Cryptophyta and Pyrrophyta increased significantly.
- \textit{Alternanthera philoxeroides}, \textit{Cynodon dactylon}, and \textit{Lobelia chinensis} were suitable for shoreline remediation.
INTRODUCTION

Reservoir construction is an important means to utilize water resources and hydro-energy efficiently. It alleviates the contradiction between the lack of water resources and the demand for a large amount of electric energy to a great extent. However, reservoir construction will also cause a series of ecological and environmental problems, such as changing the original ecosystem, causing water quality deterioration or the formation of water blooms (Joung et al. 2011; Xue et al. 2018). Thus, the above problems should be considered in the process of reservoir design and construction so as to formulate a series of ecological compensation or restoration measures. Particularly, the prediction of the influence of reservoir impoundment on water quality and phytoplankton community is the basis of ecological compensation or restoration.

Phytoplankton are the primary producers in rivers and reservoirs playing critical roles in maintaining the health and balance of aquatic ecosystems. Mhlanga et al. (2020) monitored phytoplankton community in the Tugwi-Mukosi reservoir (Zimbabwe) 9 months after impoundment. Their results showed that Cyanophyta, dominated by Microcystis aeruginosa and Aulacoseira granulata, was the predominant phylum accounted for 50–70% in the total phytoplankton community. Wang et al. (2014) found that reservoir impoundment affected silicon cycling thereby affecting the total amount of phytoplankton and the proportion of diatoms. Wu et al. (2015) compared water quality and phytoplankton community composition between rivers and reservoirs before and after impoundment of the Three Gorges Reservoir. Their results showed that the proportion of diatoms decreased significantly but dinoflagellate increased gradually after impoundment. Bi et al. (2010) analyzed the variation in phytoplankton community in the Xiangxi River before and after impoundment. Their results showed that phytoplankton diversity decreased after impoundment. These results showed that although the variations in phytoplankton community caused by reservoir impoundment in different reservoirs showed a similar pattern, there was still much uncertainty due to differences in natural geographic conditions and species of indigenous phytoplankton.

Generally, phytoplankton community variation was mainly induced by hydrodynamics changes after reservoir impoundment (Jati et al. 2017a, 2017b). de Souza et al. (2016) showed that reservoir impoundment directly affected the hydrodynamics, mixing and underwater light field, thereby influencing the composition of phytoplankton functional groups. In addition, the influx of exogenous pollution after reservoir construction also directly affected the composition of phytoplankton community. Domingues et al. (2007) analyzed the controlling factors of phytoplankton community in the Guadiana upper estuary and indicated that increased nitrogen concentration and slowed water flow rate were the most important trigger factors for cyanobacterial proliferation. Factors influencing the phytoplankton community after reservoir impoundment were extremely complex. Thus, further studies were still needed to obtain more reliable changing patterns and driving factors to develop preventive measures.

Beside phytoplankton, shoreline vegetation was essential for water purification and the health of benthic fauna in reservoirs. At the same time, knowledge of the effects of reservoir impoundment on shoreline vegetation was also of great value guiding us in the selection of suitable plants for shoreline vegetation remediation. Ye et al. (2015) demonstrated that shoreline vegetation upstream of the Three Gorges Reservoir (China) was dominated by Echinochloa crusgalli, Bidens tripartita and Cynodon dactylon. Hill et al. (1998) established a hydrological model for predicting the effects of reservoir impoundment on the shoreline vegetation. However, our knowledge about the effect of reservoir impoundment on shoreline vegetation communities was still insufficient.

In recent years, a space-time substitution method was widely employed to predict some ecological processes, such as the effects of vegetation succession on soil organic carbon (Thomaz et al. 2012; Damgaard 2019). Inspired by this method, the aim of the current study was to predict the effects of reservoir impoundment on phytoplankton.
and shoreline vegetation communities using the space-time substitution method. In the current study, the Huangjinxia Reservoir under construction on the Han River was selected as the research object because the Han River is the main water source of the middle route of China’s South-to-North Water Diversion Project. In addition, there was a reservoir (Shiquan Reservoir) built 40 years ago that can be used as a reference which was located 40 km downstream of the Huangjinxia Reservoir.

**METHODOLOGY**

**Study area and sampling sites**

The Huangjinxia Reservoir under construction is located upstream of the Han River. As shown in Figure 1, a reservoir already in operation (Shiquan Reservoir) is located 40 km downstream of the Huangjinxia Reservoir. The average annual precipitation was 890 mm, and the perennially mean temperature was 14.6 °C in this area. The space-time substitution method could thus be carried out by comparing the water quality, phytoplankton community and shoreline vegetation community. Three sampling sites were set up upstream of each reservoir.

**Samples collection**

Sampling was carried out in September 2020 when the Shiquan Reservoir had filled. At each site, three samples in a cross-section were sampled and mixed. Surface water samples were collected 0.5 meter below the surface with a plexiglass water sampler (3 L). The mixed water samples (1 L) were stored in plastic bottles in car refrigerator for water quality analysis. In addition, another 1-L mixed water sample was fixed with 15 mL Lugol’s iodine solution for phytoplankton identification and counting. All samples were translated to the laboratory as quickly as possible.

**Water quality analysis and phytoplankton counting**

Water samples for water quality analysis were divided into two groups. One group was directly used for the total nitrogen (TN) and total phosphorus (TP) analysis. The other group was filtered through 0.45 μm cellulose membranes, and the filtrate was used for the analysis of the total dissolved nitrogen.
(TDN), total dissolved phosphorus (TDP), ammonia (NH₄⁺-N) and nitrate (NO₃⁻-N). Water quality analysis was measured using a spectrophotometer (UV-1780, Shimadzu, Japan) according to the methods described in the Examination of Water and Wastewater Protocols (Chinese EPA 2002).

After 48-h sedimentation, the supernatant of the water sample for phytoplankton counting was siphoned into a small-bore silicone bottle with a volume of 30 mL for phytoplankton genera identification (Eker et al. 2000) using an optical microscope (CX31, Olympus, Tokyo, Japan). Phytoplankton identification and counting were according to Hözel & Croome (1999).

Survey of shoreline vegetation

Three 1×1 m herb quadrates were investigated at each sampling site. The quadrats at each site were randomly selected, and the interval was larger than 10 m. The plant species in the quadrats were identified following the description of Van der Meijden (2005).

Data analysis

Data analysis was performed using SPSS version 20.0 (SPSS Inc., Chicago, IL, USA). The alpha diversity indexes of phytoplankton communities, including Richness index (H), Shannon–Wiener index (H'), Simpson's diversity index (D), Pielou’s evenness index (J) and Berger–Parker dominance index (D') were calculated using the following equations as follows, respectively:

\[
H = (S - 1)/\ln N \quad \text{(1)}
\]

\[
H' = -\sum_{i=1}^{S} P_i \ln P_i \quad \text{(2)}
\]

\[
D = 1 - \sum_{i=1}^{S} (P_i)^2 \quad \text{(3)}
\]

\[
J = H'/H_{\text{max}}, \quad H_{\text{max}} = \ln S \quad \text{(4)}
\]

\[
D' = N_{\text{max}}/N \quad \text{(5)}
\]

where \( S \) is the number of phytoplankton genera found at each sampling site; \( N \) is the total number of phytoplankton individuals found at each site; \( P_i = N_i/N \), with \( N_i \) as the number of phytoplankton individuals in the \( i \)th genus; and \( N_{\text{max}} \) is the number of phytoplankton individuals in the most abundant genus.

The relative dominance of plants is calculated using the following equation as follows:

\[
R = \frac{\sum N_iV_1}{T \cdot V_2} \quad \text{(6)}
\]

where \( R \) is the degree of relative dominance; \( N \) is the number of a scale’s occupying; \( V_1 \) is the value of the scale fields; \( T \) is the total number of fields of weed community cluster; and \( V_2 \) is the value of the highest scale.

RESULTS

Water quality

The average value of TN and TDN decreased slightly from the front of the Shiquan Reservoir to the end of it (Figure 2(a) and 2(b)). The space-time substitution method indicated that the average values of TP increased from 0.049 to 0.279 mg L⁻¹ after reservoir impoundment from H3 to S3 (Figure 2(c)). In addition, the average values of TDP decreased gradually from the Huangjinxia Reservoir to the Shiquan Reservoir (Figure 2(d)). Ammonia concentration decreased, but nitrate concentration increased in front of the Shiquan Reservoir to the end of it (Figure 2(e) and 2(f)).

Phytoplankton community composition

A total of six phyla and 51 genera of phytoplankton were identified in the current study. There were distinct differences in the composition of phytoplankton before and after reservoir impoundment (Figure 3). The percentage of Bacillariophyte biomass exceeded 95% before the reservoir impoundment. However, it was gradually decreased to 75% after the reservoir impoundment. Meanwhile, the biomass of Chlorophyta, Cryptophyta and Pyrrophyta increased significantly, accounting for 32, 20 and 13% of the total biomass, respectively, after reservoir impoundment.
Figure 2 | Water quality in the Huangjinxia Reservoir (H1–H3) under construction and the Shiquan Reservoir (S1–S3) in operation.
After the reservoir impoundment, the biomass of Pyrrophyta (accounted for 85.41%) in the area of 10 km around the reservoir was exceptionally high. The 10 most dominant genera were Melosira, Cymbella, Fragilaria, Achnanthes, Navicula, Cocconeis, Cryptomonas, Nitzschia, Euglena and Peridiniopsis (Figure 4). The dominant genera before reservoir impoundment (H1–H3) were Cymbella (53.8%), Melosira (12.8%) and Navicula (13.4%). However, Peridiniopsis, Cryptomonas, Euglena and Melosira became dominant genera after reservoir impoundment. The phytoplankton biodiversity of the Huangjinxia Reservoir was completely opposite to that of the Shiquan Reservoir (Figure 5). All the diversity indices showed a decreasing trend from H1 to H3 and an increasing trend from S1 to S3 (Figure 5(a)–5(e)), except for the Berger–Parker dominance index.

Shoreline vegetation community composition

Figure 6 shows that C. dactylon (65.3%), Polygonum hydropiper (51.7%) and Aster subulatus (50.3%) were the dominant shoreline vegetation before the reservoir impoundment, whereas after the reservoir impoundment, the dominant species shifted to Alternanthera philoxeroides (62.3%), Lobelia chinensis (55.7%) and C. dactylon (53.9%). In addition, the plant richness decreased gradually from the front of the Shiquan Reservoir to the end of it.

DISCUSSION

Our results showed that reservoir impoundment may increase the concentration of TP and NH₄⁺-N. On the contrary, the concentration of TN and TDP would be reduced after reservoir impoundment. Zhao et al. (2013) analyzed variation in water quality of the Three Gorges Reservoir from 2006 to 2011 and found that reservoir impoundment...
led to a dissolved oxygen (DO) depletion. Nitrification would be limited by lower DO concentration, and thus the concentration of ammonia increased and nitrate concentration decreased. Reservoir impoundment also slowed down water flow thereby promoting the growth of phytoplankton. The growing phytoplankton assimilate dissolved phosphorus and thus resulted in decreasing TDP. Phytoplankton often accumulated in the upper layers of water.
The accumulated phytoplankton biomass directly increased the measured TP concentration because of the high phosphorus content of phytoplankton.

In the current study, Bacillariophyta was dominated in the lotic natural river without reservoir. However, in the reservoir, Pyrrophyta and Cryptophyta were dominated. Although both phyla were considered to be mainly autotrophic, Grujcic et al. (2018) indicated that Cryptophyta was the major bacterivore in freshwater reservoir in summer. In addition, Pyrrophyta was also found to prey on planktonic ciliate (Setälä et al. 2005). Thus, it could be deduced that the dominance of both Pyrrophyta and Cryptophyta was resulted from abundant bacteria and ciliates in the reservoir (Thouvenot et al. 1999; Šimek et al. 2001). Our knowledge in this area was still very scarce and needed to be explored in future research.

The proportion of Chlorophyta in the reservoir area near the dam reached one-third of the total phytoplankton, but

| Figure 6 | Shoreline vegetation community in the Huangjinxia Reservoir (H1–H3) under construction and the Shiquan Reservoir (S1–S3) in operation: (a) H1, (b) H2, (c) H3, (d) S1, (e) S2, and (f) S3. |

| Relative dominance | (a) 0% 50% 100% | (b) 0% 50% 100% | (c) 0% 50% 100% |
|-------------------|-----------------|-----------------|-----------------|
| Artemisia sacrorum | Conyza bonariensis | Asplenium trichomanes |
| Aster subulatus    | Acalypa brachystachya | Portulaca oleracea |
| Cynodon dactylon  | Artemisia capillaris | Cyperus iria |
| Polygonum hydropiper | Erigeron annuus | Amananthus spinosus |
| Alternanthera philoxeroides | Polygonum hydropiper | Phyllanthus urinaria |
|                   | Duchesnea indica | Polygonum hydropiper |
|                   | Cynodon dactylon | Digitaria sanguinalis |
|                   | Setaria viridis | Homals scabens |
|                   | Veraraum nigrum | Cynodon dactylon |
|                   | Artemisia mongolica | Conyza canadensis |
|                   | Triarrhena sacchariflora | OxaIs corniculata |
|                   | Digitaria sanguinalis | Setaria viridis |
|                   | Equisetum hyemale | Cyperus rotundus |
|                   |                   | Echinochloa crusgalli |
|                   |                   | Asterol subulatus |
|                   |                   | Uspinaria ambrostioides |
|                   |                   | Alternanthera carvifolia |
|                   |                   | Adina pilifera |

| Relative dominance | (d) 0% 50% 100% | (e) 0% 50% 100% | (f) 0% 50% 100% |
|-------------------|-----------------|-----------------|-----------------|
| Cynodon dactylon  | Cynodon dactylon | Coreopsis basalis |
| Aster subulatus    | Aster subulatus | Polygonum bistorta |
| Phyllanthus urinaria | Phyllanthus urinaria | Bidens tripartita |
| Lobelia chinensis | Lobelia chinensis | Rorippa indica |
| Eclipta prostrata | Eclipta prostrata | Mazus japonicus |
| Alternanthera philoxeroides | Alternanthera philoxeroides | Polygonum hydropiper |
| Polygonum hydropiper | Polygonum hydropiper | Ranunculus japonicus |
|                   |                   | Bidens pilosa |
|                   |                   | Cyperus rotundus |
|                   |                   | Eclipta prostrata |
|                   |                   | Hedvolda diffusa |
|                   |                   | Cynodon dactylon |
|                   |                   | Cynodon dactylon |
|                   |                   | Alternanthera philoxeroides |
|                   |                   | Lobelia chinensis |
Bacillariophyta was dominated in the natural river without reservoir. Our investigation showed that TP concentration in the reservoir, which was slightly higher than the value in the upstream river, was not significant. In addition, the concentration of TN was reduced due to reservoir impoundment. Although Bacillariophyta was always found in oligotrophic conditions, Chlorophyta and cyanobacteria were abundant in eutrophic conditions. Nevertheless, nutrient concentration would not trigger the succession from Bacillariophyta to Chlorophyta because reservoir impoundment did not contribute to significant variation in nutrient levels. Rivers were usually considered as lotic ecosystems, which were in favor of Bacillariophyta. Reservoirs built lentic ecosystems in which cyanobacteria and Chlorophyta were always dominated (Joung et al. 2013; Xue et al. 2018). Thus, the succession from Bacillariophyta to Chlorophyta would be caused by the lower water flow after reservoir impoundment.

_Cymbella_ and _Navicula_ were the dominant genera in Bacillariophyta in the natural river without reservoir. However, the proportion of genera of _Melosira_ and _Nitzschia_, which were always dominated in rivers around the world (Lange & Rada 1993; Al-Saadi et al. 2000; Devercelli et al. 2014), was relatively low in this study area. Nevertheless, _Cymbella_ and _Navicula_ were always found in mountain ponds in the area (Chang et al. 2021). In addition, _Navicula_ was also a predominant genus in an artificial lake not far from our study area (Wei et al. 2020). Thus, the dominance of _Cymbella_ and _Navicula_ in the Han River in the current study would be governed by geographical factors, such as dispersal.

Compared with sites H1–H3, the proportion of _Euglena_, _Cryptomonas_ and _Peridiniopsis_ increased in sites S1–S3. _Peridiniopsis_ was a dominant genus in the Three Gorges Reservoir and some other reservoirs (Xu et al. 2010; Korneva et al. 2015; Zarei Darki & Krakhmalnyi 2019). A large proportion of Cryptomonas was also found in the Pa’ltang Reservoir, Korea in summer (Han et al. 2002). Tan et al. (2019) found that the growth of _Euglena_ was gradually inhibited with increasing flow velocity. The environmental factors controlling the growth of _Euglena_, _Cryptomonas_ and _Peridiniopsis_ were not clear so far. However, all these genera were phytoplankton with flagella moving initiative. Thus, abundant light and food may be the main factors affecting the accumulation of these phytoplankton.

Although reservoir impoundment slightly affected phytoplankton diversity, there were only some small fluctuations in the diversity index but there was no obvious downward trend. Li et al. (2012) indicated that phytoplankton diversity clearly decreased due to the high dilution effect caused by reservoir impoundment. Decreasing phytoplankton diversity caused by reservoir impoundment was also reported by Paulette et al. (2011). The different results found in our study were most likely due to lower nutrient levels and relatively abundant water in the study area. However, the shoreline plant diversity decreased obviously due to reservoir impoundment. Su et al. (2015) also found that the total number of plant species decreased obviously with the increase of the years after the Three Gorges Reservoir impoundment. Nilsson & Keddy (1988) indicated that the water level was the main factor controlling shoreline vegetation richness and species community. Thus, the decreasing plant diversity was due to the simplification of the habitat caused by the increasing water level, which led to the direct extinction of some terrestrial plants.

Our results also showed that the upland plants were almost extinct. However, _A. philoxeroides_, _C. dactylon_ and _L. chinensis_ were dominated in the shoreline in the Shiquan Reservoir. This result was similar to the Three Gorges Reservoir (Ye et al. 2013). Similarly, _C. dactylon_ and _Abutilon theophrasti_ were the dominant species in the shoreline of the Danjiangkou Reservoir, which was built in the middle and lower reaches of the Han River (Liu et al. 2014). Thus, _A. philoxeroides_, _C. dactylon_ and _L. chinensis_ would be the plants suitable for living in the shoreline of reservoirs in this area.

**CONCLUSION**

Our results showed that Bacillariophyta was dominated in the lotic natural river without reservoir. However, in the reservoir, Pyrophyta and Cryptophyta were dominated. The proportion of Chlorophyta in the reservoir area near the dam reached one-third of the total phytoplankton, but Bacillariophyta was dominated in the natural river without reservoir. The succession from Bacillariophyta to Chlorophyta would be caused by the lower water flow after reservoir impoundment. _A. philoxeroides_ (65.5%),
C. dactylon (51.7%) and L. chinensis (50.3%) were the dominant shoreline vegetation before the reservoir impoundment, whereas after the reservoir impoundment, the dominant species shifted to B. tripartite, C. dactylon and L. chinensis. Our results suggested that the percentage of bloom-forming phytoplankton would gradually increase after the reservoir impoundment. In addition, A. philoxeroids, C. dactylon and L. chinensis would be the plants suitable for living in the shoreline of reservoirs in this area.

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DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

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