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Response Characteristics of Phytoplankton Communities in Plateau Shallow Lakes to Enclosure-Based Ecological Restoration

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Abstract: *In this study, an in situ ecological restoration experiment was conducted using methods such as enclosure wave suppression, sediment exposure, and plant cultivation to investigate the effects of different restoration strategies on water quality, submerged plants, and phytoplankton communities. The results indicated that combining plant cultivation with enclosure wave suppression effectively restored the submerged plant. Wave suppression alone supported natural plant recovery but with significantly lower coverage and biomass than artificial planting. Water quality improvement was most notable in the closed enclosure + sediment exposure + plant cultivation (closed enclosure + sediment exposure restoration experiment, CS) group compared to the permeable enclosure + plant cultivation (open enclosure restoration experiment, OE) and closed enclosure wave suppression (closed enclosure restoration experiment, CE) groups. The OE group exhibited the highest phytoplankton species richness (204 species), followed by the CS (187 species) and CE groups (170 species). However, the phytoplankton cell density was highest in the CE group (0.75–6.61×10^6 cells/L), moderate in the OE group (0.26–1.96×10^6 cells/L), and lowest in the CS group (0.08–0.47×10^6 cells/L), highlighting the superior water ecological improvement achieved by the CS measures. Non-metric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) identified distinct algal community structures across restoration strategies, with the OE group displaying the highest variability. Redundancy analysis (RDA) revealed that the phytoplankton communities in the CE group were influenced by water temperature (WT), ammonium nitrogen (NH^+_4-N), nitrate nitrogen (NO^-_3-N), and dissolved oxygen (DO), whereas those in the OE group were mainly affected by WT and NO^-_3-N. In the CS group, the key factors included WT, chemical oxygen demand (COD_{Mn}), NH^+_4-N, and pH. This study highlights the ecological benefits of different restoration measures and could provide valuable insights into lake ecological restoration.*

Keywords: *Phytoplankton; Water ecological restoration; Enclosure wave suppression; Submerged plants*

1. Introduction

Eutrophication is a critical environmental issue affecting aquatic ecosystems globally [1,2] and is recognized as a primary concern for lakes worldwide by restoration practitioners [3]. Since 1990, water quality in Africa, Asia, and Latin America has declined significantly, with over 75% of closed water bodies, such as lakes, ponds, and reservoirs, experiencing some degree of eutrophication [4]. This process elevates nutrient concentrations, causing adverse effects such as algal blooms, aquatic vegetation decline, and fish mortality, ultimately causing ecosystem degradation or collapse [5–8]. Beyond ecological health and biodiversity losses, eutrophication poses serious challenges to water supply security, fishery production, and tourism.

Submerged plants are essential for maintaining water clarity in shallow lakes by providing structural habitats and food for aquatic animals, competing with algae for light and nutrients, reducing the sediment resuspension, and enhancing the oxidation of fertile sediments [5,9,10]. Their restoration is widely regarded as a critical measure for controlling eutrophication and has garnered significant attention. However, their survival and recovery are hindered by challenges such as pollutant toxicity, insufficient light penetration in turbid waters, difficulty in rooting within soft sediments, and physical damage caused by waves and

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aquatic herbivores [11–17]. Strategies such as water level regulation, dredging, transplantation, and biomanipulation have been employed to promote their recovery, whereas the effectiveness of these methods depends on factors such as the experimental duration and size of the water body [11,18–23].

The restoration of submerged plants can profoundly affect the structure and function of phytoplankton communities [24]. Following the recovery of submerged plants, changes are often observed in the species composition, biomass, and diversity of phytoplankton communities [25]. Submerged plants can inhibit the growth of phytoplankton by reducing suspended solids, nutrient concentrations, and increasing water transparency [26]. They can also directly suppress specific phytoplankton species through the release of allelopathic substances [27]. Studies have suggested that submerged plant restoration can reduce phytoplankton biomass and chlorophyll-a concentrations, along with increased zooplankton density and biomass, reflecting a top-down control effect on phytoplankton communities [28]. However, phytoplankton responses vary across lakes and restoration strategies, highlighting the need for further investigation into the underlying ecological mechanisms.

Caohai Lake in Guizhou, China, is a typical plateau wetland ecosystem that serves as a critical wintering habitat for rare waterbirds, including black-necked cranes. The health of aquatic ecosystems directly affects the habitats of these species. Despite significant governmental efforts to protect the lake, a large-scale decline in submerged vegetation was observed in some areas beginning in July 2020. By 2021, submerged vegetation had nearly entirely disappeared [29]. To address this, enclosure-based restoration was attempted. This study conducted three in situ enclosure restoration experiments in Caohai Lake to assess phytoplankton species and density, analyze the response characteristics of phytoplankton communities to different restoration measures, and identify the key factors driving these changes.

2. Materials and methods

2.1. Study area and sampling points

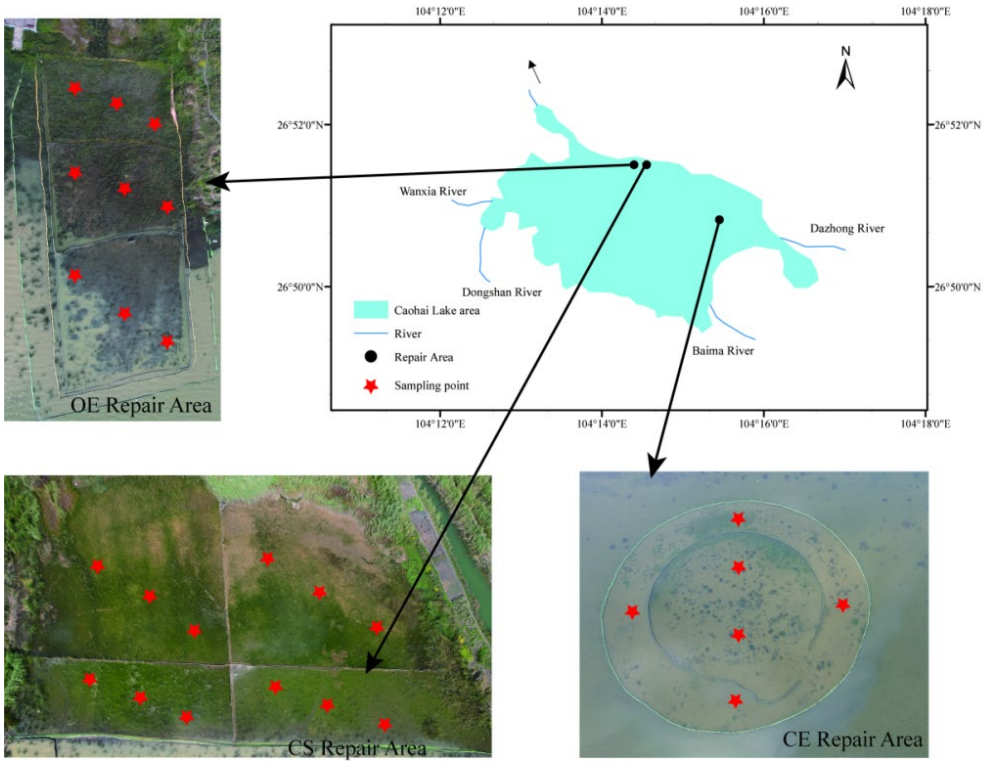

Figure 1: Schematic diagram of the restoration groups and sampling points.

To identify effective water ecological restoration methods for areas with strong waves and high sediment organic matter content, three in situ enclosure-based ecological restoration experiments were conducted in the northern part of Caohai Lake (Figure 1). These experiments included (1) a closed enclosure restoration experiment (CE), characterized by minimal water exchange between the enclosure and the surrounding lake,with an average depth of 0.43 m; (2) an open enclosure restoration experiment (OE), allowing strong water flow between the enclosure and the lake,with an average depth of 0.30 m;

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and (3) a closed enclosure + sediment exposure(From May 2023 to July 2023, due to water level regulation, the water volume in Caohai rapidly decreased, resulting in the exposure of anhydrous sediments in the experimental area. By August 2023, the water level began to rise again.) restoration experiment (CS), involving reduced water exchange, lowered water level, and two months of natural sediment exposure, with an average depth of 0.26 m. Each enclosure covered an area of approximately 6666.7 m2. Grass carp (Ctenopharyngodon idella), common carp (Cyprinus carpio), and crucian carp (Carassius auratus) were removed from the enclosures, and submerged plants, including Vallisneria natans, Potamogeton wrightii, and Myriophyllum spicatum, were planted.

Environmental variables and phytoplankton were monitored from August 2023 to January 2024, while submerged plants were surveyed monthly from August to October 2023. The first experiment started on August 5, 2023, once a month, and ended on January 19, 2024. Among the three restoration groups (Figure 1), the CE group was divided into two areas, each containing one submerged plant survey point and three water quality and phytoplankton sampling points, for a total of six sampling points. The OE group was divided into three areas, each containing one submerged plant survey point and three water quality and phytoplankton sampling points. The CS group was divided into four areas with one submerged plant survey point and three water quality and phytoplankton sampling points in each area.

2.2. Sample collection and analysis

2.2.1. Water quality

From August 2023 to January 2024, a portable water quality analyzer (HQ30d, Hach, Loveland, CO, USA) was used to measure overlying water parameters, including temperature (WT), pH, and dissolved oxygen (DO). Water transparency (SD) was assessed using a Secchi disk. At each sampling point, 1 L of overlying water was collected at a depth of 0.2 m to analyze total nitrogen (TN), total phosphorus (TP), ammonium nitrogen (NH^+_4-N), nitrate nitrogen (NO^-_3-N), chemical oxygen demand (CODMn), and chlorophyll-a (Chl a). These parameters were analyzed in accordance with Standard Methods for the Examination of Water and Wastewater [30].

2.2.2. Phytoplankton collection, identification, and enumeration

Phytoplankton samples were collected for qualitative and quantitative analyses. The qualitative samples were obtained using a No. 25 plankton net , towed slowly in a figure-eight motion at the depth of 0.2 m for 8 min. The samples were then concentrated and preserved in 1-2 mL formaldehyde solution. For quantitative analysis, collect 1L of overlying water, let it stand for 48 hours, and use a siphon to remove the supernatant. Transfer the remaining 20-50 ml into a 50 ml volumetric flask. Fix the concentrate with 10-15 mL of Lugo iodine solution[31]. Phytoplankton identification was conducted using Freshwater Algae in China: Systematics, Taxonomy and Ecology [32], Use a 0.1 mL plankton counting box to count under a 40 × objective lens. Observe rows 2, 5, and 8 of the phytoplankton counting box one by one, with a total of 30 small squares. Classify and count all phytoplankton cells in each small square, and record the classification counting results of each small square. Count twice for each sample.

2.2.3. Submerged plant survey

At each sampling point, three to five quadrats (1 × 1 m) were established. Submerged plants were collected using a custom underwater sickle (25 cm × 25 cm). The species were identified visually, and the submerged plant coverage (SPC%) was calculated using Equation (1) [33]. Measure submerged plant biomass (SPB, g/m^2) and fresh weight by washing, draining, and weighing collected plants.

$$\mathrm{SPC}(\%) = \frac{\text{Total area covered by submerged plants in the quadrat}}{\text{Total quadrat area}} \times 100\% \quad (1)$$

2.3. Data processing and analysis

2.3.1. Phytoplankton index calculation formulas

Phytoplankton density, Shannon-Wiener diversity index (H'), Pielou's evenness index (J), and species dominance (y) were calculated using their respective formulas [34–36].

$$H' = -\sum_{i=1}^{S} \left(\frac{ni}{N}\right) \log_2 \left(\frac{ni}{N}\right) \quad (2)$$

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

$$y = Pi \times fi, Pi = ni / N \tag{4}$$

where ni represents the number of individuals of a single species, N represents the total number of individuals in all samples, S represents the total number of phytoplankton species in the sample, fi represents the frequency of the i-th phytoplankton species, and Pi represents the percentage of the i-th phytoplankton species in the total individual count. Species were considered dominant if $y \geq 0.02$.

2.3.2. Statistical analysis

The data processing and visualization were performed using Origin 2022, Canon 5, and R (version 4.4.1). The R package vegan (version 2.4.3) was used for non-metric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) to analyze phytoplankton community structures under the three restoration strategies. Redundancy analysis (RDA) was conducted using Canon 5, and Monte Carlo permutation tests were applied to evaluate the significance of environmental factors.

To enhance data uniformity and normality, phytoplankton density, submerged plant biomass, and environmental factors (excluding pH) were subjected to Hellinger and log transformations (log(x+1)). For the network analysis, Spearman correlation coefficients (ρ) > 0.6 and p-values < 0.01 were used as thresholds[37]. The network visualization was conducted using Gephi (version 0.10.1)..

3. Results and analysis

3.1. Physicochemical characteristics of water

Table 1 summarizes the physicochemical characteristics of water under different restoration measures. During the investigation, the pH and DO levels in all three restoration groups followed similar trends: pH initially increased and then decreased, whereas the DO levels increased, decreased, and increased again, exhibiting an overall increasing trend. Except for WT, significant variations in physicochemical characteristics were observed among the three restoration strategies and across different months. Notably, the CS restoration group significantly reduced nutrient indicators after restoration, while TN and NH^+_4-N increased, and TP and NO^-_3-N decreased in the other two groups. These findings indicated that the CS restoration strategy substantially improved water quality(Figure 2).

Table 1:Physicochemical characteristics of water under different restoration strategies.

Water quality parameter	Sample plot	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.
WT (℃)	CE^A	22.42 ± 0.77^a	19.91 ± 0.12^b	14.27 ± 0.23^c	15.83 ± 0.28^d	6.31 ± 0.17^e	6.60 ± 0.08^e
	OE^A	26.45 ± 0.82^a	25.00 ± 0.77^b	18.21 ± 0.63^c	14.70 ± 0.73^d	5.55 ± 0.20^f	6.51 ± 0.21^e
	CS^A	26.70 ± 0.66^a	23.96 ± 0.54^b	18.25 ± 0.36^c	15.73 ± 0.31^d	5.40 ± 0.11^f	6.33 ± 0.13^e
TN (mg/L)	CE^A	2.66 ± 0.12^a	1.95 ± 0.08^c	1.87 ± 0.03^c	1.89 ± 0.07^c	2.38 ± 0.12^b	2.59 ± 0.06^a
	OE^B	1.02 ± 0.05^b	1.32 ± 0.09^a	1.33 ± 0.25^a	1.29 ± 0.18^a	0.99 ± 0.06^b	1.33 ± 0.17^a
	CS^B	0.82 ± 0.09^e	0.98 ± 0.09^d	1.26 ± 0.10^b	1.11 ± 0.04^c	1.79 ± 0.07^a	$1.17\pm0.04b^c$
TP (mg/L)	CE^A	0.06 ± 0.01^a	0.04 ± 0.01^b	0.04 ± 0.00^b	0.04 ± 0.01^b	0.02 ± 0.00^c	0.02 ± 0.00^c
	OE^B	0.03 ± 0.00^{ab}	0.04 ± 0.00^a	0.04 ± 0.01^a	0.03 ± 0.01^{ab}	0.02 ± 0.01^b	0.03 ± 0.01^b
	CS^C	0.03 ± 0.01^a	0.03 ± 0.01^{ab}	0.03 ± 0.00^b	0.02 ± 0.00^b	0.02 ± 0.00^b	0.03 ± 0.01^{ab}
DO (mg/L)	CE^B	5.83 ± 0.30^d	7.63 ± 0.25^b	7.02 ± 0.17^c	7.24 ± 0.11^c	8.47 ± 0.09^a	8.29 ± 0.08^a
	OE^{AB}	7.26 ± 0.48^c	8.11 ± 0.44^b	6.56 ± 0.33^d	7.30 ± 0.25^c	7.30 ± 0.25^c	8.67 ± 0.30^a
	CS^A	8.08 ± 0.86^b	8.98 ± 0.54^a	6.52 ± 0.16^d	7.66 ± 0.27^{bc}	7.41 ± 0.28^c	8.68 ± 0.33^a
COD_{Mn} (mg/L)	CE^A	7.06 ± 0.36^c	7.35 ± 0.18^{bc}	7.81 ± 0.18^{ab}	7.35 ± 0.21^{bc}	7.61 ± 0.27^{ab}	7.83 ± 0.28^a
	OE^B	5.18 ± 0.24^c	6.50 ± 0.22^b	6.70 ± 0.45^b	6.73 ± 0.35^b	8.41 ± 1.07^a	6.47 ± 1.39^b
	CS^B	4.64 ± 0.15^d	6.86 ± 0.17^c	6.90 ± 0.32^c	7.01 ± 0.16^c	7.81 ± 0.40^b	8.28 ± 0.41^a
NH_4^+-N	CE^A	2.15 ± 0.17^a	0.99 ± 0.07^d	0.98 ± 0.04^d	1.09 ± 0.02^d	1.58 ± 0.05^c	1.96 ± 0.04^b

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(mg/L)	OE^{B}	0.29 ± 0.06^{c}	0.52 ± 0.05^{b}	0.81 ± 0.04^{a}	0.53 ± 0.02^{b}	0.49 ± 0.09^{b}	0.77 ± 0.23^{a}
	CS^{B}	0.36 ± 0.05^{e}	0.42 ± 0.04^{d}	0.56 ± 0.04^{c}	0.42 ± 0.03^{d}	1.34 ± 0.04^{a}	0.69 ± 0.03^{b}
pH	CE^{C}	7.94 ± 0.13^{c}	8.13 ± 0.08^{b}	8.33 ± 0.08^{a}	8.24 ± 0.14^{ab}	7.87 ± 0.05^{c}	7.78 ± 0.08^{c}
	OE^{B}	8.16 ± 0.37^{bc}	9.01 ± 0.30^{a}	8.56 ± 0.42^{ab}	8.16 ± 0.25^{bc}	7.92 ± 0.29^{c}	7.96 ± 0.24^{c}
	CS^{A}	8.25 ± 0.17^{c}	8.99 ± 0.46^{a}	8.83 ± 0.25^{ab}	8.96 ± 0.22^{ab}	8.64 ± 0.23^{b}	7.95 ± 0.18^{c}
NO_3^--N (mg/L)	CE^{A}	0.19 ± 0.03^{c}	0.26 ± 0.07^{b}	0.18 ± 0.02^{c}	0.39 ± 0.02^{a}	0.33 ± 0.05^{a}	0.33 ± 0.02^{a}
	OE^{B}	0.30 ± 0.08^{ab}	0.12 ± 0.08^{c}	0.10 ± 0.01^{c}	0.23 ± 0.03^{b}	0.22 ± 0.03^{b}	0.33 ± 0.07^{a}
	CS^{B}	0.11 ± 0.04^{d}	0.18 ± 0.06^{bc}	0.14 ± 0.04^{cd}	0.23 ± 0.02^{a}	0.22 ± 0.02^{ab}	0.24 ± 0.01^{a}

Note: Lowercase letters indicate ANOVA differences between months. Uppercase letters indicate ANOVA differences among the three restoration strategies. CE: Closed enclosure restoration experiment; OE: Open enclosure restoration experiment; CS: Closed enclosure + sediment exposure restoration experiment.

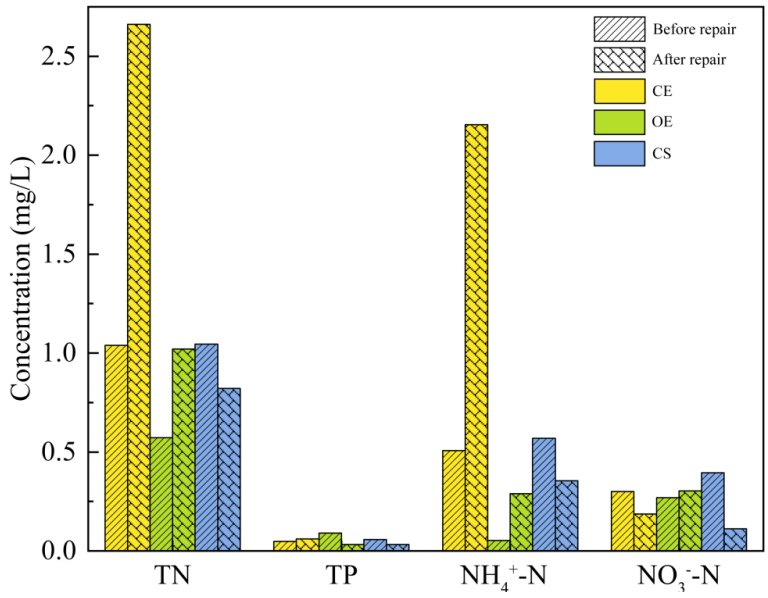

Figure 2: Changes in TN, TP, NH_4^+-N,NO_3^--N in water quality before and after

3.2. Submerged vegetation coverage and biomass

Artificial planting effectively restored aquatic vegetation in the OE and CS groups, achieving vegetation coverage exceeding 95% (Figure 3). In contrast, the CE group, which lacked artificial planting, had the lowest biomass and coverage of aquatic vegetation.

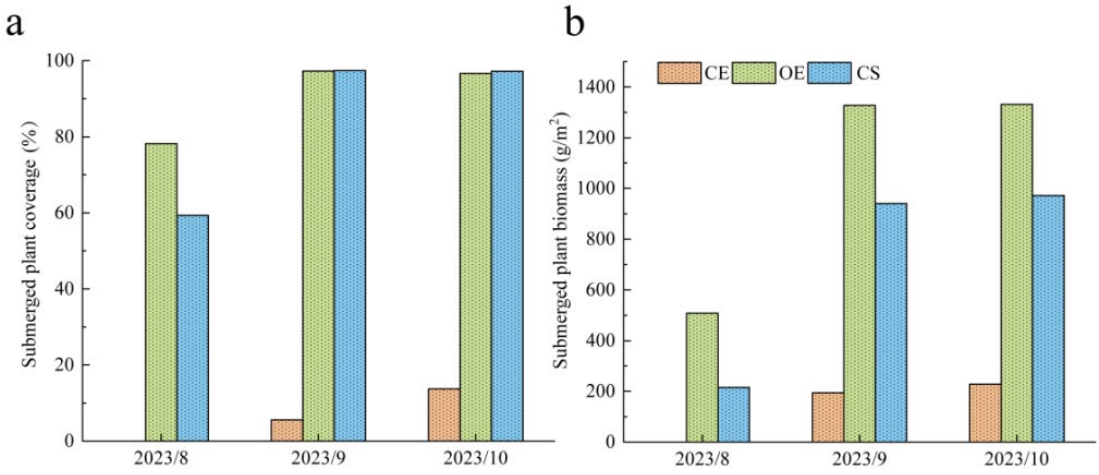

Figure 3: Monthly changes in submerged vegetation coverage and biomass. (a) Submerged vegetation coverage; (b) submerged vegetation biomass.

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3.3. Phytoplankton species composition

During the survey, 170 phytoplankton species were identified in the CE restoration group, including Cyanophyta (12 species, 7.06%), Bacillariophyta (62 species, 36.47%), and Chlorophyta (82 species, 48.24%). In the OE and CS groups, 204 species were identified, including Cyanophyta (25 species; 12.25%), Bacillariophyta (66 species; 32.35%), and Chlorophyta (87 species; 42.65%). As shown in Figure 3, the relative abundances of other phyla in all three enclosures followed the order: Euglenophyta > Pyrrophyta > Chrysophyta > Cryptophyta (Figure 4).

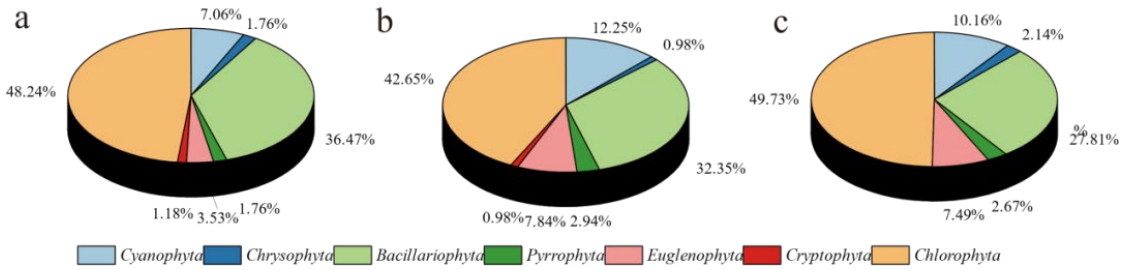

Figure 4:Composition of phytoplankton species. (a) CE restoration group; (b) OE restoration group; (c) CS restoration group.

3.4. Phytoplankton ecological characteristics

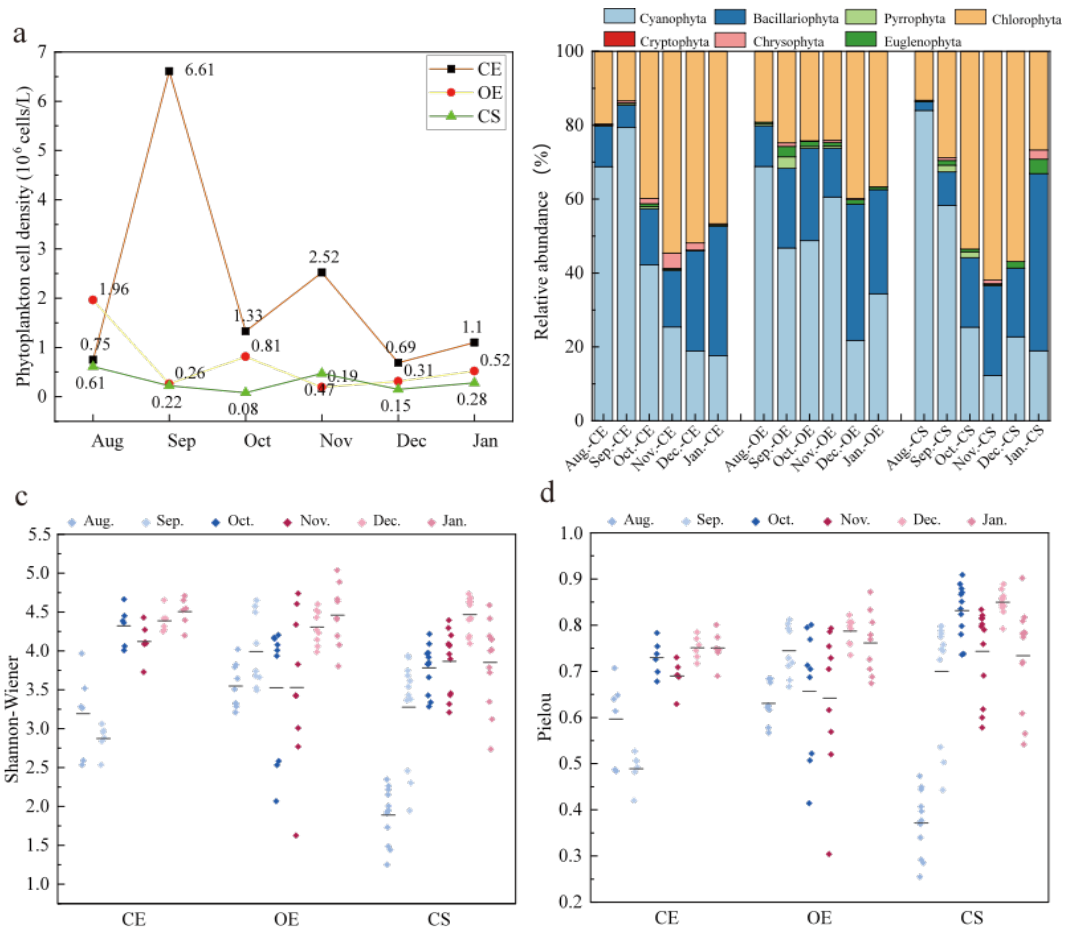

Figure 5: (a) Phytoplankton density, (b) relative abundance and chlorophyll a, (c) Shannon-Wiener index, and (d) Pielou index.

As shown in Figure 5a, phytoplankton density in the CE restoration group peaked in September and dropped to its lowest in November, following an initial increase and subsequent fluctuating decline, ranging from 0.75 to 6.61 × 10^6 cells/L. In the OE group, the density was lowest in October and highest in August, presenting an overall trend of initial decline followed by a gradual increase, ranging from 0.26

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to 1.96×10^6 cells/L. In the CS group, the density was lowest in October and peaked in August, displaying a trend of decline, increase, and then decline, with a range of 0.08 to 0.47×10^6 cells/L. The relative phytoplankton composition in all three groups was dominated by Cyanophyta, Bacillariophyta, and Chlorophyta (Figure 5b). The CE group exhibited the highest overall phytoplankton density, whereas the CS group exhibited the lowest density. Cyanophyta maintained dominance throughout the study period, with higher relative abundance in August and September, whereas Chlorophyta and Bacillariophyta were more prevalent in other months. The Shannon-Wiener and Pielou indices for phytoplankton communities (Figures 5c and 5d) were lower in the CE and OE groups but higher in the CS group. The low algal density combined with the high diversity in the CS group suggested healthier water quality, indicating that sediment exposure effectively supported the restoration efforts.

The numbers of dominant species in the CE, OE, and CS groups were 20, 26, and 22, respectively (Table 2). The shared dominant species included *Merismopedia punctata*, *Merismopedia tenuissima*, *Gomphosphaeria aponina*, *Melosira granulata*, *Synedra acus,* and *Scenedesmus quadricauda*. The OE group exhibited the highest diversity of dominant species, which may contribute to the development of a stable community structure.

The average Chl a content was the highest in the CE group (5.53 μg/L), followed by the OE group (4.55 μg/L) and the CS group (4.12 μg/L). Significant monthly variations in Chl a were observed in the CE and CS groups, with the CE group showing significantly higher Chl a levels in September ($P < 0.05$) and the CS group peaking in December ($P < 0.05$) (Figure 6).

Table 2:Dominant genera in the three restoration methods.

Type	Month	Dominant species
CE	Aug.	*Merismopedia punctata*, *Merismopedia tenuissima*, *Gomphosphaeria aponina*, *Oscillatoria subtillissima*, *Melosira granulata*, *Nitzschia acicularis*, *Monactinus simplex* (Meyen) Corda, and *Scenedesmus quadricauda*
	Sep.	*Merismopedia punctata*, *Merismopedia tenuissima*, *Microcystis wesenbergii*, *Microcystis aeruginosa*, *Synedra acus*, and *Scenedesmus quadricauda*
	Oct.	*Merismopedia punctata*, *Merismopedia tenuissima*, *Gomphosphaeria aponina*, *Melosira granulata*, *Synedra acus*, *Dictyosphaeria cavernosa*, *Monactinus simplex* (Meyen) Corda, and *Scenedesmus quadricauda*
	Nov.	*Merismopedia punctata*, *Oscillatoria subtillissima*, *Kephyrion* sp, *Melosira granulata*, *Stephanocyclus meneghinianus* (Kützing) Kulikovskiy, Genkal & Kociolek, *Scenedesmus quadricauda*, *Desmodesmus perforatus* (Lemmermann) E.Hegewald, *Desmodesmus spinosus* (Chodat) E.Hegewald, and *Tetradesmus lagerheimii* M.J.Wynne & Guiry
	Dec.	*Merismopedia punctata*, *Gomphosphaeria aponina*, *Melosira granulata*, *Synedra acus*, *Craticula simplex* (Krasske) Levkov, *Pediastrum duplex*, *Scenedesmus quadricauda*, and *Desmodesmus perforatus* (Lemmermann) E.Hegewald
	Jan.	*Merismopedia punctata*, *Gomphosphaeria aponina*, *Oscillatoria subtillissima*, *Melosira granulata*, *Synedra acus*, *Pediastrum duplex*, *Scenedesmus quadricauda*, and *Desmodesmus perforatus* (Lemmermann) E.Hegewald
OE	Aug.	*Merismopedia punctata*, *Merismopedia tenuissima*, *Aphanocapsa delicatissima*, *Gomphosphaeria aponina*, *Melosira granulata*, *Synedra acus*, *Dictyosphaeria cavernosa*, and *Scenedesmus quadricauda*
	Sep.	*Merismopedia punctata*, *Merismopedia elegans*, *Pseudanabaena mucicola*, *Synedra acus*, *Craticula simplex* (Krasske) Levkov, *Navicula radiosa*, *Scenedesmus quadricauda*, and *Ulothrix tenerrima*
	Oct.	*Merismopedia punctata*, *Microcystis pseudofilamentosa*, *Microcystis flos-aquae*, *Synedra acus*, *Ulnaria ulna* (Nitzsch) Compère, *Craticula simplex* (Krasske) Levkov, *Nitzschia sublinearis*, and *Eudorina elegans*
	Nov.	*Merismopedia punctata*, *Aphanocapsa delicatissima*, *Microcystis aeruginosa*, *Oscillatoria subtillissima*, *Synedra acus*, *Scenedesmus quadricauda*, and *Mougeotia* sp.
	Dec.	*Merismopedia punctata*, *Microcystis wesenbergii*, *Oscillatoria princeps*, *Melosira granulata*, *Synedra acus*, *Craticula simplex* (Krasske) Levkov, *Gogorevia exilis* (Kützing) Kulikovskiy & Kociolek,

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		Pediastrum duplex, and *Scenedesmus quadricauda*
	Jan.	*Merismopedia punctata*, *Gomphosphaeria aponina*, *Microcystis aeruginosa*, *Synedra acus*, *Nitzschia palea*, and *Scenedesmus quadricauda*
CS	Aug.	*Merismopedia punctata*, *Merismopedia tenuissima*, *Gomphosphaeria aponina*, *Tetrachlorella alternans*, and *Scenedesmus quadricauda*
	Sep.	*Merismopedia punctata*, *Merismopedia elegans*, *Chroococcus minutus*, *Melosira granulata*, *Pediastrum duplex*, and *Ulothrix tenerrima*
	Oct.	*Merismopedia punctata*, *Melosira granulate*, *Eudorina elegans*, *Tetraedron minimum*, *Scenedesmus quadricauda*, *Scenedesmus perforates*, and *Spirogyra longata*
	Nov.	*Merismopedia punctata*, *Fragilaria crotonensis*, *Epithemia gibba* (Ehrenberg) Kützing, *Scenedesmus quadricauda*, *Spirogyra* sp., and *Mougeotia* sp.
	Dec.	*Merismopedia punctata*, *Gomphosphaeria aponina*, *Melosira granulata*, *Gogorevia exilis* (Kützing) Kulikovskiy & Kociolek, *Pandorina morum*, *Pediastrum duplex*, *Scenedesmus quadricauda*, *Desmodesmus spinosus* (Chodat) E.Hegewald, and *Mougeotia* sp.
	Jan.	*Merismopedia punctata*, *Gomphosphaeria aponina*, *Melosira granulata*, *Synedra acus*, *Scenedesmus quadricauda*

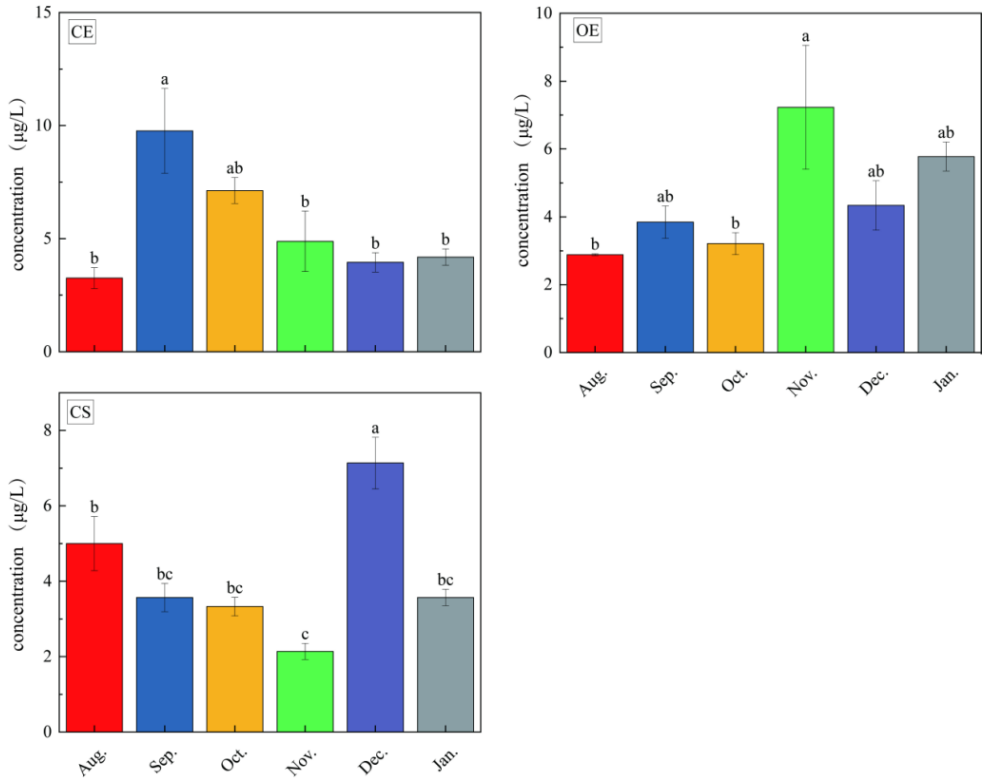

Figure 6:Significance analysis of chlorophyll in each month.

3.5. Differences in phytoplankton community structure and their relationship with environmental factors

3.5.1. NMDS and ANOSIM analysis

NMDS analysis based on Bray-Curtis distances was conducted for phytoplankton communities in the three enclosures (Figure 7a). A stress value of 0.171 indicated a good model fit. Among the groups, the confidence ellipses for the OE and CS restoration groups demonstrated minimal overlap, whereas the CE group was distinctly separated from the others, indicating that the community structure of the CE group differed from those of the OE and CS groups. Further analysis using ANOSIM (Figure 7b) revealed a dissimilarity coefficient (R) of 0.218 and structural differences (P = 0.001), suggesting that inter-group differences were greater than intra-group differences. This confirmed that phytoplankton community composition and structure varied among the three restoration groups.

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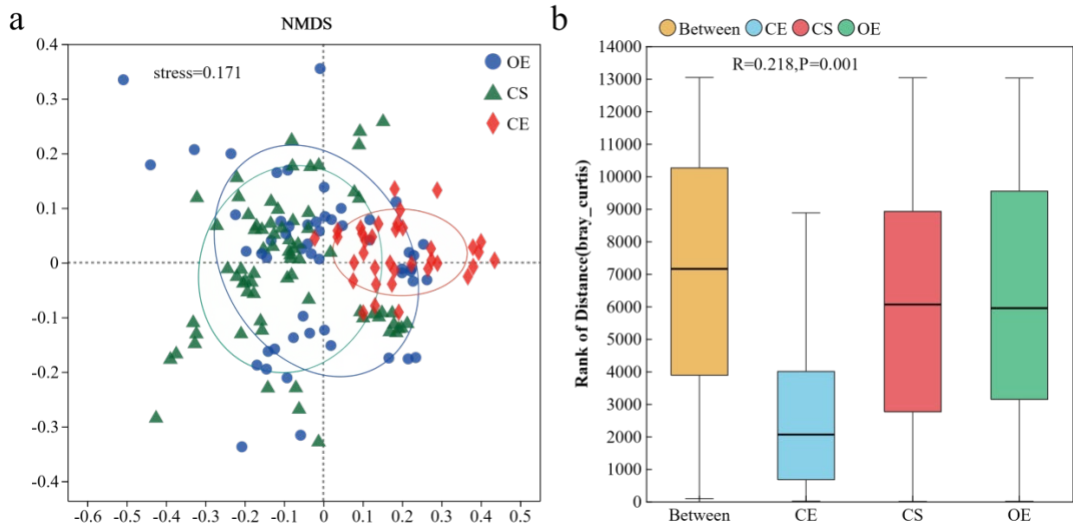

Figure 7: NMDS and ANOSIM analyses of phytoplankton community structure.

3.5.2. Redundancy analysis (RDA)

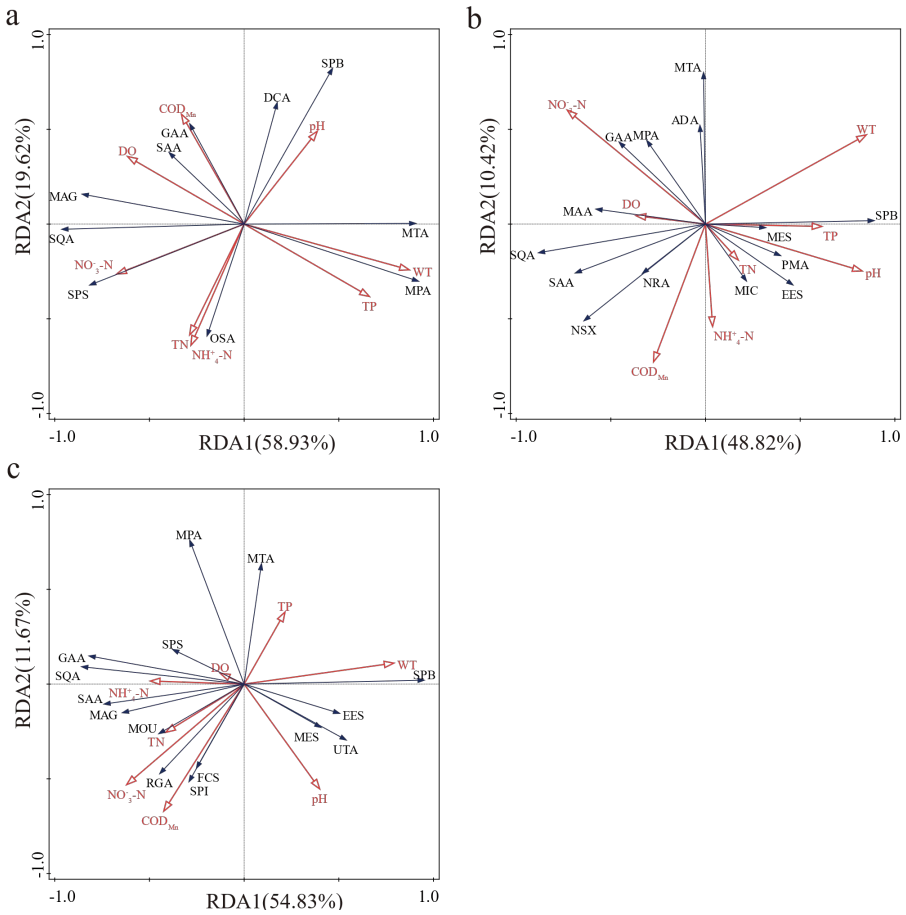

Figure 8: RDA of phytoplankton and environmental factors. (a) CE restoration group; (b) OE restoration group; (c) CS restoration group. Abbreviations: MPA, Merismopedia punctata; MTA, Merismopedia tenuissima; MES, Merismopedia elegans; AD, Aphanocapsa delicatissima; GAA, Gomphosphaeria aponina; MAA, Microcystis aeruginosa; MIC, Microcystis pseudofilamentosa; PMA, Pseudanabaena mucicola; OSA, Oscillatoria subtillissima; MAG, Melosira granulata; SAA, Synedra acus; FCS, Fragilaria crotonensis; NSX, Craticula simplex (Krasske) Levkov; NRA, Navicula radiosa; RGA, Epithemia gibba (Ehrenberg) Kützing; EES, Eudorina elegans; DCA, Dictyosphaeria cavernosa; SQA, Scenedesmus quadricauda; SPS, Scenedesmus perforates; UTA, Ulothrix tenerrima; MOU, Mougeotia sp.SPI, Spirogyra sp.SPB, submerged plant biomass.

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RDA was conducted to examine the densities of the dominant species (Y ≥ 0.04) and submerged macrophyte biomass (SPB) in relation to the environmental factors across the three restoration groups (Figure 8). In the CE zone, WT, NO^-_3-N, and DO were significantly correlated with both the phytoplankton and submerged macrophytes. The absolute dominant species *M. punctata* and *M. tenuissima* , along with SPB, were positively correlated with WT but negatively correlated with NH^+_4-N and NO^-_3-N *S. quadricauda* and *M. granulate* were positively correlated with NH^+_4-N, while *S. quadricauda*, *M. granulate*, *S. acus* , and *G. aponina* were positively correlated with NO^-_3-N. In the OE zone, WT and NO^-_3-N were the primary explanatory variables, accounting for 37.6% and 17.5% (Table 3) of variance, respectively *M. tenuissima* and SPB were positively correlated with WT, whereas *M. punctata* was negatively correlated with WT and positively correlated with NO^-_3-N. In the CS zone, the key explanatory variables were WT (37%), COD_{Mn} (14.2%), and NH^+_4-N (12.2%), along with pH *M. tenuissima* was positively correlated with these variables, whereas *G. aponina*, *S. quadricauda*, *S. acus*, and *M. granulate* were negatively correlated. *M. punctata* exhibited negative correlations with WT, COD_{Mn}, and pH but a positive correlation with NH^+_4-N.

Table 3:Results of forward selection of environmental factors in RDA based on phytoplankton community variation and submerged plant biomass.

	Environmental factors	Explanation (%)	Contribution (%)	pseudo-F	*P*
CE restoration group	WT	46.5	51.7	8.7	0.002
	NO_3^--N	13.4	14.9	3.9	0.02
	NH_4^+-N	12.2	13.5	2.7	0.046
	DO	10	11.1	3.9	0.008
	TP	2.7	3	1.1	0.426
	COD_{Mn}	2	2.2	0.8	0.65
	pH	2.1	2.3	0.7	0.56
	TN	1.1	1.3	0.3	0.824
OE restoration group	WT	37.6	54.6	9.6	0.002
	NO_3^--N	17.5	25.4	5.8	0.006
	TN	2.7	3.9	0.9	0.486
	NH_4^+-N	3.1	4.4	1	0.404
	pH	2.4	3.5	0.8	0.484
	DO	2.2	3.2	0.7	0.628
	COD_{Mn}	1.9	2.8	0.6	0.634
	TP	1.5	2.2	0.4	0.83

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CS restoration group	WT	37	45.2	12.9	0.002
	COD_{Mn}	14.2	17.3	6.1	0.006
	NH_4^+-N	12.2	14.8	6.6	0.002
	pH	9.4	11.5	6.5	0.002
	TN	3.2	3.9	2.4	0.068
	DO	2.9	3.6	2.3	0.074
	NO_3^--N	1	1.2	0.8	0.48
	TP	2.1	2.5	1.7	0.148

3.5.3. Correlation network analysis

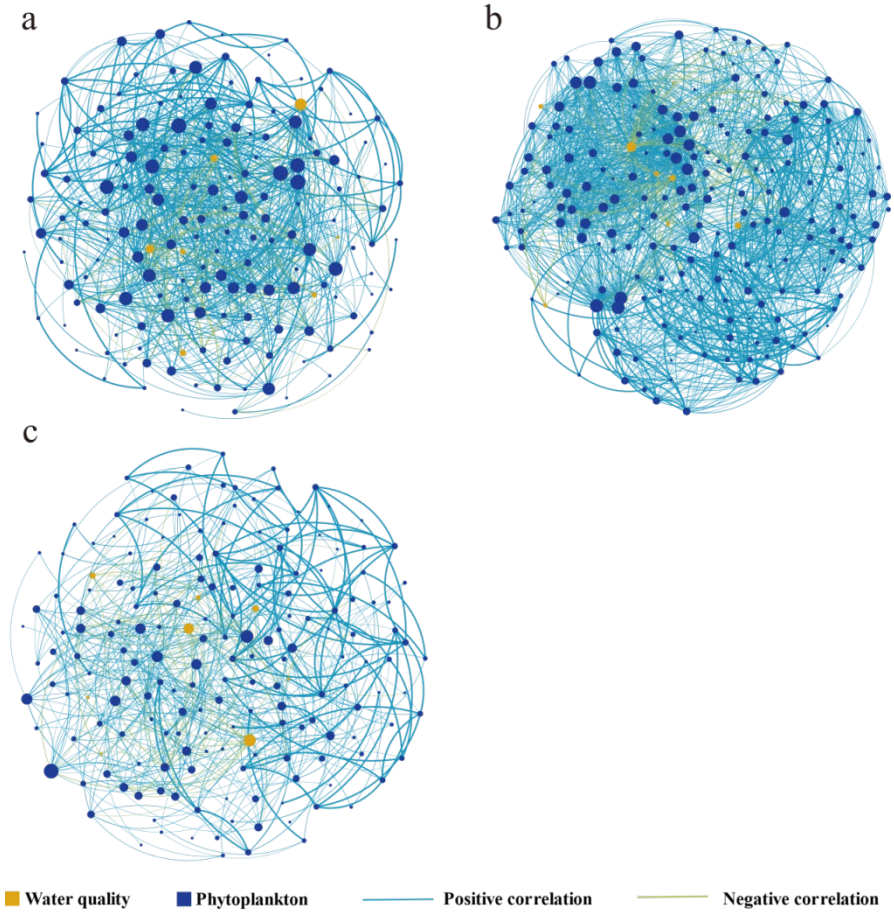

Figure 9:Coexisting phytoplankton and water parameter networks based on correlation analysis. (a) CE restoration group; (b) OE restoration group; (c) CS restoration group.

Network analysis revealed the ecological dynamics of phytoplankton communities across the three restoration groups (Figure 9). The OE group demonstrated the highest network complexity and connectivity, as indicated by the higher values of topology coefficients, including node count (209)(Table 4), edge count (1613), positive correlation proportion (93.68%), and network density (0.074), reflecting stronger synergistic interactions. In contrast, the CE group, which exhibited slightly higher clustering coefficients and average clustering coefficients indicative of stronger local connectivity, had a lower

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overall network density and connectivity than the OE group. The CS group presented the lowest values for most network coefficients, particularly the edge count (509) and average weighted degree (3.904), suggesting a sparse network structure. These findings indicated that the structure and function of phytoplankton community networks varied significantly under different restoration strategies.

Table 4 Topological coefficients of correlation network based on phytoplankton community.

Topological coefficients	CE	OE	CS
Number_of_nodes	167	209	182
Number_of_edges	738	1613	509
Positive correlation (%)	90.24%	93.68%	88.61%
Negative correlation (%)	9.76%	6.32%	11.39%
Average_degree	8.838	15.435	5.593
Average_path_length	2.758	2.071	2.725
Network_diameter	6.829	5.682	6.672
Network_density	0.053	0.074	0.031
Clustering_coefficient	0.453	0.395	0.304
Average_clustering_coeff	0.502	0.466	0.413
Average_weighted_degree	7.038	10.963	3.904
Modularity	0.588	0.607	0.665

4. Discussion

Among the three in situ restoration enclosures in the northern part of Caohai Lake, the closed enclosure with sediment exposure (CS) demonstrated significant water quality improvements, including substantial nutrient reductions and increased dissolved oxygen levels. These outcomes could be attributed to the sediment exposure, which inhibited the nutrient release and mitigates eutrophication [38,39]. Similar findings have been reported by researchers who tested three drying intensities and durations (10, 30, and 90 d) and observed lower nutrient release rates under the most intense and prolonged drying conditions after rehydration [40]. Zhou et al. [41] suggested that the increased dissolved oxygen levels further suppressed the pollutant release, reinforcing the effectiveness of sediment exposure in controlling nutrient leaching. Thus, sediment exposure is a viable strategy for ecological restoration.

During the survey, 281 phytoplankton species were identified across the three restoration methods in Caohai Lake, and the species composition and relative abundance predominantly consisted of cyanobacteria, green algae, and diatoms, which are typical of subtropical eutrophic lakes [42–44]. Cyanobacteria dominated all restoration groups, exhibiting a higher relative abundance in August and September and lower levels in other months, which is consistent with the findings of Feng et al. [45]. Tan et al. [46] conducted a study using the simulated warming to the culture winter sediments from Lake Taihu, discovering that the green algae dominated at 12.5°C and 16°C, while cyanobacteria prevailed at the temperatures above 19.5°C [46]. Other studies have similarly indicated that cyanobacteria can thrive at higher temperatures, whereas green algae and diatoms dominate at lower temperatures [47–49]. Consequently, the relative abundance of green algae and diatoms increased during cooler months. The diversity indices for the CE and CS restoration groups were lowest in August and September, likely because of the rapid proliferation of cyanobacteria under high temperatures [50]. In the CS restoration group, as the water levels rose in August and September, the restoration of water volume from the previously dry state caused significant environmental changes, enabling the survival of a few highly adaptable species. Over time, environmental stabilization, improved nutrient cycling and availability, enhanced habitat heterogeneity, and migration of new species can collectively promote community diversity [51–53]. However, further research is required to evaluate the sustainability of this diversity and its long-term effects on ecological stability. Throughout the investigation, the CE group maintained water coverage but lacked connectivity with the lake, limiting nutrient replenishment and species exchange, which likely suppressed the phytoplankton diversity. In contrast, water exchange in the OE group

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facilitated nutrient flux and species migration, thereby facilitating the maintenance of higher phytoplankton diversity [54,55].Additionally, chlorophyll-a levels in the CE restoration group showed a significant increase in September, which may be related to elevated temperatures promoting cyanobacterial proliferation. Rising WT accelerated phytoplankton metabolism, with cyanobacteria exhibiting enhanced competitive advantages under thermal stress[56]. The enclosed environment of the CE group led to nutrient accumulation (NH_4^+-N and NO_3^--N, Table 1), further stimulating algal biomass[57]. The chlorophyll-a peak observed in the CS group during December could be attributed to short-term nutrient release following sediment desiccation and the dominance of diatoms/green algae under lower temperatures[58]. In contrast, the OE group demonstrated minimal chlorophyll-a fluctuations, potentially resulting from water exchange diluting nutrient concentrations and submerged macrophytes suppressing algal growth through competition for light and nutrients[59].

WT was a key environmental factor influencing phytoplankton and submerged plants across all three restoration groups, with significant correlations ($P < 0.01$). Similar findings have been reported, such as studies of phytoplankton communities in Wuhan lakes, where WT was identified as a critical factor [60], and research by Wang et al. [61] highlighted the importance of WT in different restoration groups in Nanhu, Jiaxing. WT can affect phytoplankton growth [62] by promoting photosynthesis and respiration, thereby enhancing reproduction [63]. In the CE group, WT was positively correlated with MPA because of poor submerged plant recovery and constant water coverage, which retained more nutrients [64,65], favoring MPA growth. Temperature was positively correlated with MPA in the CE restoration group. In the OE area, water exchange with the lake diluted some nutrients, and the successful recovery of submerged plants suppressed cyanobacterial growth [66,67], leading to a negative correlation between temperature and MPA. In the CS restoration group, whereas there was no water exchange with the lake, sediment exposure reduced nutrient release, and the recovery of submerged plants also suppressed cyanobacteria growth [48,68], resulting in a similar negative correlation. CODMn and pH, key indicators of environmental water conditions, were significantly affected in the CS restoration group ($P < 0.01$). Their variations were closely linked to organic matter decomposition, microbial activity [69,70], phytoplankton community structure, and submerged plant growth. In the CS restoration group, water isolation and sediment exposure increased the rate of organic matter decomposition, increasing the CODMn concentrations and influencing the phytoplankton species distribution. Following the recovery of submerged plants, photosynthesis consumes CO2, increasing the water pH [71]. Within the optimal pH range, phytoplankton biomass increased [72].

The network structure reflects the complexity and stability of the communities [73]. In lake ecosystems, competition among phytoplankton fluctuates with environmental changes, causing dynamic shifts in the community composition. In the constructed network, the OE restoration group exhibited the highest values for edges, nodes, average degree, network density, average weighted degree, and positive correlation proportion, along with the lowest values for average path length and network diameter. These metrics indicate strong interactions between phytoplankton species and the establishment of a more stable and coordinated ecological network [74,75]. Similarly, Peng et al. [76] suggested that recirculating aquaculture ponds in rice paddy-pond systems had a greater buffering capacity and more complex community structures than traditional ponds. These findings suggest that water exchange between enclosures and lakes can enhance the adaptability and stability of phytoplankton communities in response to environmental change.

5. Conclusion

This study examined the response characteristics of water quality, submerged plant communities, and phytoplankton communities to different restoration measures, including enclosure wave suppression, sediment exposure, and plant cultivation.

(1) Enclosure wave suppression effectively restored aquatic vegetation through planting while also facilitating its natural recovery.

(2) Among the various combinations of enclosure wave suppression, sediment exposure, and plant cultivation, the sediment exposure treatment group achieved the greatest water quality improvement, highest phytoplankton species diversity, and lowest algal cell density. These results highlight the critical role of sediments in water ecological restoration and demonstrate that sediment exposure is an effective measure for mitigating sediment-related impacts.

(3) This study highlights the distinct impacts of various restoration measures on the ecological structure and function of water bodies, offering valuable guidance for practical aquatic ecological

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restoration efforts.

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