

Deciphering the algal successional trajectories and ecological regulation mechanisms during the cooling phase: A case study of a eutrophic urban lake

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ABSTRACT

Global rise in eutrophication has brought out various types of algal blooms. However, research on eutrophic lakes has predominantly focused on the risks and drivers of harmful algal blooms (HABs), while spatial and temporal data on algal community dynamics under low-temperature conditions remain limited. This data gap has hindered a comprehensive understanding of algal succession and its ecological effects. Through high-frequency, in-situ, multi-site vertical observations in a typical eutrophic urban lake, this study provides the first systematic analysis of algal community succession across three key dimensions: total algal biomass, community structure, and vertical distribution. The results show a significant decline in Cyanobacteria with decreasing water temperature (WT). However, total average algal concentration (TAC) does not continuously decrease. Instead, it peaks at 47.45 µg/L at 6 °C, due to a relatively high Fv/Fm (0.4–0.6) and a notable increase in Cryptophyta relative abundance (3.88 %–87.20 %). In Stage A (Gradual cooling), a diverse algal community comprising multiple phyla coexists, primarily concentrated in the surface layer (0.4 m), exhibiting clear vertical niche differentiation. As succession progresses (Rapid cooling and Gradual warming), Cryptophyta gradually replace Cyanobacteria, Chlorophyta, and Diatom, occupying their vacated ecological niches and shifting the peak of algal biomass to the mid-water layer (0.8 m). Mantel tests identified synergistic drivers, including WT, algal nutrient availability (TN, TP, COD), and algal competition. Notably, Cryptophyta succession contributed to increased SD and DO levels, underscoring the role of interspecific competition and succession in maintaining ecosystem stability during WT shifts. Our findings enhance the understanding of algal community succession and their potential role in supporting long-term ecosystem stability, offering insights for aquatic ecosystem restoration and algal bloom management.

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1. Introduction

Water, the lifeblood of urban development, and the United Nations World Water Development Report 2024 emphasizes the imperative of health aquatic ecosystems for prosperity and peace [1]. As primary producers, algae drive material and energy cycles, fundamentally shaping the structure and function of aquatic ecosystems. The high species diversity of algae, coupled with their sensitivity to environmental fluctuations, makes algal community dynamics a multifactorial process influenced by both external environmental conditions and internal ecological interactions [2,3]. Shifts in biomass, species composition, and community structure serve as key indicators of environmental gradients and ecosystem characteristics [4]. Therefore, advancing our understanding of algal community succession and its ecological effects is crucial for developing effective aquatic ecosystem restoration strategies.

Rapid urbanization and escalating human activities introduce pollutants into urban water bodies through various pathways, resulting in pollution loads that exceed eutrophication thresholds (TN > 0.2 mg/L, TP > 0.02 mg/L, Chla > 10 µg/L) [5]. Concurrently, the global rise in eutrophication has brought out various types of algal blooms, and harmful algal blooms (HABs) have emerged as a major global ecological issue, acting as key indicators of ecological imbalance in aquatic ecosystems [6]. The imbalance profoundly threatens the hydrological, physical, and chemical properties of urban water bodies, leading to phenomena such as a decline in biodiversity, habitat degradation, and the resurgence of black and odorous water bodies [7]. This has precipitated an unprecedented crisis, risking further functional degradation of aquatic ecosystems.

In recent decades, there has been an increasing attention on algal blooms in both domestic and international research to address this ongoing crisis. However, most studies on eutrophic lakes have predominantly focused on how to mitigate the negative effects of HABs, thereby investigating their risks and drivers [8–10]. For example, Ji et al. demonstrated that monitoring the annual cycle of Cyanobacteria blooms in Lake Taihu has revealed the substantial presence of dormant Cyanobacteria seeds in winter sediments due to unfavorable growth conditions [11]. When temperature and light conditions become favorable for blooms, they rapidly re-suspended, leading to algal biomass stratification, thereby impacting the occurrence of Cyanobacteria blooms [12]. Wu et al. used numerical simulations and laboratory analysis to identify key factors affecting the vertical migration of Cyanobacteria and the formation of blooms [13]. Additionally, a growing number of studies have observed these blooms exhibit distinct seasonal patterns, such as Diatom blooms in winter and Cyanobacteria blooms in summer [14,15]. However, limited information is available on the dynamics of algal communities during winter periods. Most existing studies focus on the overwintering and decline of Cyanobacteria [12]. Consequently, current studies have largely neglected the succession of algal communities during winter and their potential role in supporting long-term ecosystem stability. It remains uncertain whether blooms in eutrophic water bodies during winter will dissipate or whether alternative bloom states will emerge. To address this gap, a deeper understanding of algal community succession in winter is essential.

Considering urban lakes are typically small, shallow, and highly canalized, with limited environmental capacity and weak self-purification capabilities, there is an urgent need to protect eutrophic urban lakes in the face of evolving environmental challenges [16]. This study conducted high-frequency, in-situ observations of algal community dynamics in a typical eutrophic urban lake. The specific aims of the study were: (1) to discuss the patterns of algal community succession under low-temperature, (2) to explore the role of algal succession in ecosystem self-regulation, and (3) to reveal the key drivers of algal succession and the regulation mechanisms mediated by algal succession. The findings of this study offer valuable insights for aquatic ecosystem restoration and algal bloom management from a community succession perspective, thereby boosting the precision and efficiency of urban

water environmental stewardship.

2. Materials and methods

2.1. Study site and field sampling

This study was conducted at Tongling West Lake, a shallow eutrophic urban lake located in the central-western part of Xilianwei, Tongling City, Anhui Province (30°59'N, 117°50'E). This lake has a watershed area of 1.61 km² and an average depth of 1.75 m (Fig. 1). The study site has a humid subtropical monsoon climate, with an annual mean temperature of 17.4 °C and an annual mean precipitation of 1058 mm. Its primary ecosystem services include enhancing urban landscapes, providing non-potable water storage, recreational access, stormwater retention, and supporting ecological restoration. Compared with large open water bodies, Tongling West Lake is a semi-enclosed shallow system with limited hydrological connectivity, low self-purification capacity, and a single recharge source. These characteristics make it highly susceptible to anthropogenic disturbances, with an elevated risk of water quality deterioration and algal blooms.

Between September 2024 and January 2025, vertical monitoring of the algal community and field sampling were conducted at key locations, including the upstream, lake region, and downstream. A total of 35 sites were set up to assess external environmental conditions and algal community characteristics. Vertical observations were conducted weekly at all 35 sites, while monthly field sampling took place at 18 sites (Fig. 1) (Fig. S1).

Preliminary vertical observations revealed no significant difference in Chla concentration between adjacent layers at depths of less than 0.1 m. However, data collected at depths of 0.2 m and 0.5 m often failed to accurately represent the vertical distribution of algal biomass [17]. Therefore, vertical monitoring was performed with a resolution of 0.1 m per layer. At each site, 1 L water samples were collected using a plexiglass water sampler, stored in a dark environment, and frozen until laboratory analysis.

2.2. Analytical methods

Algal biomass and community structure were measured using the algal analysis instrument (AGHJ-AFS-II) [18]. The maximum quantum yield of photosystem II (Fv/Fm) was measured using the primary productivity fluorescence kinetics analyzer (AGHJ-OGFS) [19]. Key sampling points (8) were selected according to the "Lake Eutrophication Survey Specification." Water samples were collected at depths of 0.5 m, 1.0 m, and 1.5 m, and magnesium carbonate saturated suspension was added. The samples were filtered using glass fiber membranes (0.45 µm), stored in the dark at low temperatures, and promptly transported back to the laboratory for chlorophyll-a concentration analysis according to national standard methods. The AGHJ-AFS-II measurements showed a relative deviation of less than 10 % compared to the standard method. Additionally, to validate the accuracy of the in-situ monitoring data, monthly sampling and microscopic analysis of Tongling West Lake samples were conducted using the method described by Peng et al. The results confirmed that the dominant algae species observed were consistent with the in-situ data.

The conventional physicochemical parameters, including water temperature (WT), dissolved oxygen (DO), pH, and electrical conductivity (EC), were measured in situ using the YSI multiparameter water quality meter (Thermo Fisher Scientific, Waltham, MA, USA). Secchi depth (SD) was measured using a Secchi disk. The concentrations of the chemical oxygen demand (COD_{Mn}), total phosphorus (TP), total nitrogen (TN), and ammonium nitrogen (NH₃-N) were measured using standard methods [10]. Meteorological data were provided by the Tongling Ecological Environment Monitoring Center (Table S2).

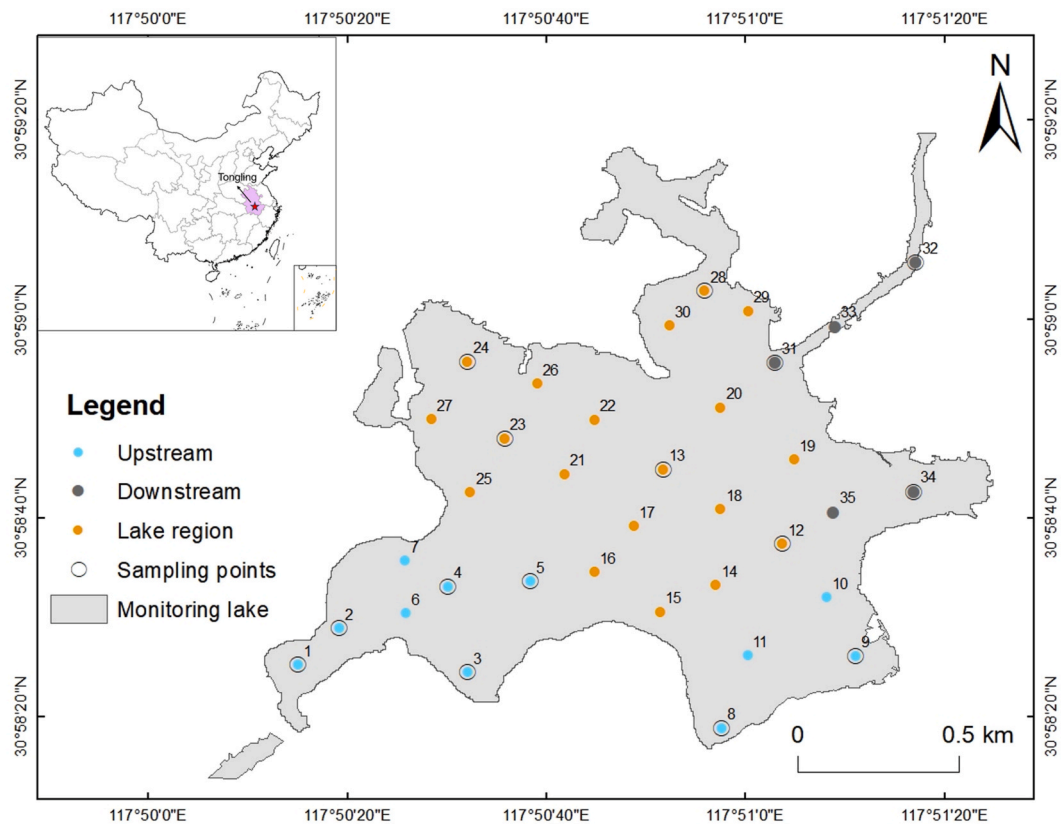


Fig. 1. Location of 35 monitoring sites and overall analysis framework. In the study site diagram, blue, yellow, and black circles represent the upstream (1–11), lake region (12–30), and downstream (31–35), respectively. Sampling points are marked with hollow circles.

2.3. Data processing

The trophic level of the urban lake was assessed using the Trophic Level Index (TLI) [20]. Water quality was evaluated using the Water Quality Index (WQI), which was calculated following the method outlined by Tian et al. [21]. Based on the WQI values, water quality was classified into five categories: excellent, good, fair, poor, and very poor.

The vertical average algal concentration (VAC) was estimated using vertical Chla data, which reflects the level of algal biomass in the water column. The formula is expressed in Equation (1):

$$VAC = \frac{\sum_{i=1}^n C_i}{n} \quad (1)$$

Where, n is the number of layers in the water column, C_i represents the algal biomass in the i -th layer, measured as chlorophyll-a concentration.

The total average algal concentration (TAC) was determined as the ratio of total algal mass (TAM) to the lake's storage capacity (SC). The calculation for TAM is shown in Equation (3), and SC data is provided by the lake management authority:

$$TAC = \frac{TAM}{SC} \quad (2)$$

$$TAM = \frac{S}{N} \times \sum_{j=1}^N \int_0^{d_{max}} C_j(z) dz \quad (3)$$

Where, S is the area of the lake, N is the number of the site, d_{max} is the maximum depth of the site, and $C_j(z)$ is the distribution of Chla concentration with depth.

2.4. Statistical analysis

Data were processed and visualized using Origin 2021. Statistical analysis was conducted using IBM SPSS26. The results are presented as mean $\pm$ standard deviation, and statistical significance was assessed using analysis of variance (ANOVA). Analysis of variance was used to test the significance of the results, and $p < 0.05$ was considered statistically significant. Mantel-test network heatmaps were analyzed using R Studio 4.3.0.

3. Results

3.1. Water trophic levels and water quality

During the monitoring period (September 23, 2024 to January 24, 2025), the study site exhibited high concentrations of TN, TP, $\text{NH}_3\text{-N}$, and COD_{Mn} (Fig. S2). The TLI values were 64.29 ± 4.79 , ranging from 52.35 to 75.77, categorizing the site as middle eutrophic. Further analysis of the WQI revealed an average value of 54.01 ± 7.92 , ranging from 37.92 to 72.50. Water quality was classified as "fair" at 33 % of the sites and "poor" at 67 % (Fig. S3) [21].

Fig. 2 illustrates the long-term variations in key physicochemical parameters. The WT in the lake ranged from 6.65 to 25.93 °C, with an average of 15.10 ± 6.93 °C. Significant fluctuations in WT were observed throughout primarily due to changes in the surrounding ambient temperature (Fig. 2a). The average DO concentration was 9.52 ± 3.39 mg/L. DO levels were consistently higher in the upstream region compared to the lake and downstream areas. A notable decrease in DO was observed from November 11 to November 23 (6.14 ± 1.77 mg/L), and then DO levels recovered to relatively higher concentrations (11.19 ± 3.15 mg/L) (Fig. 2b). The SD, which effectively reflects water clarity, remained low from September 23 to December 15, averaging $20.13 \pm$

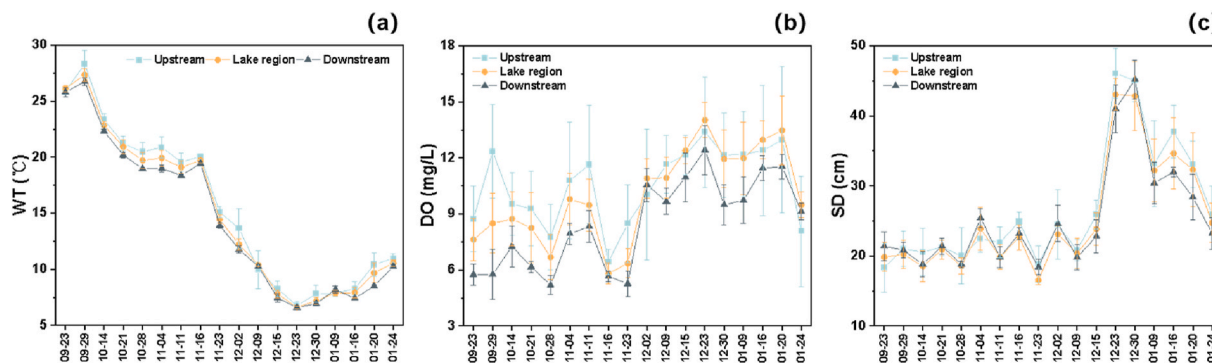


Fig. 2. Variations in key physicochemical parameters in the eutrophic lake from September 2024 to January. (a), (b), and (c) illustrate the variations in WT, DO, and SD. The data for the upstream, lake region, and downstream are represented by the average values and standard deviations of monitoring sites 1–11, 12–30, and 31–35, respectively.

5.13 cm. Following this period, SD levels increased significantly, reaching an average of 41.73 ± 9.64 cm over 15 days. After January, SD levels gradually declined, reaching 23.2 ± 2.28 cm on January 24 (Fig. 2c).

3.2. Dynamics of algal successional trajectories

To comprehensively understand algal successional trajectories, this study provides the first systematic analysis of algal community succession across three key dimensions: total algal biomass, community structure, and vertical distribution. These insights are essential for understanding the seasonal dynamics of algal blooms and assessing associated risks.

As illustrated in Fig. 3, the mean values of VAC and TAC during the study period were 26.59 ± 16.18 $\mu\text{g/L}$ and 27.79 ± 10.01 $\mu\text{g/L}$, respectively, indicating a significant risk of harmful algal blooms (HABs) (Fig. 3a and b) [10]. Despite a decrease in WT, TAC did not experience a notable decline during winter. Instead, it displayed a dynamic pattern of growth-decline-regrowth, with two distinct TAC peaks observed on November 11 and December 23 (Fig. 3b). Concurrent monitoring of Fv/Fm revealed that values from September 2024 to January 2025 suggested considerable growth potential for the algae (Fig. 3c). This observation data can help to explain the rapid algal growth following the retreat on November 23 [22]. Furthermore, the weak hydrodynamic conditions and high nutrient levels provided a suitable environment for the growth of phytoplankton, thereby increasing the risk of Cryptophyta bloom in aquatic ecosystems [23].

The analysis of algal biomass variations across different phyla revealed that no significant differences were observed between September 23 and November 4, with minimal fluctuations observed (Fig. 4). During this period, the concentrations of Cyanobacteria,

Chlorophyta, Diatom, and Cryptophyta were 3.33 ± 1.13 $\mu\text{g/L}$, 2.91 ± 0.96 $\mu\text{g/L}$, 5.22 ± 0.92 $\mu\text{g/L}$, and 3.74 ± 1.94 $\mu\text{g/L}$, respectively. Over time, algal biomass in the upstream, lake region, and downstream increased to varying extents, with the most pronounced growth observed in the upstream area. Between November 11 and December 9, Cryptophyta concentrations fluctuated significantly. After December 23, Cryptophyta concentrations declined, while Diatom concentrations slightly increased. Overall, the early-stage community structure was characterized by the coexistence of multiple phyla, with Cryptophyta emerging as the dominant species later on. Furthermore, we observed that the upstream areas exhibited a notably higher algal biomass than both the lake and downstream regions during the initial phase. Cyanobacteria accounted for about 20 % of this biomass, where their elevated concentrations led to increased light attenuation in the water column. This, in turn, facilitated surface blooms and concentration gradients. The northeastern winds initially directed the algae accumulation towards the upwind upstream areas (Table S2). As Cryptophyta concentrations increased, the algal biomass in the lake area eventually surpassed those in the upstream region. This shift appeared to correlate with water flow dynamics and the vertical distribution patterns of Cryptophyta once they dominated the biomass.

To further investigate this phenomenon, this study analyzed the variation in the relative abundance of algae with WT (Fig. 5). As WT decreased, the relative abundance of Cyanobacteria dropped from 28.76 % to 2.56 %. In contrast, the decrease in the relative abundance of Chlorophyta is less pronounced. From September 23 to November 16, the relative abundance of Chlorophyta decreased from 32.17 % to 6.13 % and then stabilized at approximately 5 %–15 %. The relative abundance of Diatom initially remained stable, but a dramatic decline occurred after the rapid cooling on November 23 (14.5 °C). By the lowest recorded WT on December 23 (6.65 °C), the relative abundance

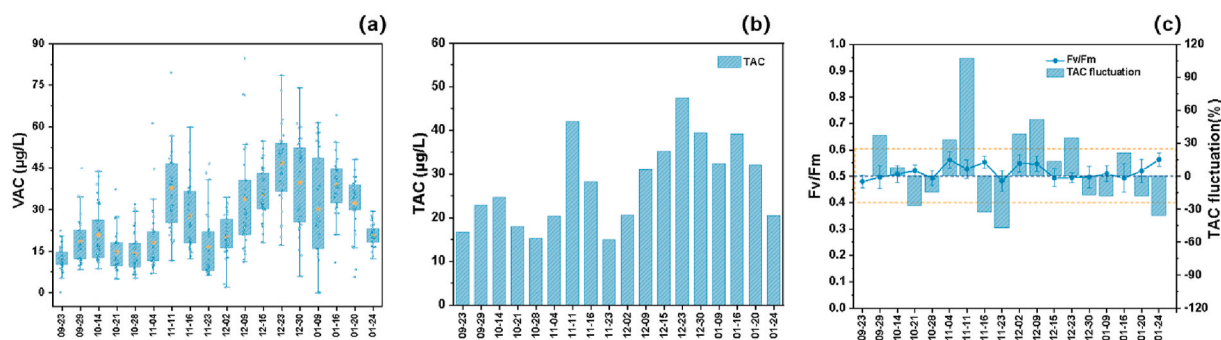


Fig. 3. Variations in algal biomass in the eutrophic lake from September 2024 to January 2025. (a) Shows the boxplot of VAC at 35 monitoring sites, with the orange symbol representing the mean VAC across all sites, (b) depicts the TAC in the lake, and (c) illustrates the rate of change in TAC along with the mean and standard deviation of Fv/Fm across the 35 monitoring sites.

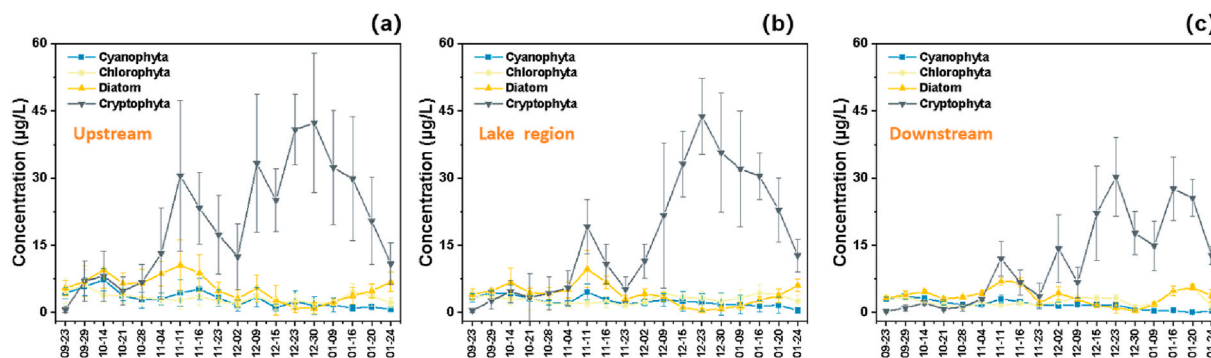


Fig. 4. Variations in algal biomass across different phyla in the eutrophic lake from September 2024 to January 2025. (a), (b), and (c) represent the algal biomass changes in the upstream, lake region, and downstream, respectively. These variations are based on the average values and standard deviations of in-situ algal biomass across different phyla at monitoring points 1–11, 12–30, and 31–35, respectively.

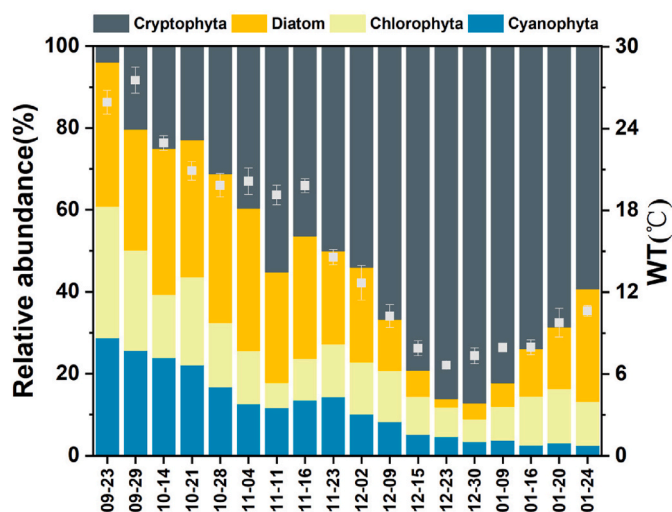


Fig. 5. Variations in relative abundance across different phyla in the eutrophic lake from September 2024 to January 2025. The relative abundance was calculated from the VAC average of 35 sites, and the gray symbols are the mean and standard deviation of WT.

of Diatom had fallen to its lowest level, reaching only 2.01 %. However, as WT increased, Diatom abundance partially recovered, reaching 27.50 % by January 24. In contrast, fluctuations in the relative abundance of Cryptophyta were more pronounced, rising from 3.88 % to 87.20 % during the study period (Fig. 5). Overall, algal community succession in the study area is jointly shaped by water temperature (WT), nutrient levels, and algal competition. Notably, different factors dominate at various stages, collectively determining the trajectory of community succession (Fig. S4). Algal biomass changes are mainly driven by Cryptophyta, though diatoms play a crucial intermediary role through competitive interactions with Cryptophyta during succession. Furthermore, microscopic analysis of samples collected during the marked increase revealed that *Microcystis* and *Dolichospermum* were the dominant species at the early stage. Later, *Cyclotella* became significantly more dominant, while *Cryptomonas* sp. and *Chroomonas* sp. played a crucial role in the prominence of Cryptophyta.

Fig. 6 shows the vertical distribution characteristics of in-situ algae biomass across different phyla. The initial vertical distribution of algae is primarily influenced by Cyanobacteria and Cryptophyta, which concentrate in the subsurface layer. As Cyanobacteria and Diatom diminish, Cryptophyta emerges as the main controlling factor in vertical distribution. However, factors such as wind speed and light availability also significantly affect algal aggregation, though these are not discussed in detail in this study.

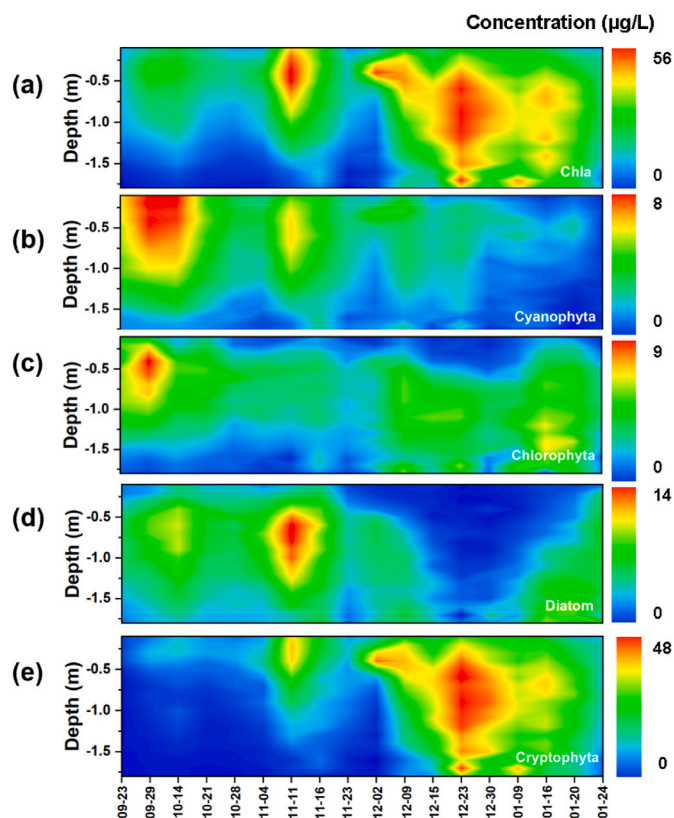


Fig. 6. Variations in the vertical distribution characteristics of in-situ algae biomass across different phyla in the eutrophic lake from September 2024 to January 2025. The vertical heat map is generated by averaging observations from all 35 sites. The data is presented for: (a) Chla, (b) Cyanobacteria, (c) Chlorophyta, (d) Diatom, and (e) Cryptophyta.

In the early stages, Cyanobacteria and Chlorophyta exhibited distinct vertical stratification within the surface layer (0–1.0 m) (Fig. 6a 6b), while Cryptophyta predominantly aggregated in the uppermost layer (0–0.5 m) (Fig. 6d). During this period, Diatom distribution in the water column was relatively uniform (Fig. 6c). As time progressed, the Cyanobacteria concentration in the surface layer significantly declined, reducing the overall vertical stratification of the algal community (Fig. 6a). However, vertical stratification re-emerged by November, with notable increases in the concentrations of Diatom and Cryptophyta. Specifically, Diatom became more concentrated in the middle layer (0.5–1.5 m), while Cryptophyta peaked in the surface layer (0–0.5 m) (Fig. 6c 6d). Subsequently, Diatom concentrations in the middle layer

decreased significantly, while Cryptophyta concentrations gradually increased, eventually occupying the entire water column (Fig. 6c 6d). By January, the concentration of Cryptophyta across the water column had decreased, accompanied by a gradual increase in Diatom concentrations from the bottom to the surface, while Cyanobacteria concentrations decreased in the middle and lower layers (Fig. 6a 6c 6d).

4. Discussion

4.1. Characteristics of the distinct stages of algal succession

This study showed that algal successional trajectories in the eutrophic urban lake exhibit distinct stage variations (Figs. 2–6). The study area experienced WT shifts by seasonal variations, and low WT characterized the study area in winter. As shown in Fig. 7a, this study divides the succession process into three stages based on WT trends and algal successional trajectories: Gradual cooling (Stage A), Rapid cooling (Stage B), and Gradual warming (Stage C).

In Stage A Fig. 7b, TAC initially shows no significant changes as Cryptophyta biomass increases. The first peak of TAC (41.99 $\mu\text{g/L}$) is formed. At the same time, the algal community structure enters the first fluctuation period, shifting from a coexistence of Cyanobacteria, Chlorophyta, and Diatom to a coexistence of Cyanobacteria, Chlorophyta, Diatom, and Cryptophyta. During this stage, the relative abundance of Cyanobacteria and Chlorophyta declines as they enter the senescence phase, likely due to their competitive advantage at higher WT. In contrast, Cryptophyta, with superior cold tolerance, can break through environmental filtering as temperatures drop and gradually fill the ecological niches vacated by Cyanobacteria and Chlorophyta [24]. Our findings also indicate a clear vertical niche differentiation in the algal community. Cryptophyta dominates in the surface layer, while Diatom proportions increase with depth. At the bottom, Diatoms are most abundant. This pattern can be explained by the flagellate structure of Cryptophyta, which enables them to move freely in the surface layer and outcompete other algae for light [25]. Diatoms, with their silica-based cell walls, are better suited to low-light, high-pressure environments [26].

As the system transitions to Stage B, the rapid decline in WT disrupts the existing ecosystem, leading to biomass reductions across all algal groups and a minimum TAC of 14.87 $\mu\text{g/L}$, accompanied by reduced photosynthetic efficiency on November 23. In Stage B Fig. 7c, TAC does not decrease further despite the continued drop in WT; instead, it rapidly increases, reaching a second peak (47.45 $\mu\text{g/L}$). Analysis of the algal biomass across different phyla shows that this growth is primarily driven by an increase in Cryptophyta, which aligns with previous studies

indicating that Cryptophyta can efficiently utilize light and organic matter under low temperatures [27,28]. During this stage, the relative abundance of Diatoms decreases suggesting a transition into the stationary or senescent phase. This shift is likely driven by continued temperature decreases, which reduce ecological niches available to Cyanobacteria and Chlorophyta. In contrast, Cryptophyta, with greater cold tolerance and efficient nutrient uptake, gradually takes over Diatom niches. From a vertical perspective, Cryptophyta's relative abundance increases throughout the water column, and the earlier stratification becomes less distinct.

In Stage C Fig. 7d, as WT rises above 10 °C, TAC begins to decrease. However, despite this decline, algal biomass and photosynthetic efficiency remains relatively high, exceeding the average of the previous two stages. At the same time, although Cryptophyta decline and Diatoms recover, Cryptophyta maintains dominance and shifts the peak algal concentration from the surface to the mid-water column (0.8 m). This shift is mainly due to the near-disappearance of Cyanobacteria, allowing Cryptophyta to move freely in the euphotic zone. This phenomenon is driven by the absence of Cyanobacteria [29].

4.2. Role of algal succession in ecosystem self-regulation

This study underscores that algal community succession not only involves changes in species composition but also plays a crucial role in maintaining ecosystem stability. Our results suggest that Cryptophyta-dominated communities exhibit distinct functional traits that enhance ecosystem stability by improving DO and SD during fluctuations in WT and under the influence of interspecies competition (Fig. 2 Fig.7).

Specifically, despite the challenging conditions in eutrophic urban lakes with poor water quality (section 3.1), we found that fluctuations in DO levels are closely related to the increases in algal biomass and high photosynthetic efficiency, as indicated by the TAC and Fv/Fm (Fig. 2) [30]. Moreover, the improvement in SD can be attributed to two key factors: First, Cryptophyta tends to aggregate less than Cyanobacteria, leading to smaller suspended solid particles, which reduces light absorption and scattering [17]. Second, during the early stages, Cyanobacteria's vertical distribution causes algal biomass to concentrate near the water surface, obstructing light penetration. As Cyanobacteria decline, Cryptophyta promotes a more evenly distributed algal biomass throughout the water column, which enhances light penetration and significantly improves SD [31]. However, it is important to note that SD shows a sharp decline after a short-term improvement. This decline is likely related to the decomposition of dead algae and the resuspension of bottom sediments due to wind and waves [32,33].

Therefore, we argue that the increase of algal biomass driven by

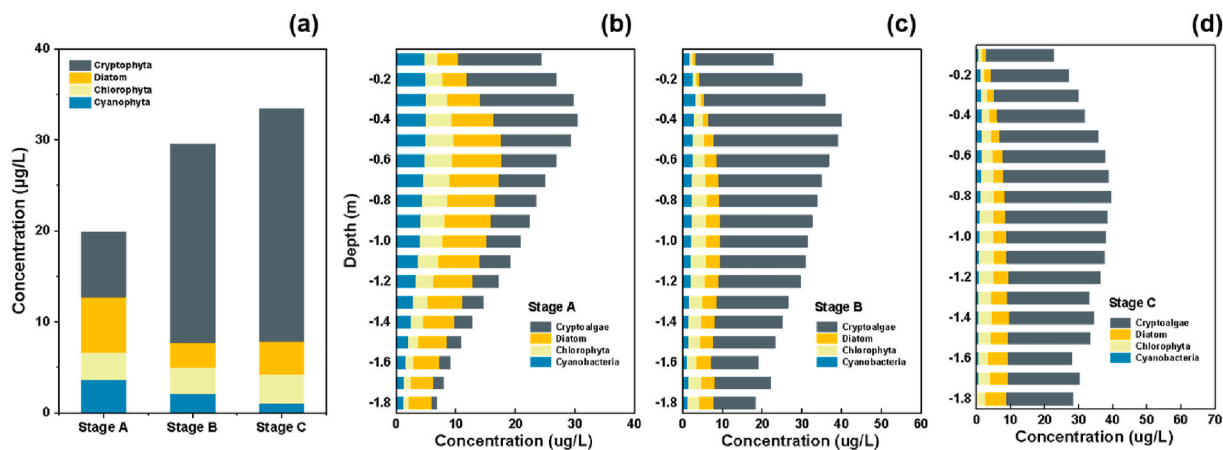


Fig. 7. Characteristics of the distinct stages of algal succession. (a) The changes in algal community composition across three distinct phases: Phase A from September 23, 2024, to November 16, 2024; Phase B from November 16, 2024, to December 23, 2024; and Phase C from December 23, 2024, to January 24, 2025, (b), (c), and (d) illustrate the vertical distribution characteristics of in-situ algal biomass across different phyla for Phases A, B, and C, respectively.

Cryptophyta-dominated communities during shifts in water temperature can help improve SD and DO levels, effectively mitigating the negative impacts of eutrophication associated with Cyanobacteria and Chlorophyta dissipation, such as oxygen depletion and the formation of anoxic, foul-smelling conditions [34]. Although Cryptophyta blooms provide short-term improvements in water quality, the consistently elevated concentrations of TN and TP in the study area, which exceed eutrophication thresholds, render the system inherently unstable. Seasonal temperature fluctuations pose a significant ecological risk, particularly when rapid shifts in community structure prevent any single species from establishing dominance. In such cases, ecological stability may be compromised, potentially leading to large-scale algal die-offs and system collapse. Additionally, as previously noted, low temperatures can severely limit the growth of most phytoplankton species, reducing the complexity and stability of phytoplankton communities during the winter months [24]. Therefore, while Cryptophyta-dominated communities play a key role in enhancing water quality in eutrophic lakes by improving DO and SD levels, their long-term success depends on improvements in external environmental conditions.

4.3. Regulation mechanisms mediated by algal succession

As previously discussed, the self-regulating phenomenon of eutrophic urban lakes is mediated by algal succession. However, algal succession is a complex and dynamic process. Numerous studies have shown that changes in environmental factors and species interactions are key drivers of this succession [2]. To deeply understand the driving mechanisms underlying ecosystem regulation, this study identifies the critical drivers of algal succession and explores the regulatory processes mediated by this succession.

Mantel analysis revealed significant differences in the relationship between algal biomass across different phyla and environmental factors at distinct stages of algal succession (Fig. S4). Furthermore, Statistical analysis of observational data based on WT revealed a shift in the algal community structure, transitioning from multi-species coexistence to the dominance of a single species with the WT gradient (Fig. 8).

At higher temperatures (25–30 °C), Cyanobacteria, Chlorophyta, and Diatom coexisted without significant differences in their relative

abundances. This stable coexistence is likely due to the formation of stress-resistant dormant spores by Cryptophyta under high temperatures, an adaptive strategy consistent with K-selection mechanisms that prioritize population stability and minimize competition [35]. During this period, the algal community, primarily driven by Cyanobacteria, was concentrated in the surface layers.

As WT decreased (10–25 °C), the relative abundance of Cyanobacteria and Chlorophyta declined, while the abundance of Cryptophyta increased significantly. During this phase, Cryptophyta reduced direct competition through niche differentiation [2,36]. Diatoms, which exhibit strong cold tolerance, maintained stable relative abundances, reflecting their resilience to environmental fluctuations and lower selection pressures [37].

When the temperature dropped to 15 °C, Cyanobacteria and Chlorophyta were gradually replaced by Cryptophyta, and niche space for further growth became increasingly limited. This shift created conditions where competition between Cryptophyta and Diatoms for dominance became a major driver of community succession. During this period, Cryptophyta, following an r-strategy, rapidly expanded to occupy available niches, while Cyanobacteria and Diatoms, adopting K-strategies, focused on long-term stability and competitive advantage. The resulting shift in survival strategies intensified competitive pressures, further altering the community structure [38,39].

At 10 °C, the ecosystem underwent a dramatic shift from multi-species coexistence to a Cryptophyta-dominated state. The increased biomass of Cryptophyta intensified competition and suppressed other algal groups, reinforcing its dominance through feedback regulation. However, this dominance was unstable; even a slight increase in temperature could enable Diatoms, with their competitive advantages, to proliferate rapidly and restore community balance [40].

Therefore, our research suggests that the key to ecosystem self-regulation lies in algal succession, driven by WT-mediated environmental filtering and dynamic shifts between r- and K-selection strategies. These interactions can be understood within the framework of modern coexistence theory, offering deeper insights into the mechanisms shaping algal community dynamics.

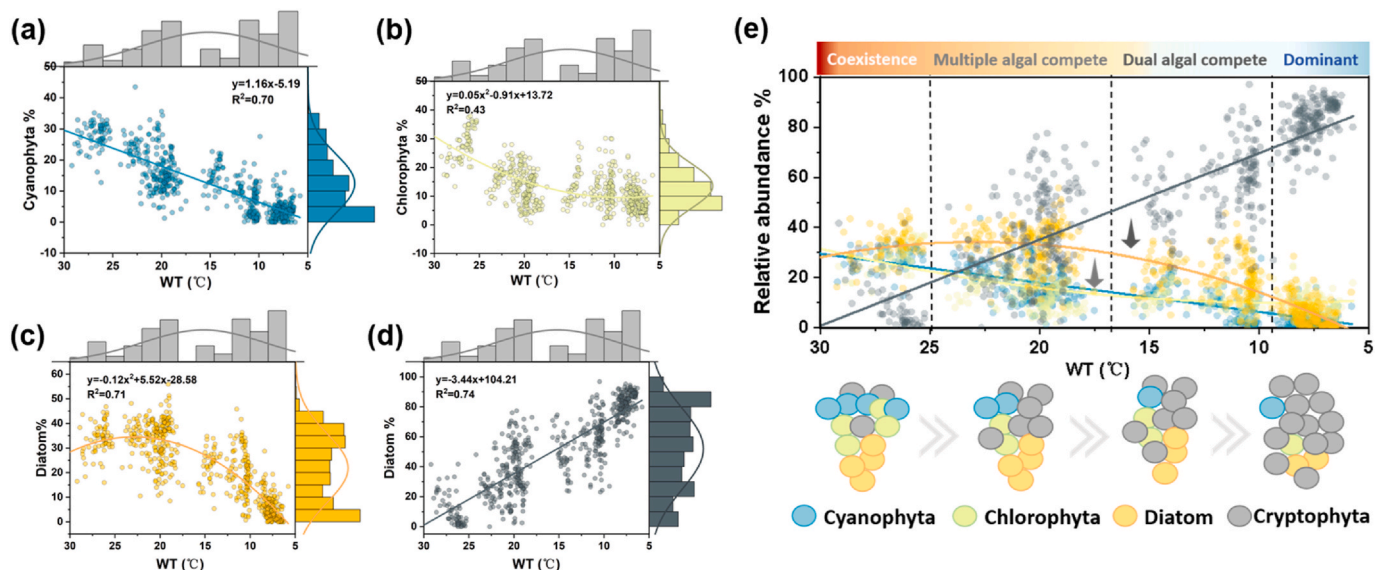


Fig. 8. Regulation mechanisms mediated by algal succession. (a), (b), (c), and (d) represent the relationships between WT and relative abundance for Cyanobacteria, Chlorophyta, Diatom, and Cryptophyta, respectively, (e) illustrates the conceptual model of algal succession based on the relationship between WT and relative abundance. At higher temperatures (25–30 °C), a co-occurrence state is observed, while a competitive state occurs when WT ranges from 10 °C to 25 °C. At lower WT, Cryptophyta dominate. Additionally, the vertical distribution characteristics of in-situ algal biomass across different phyla corresponding to these states are shown in (e).

4.4. Environmental implications and limitations

This study uses a stereoscopic monitoring approach to provide high-resolution in situ evidence that the successful succession of dominant algal species in a small eutrophic urban lake supports stable overwintering. This process mitigates the impacts of eutrophication and helps maintain long-term ecosystem stability. The outcome has addressed a crucial gap in understanding the natural patterns of algal succession and their ecological effects in eutrophic lakes, which could help us to develop or optimize ecological management strategies to mitigate eutrophication. For example, by identifying key indicators such as DO, SD, and algal successional trajectories within critical temperature ranges, it is possible to predict whether significant water quality degradation or ecological collapse will occur during the winter, thus guiding decisions on the need for management interventions. Additionally, our case study contributes to the advancement of theoretical ecology.

Nevertheless, there are two caveats to the interpretation of our studies. First, the design of this study was primarily based on field observation data to achieve a more comprehensive and objective understanding of algal succession dynamics. Therefore, no additional laboratory experiments and genomic analyses have been conducted to validate the ecosystem self-regulation mechanisms mediated by algal succession. Second, our findings from a eutrophic urban lake may not fully represent the dynamics in lakes with different levels of eutrophication or deep-water ecosystems. In the future, this novel monitoring and analytical approach can be applied to other urban lakes to validate and broaden the generalizability of the results. Additionally, we aim to further investigate the mechanisms underlying algal bloom formation and the dynamic environmental changes driven by algae from the perspective of community succession. Building on this, we will integrate algal and water quality indicators to identify ecologically relevant indicators that can inform algal bloom management and guide aquatic ecosystem restoration. Such critical knowledge will enhance our understanding of how algal succession shapes the ecological resilience and management of eutrophic urban lakes.

5. Conclusions

This study conducts high-frequency, in-situ, multi-site vertical observations in a typical eutrophic urban lake, aiming to provide the first systematic analysis of algal community succession across three key dimensions: total algal biomass, community structure, and vertical distribution. The results show that although Cyanobacteria significantly decline under low temperatures, Cryptophyta successfully replaces them through high Fv/Fm and niche restructuring, maintaining a higher TAC. Our findings suggest that WT, nutrients, and algal competition synergistically influence this succession phenomenon. Notably, the ecological succession driven by Cryptophyta-dominated communities during WT shifts can help to improve SD and DO levels, effectively mitigating the negative impacts of eutrophication. Therefore, future efforts to protect eutrophic urban lakes must focus not only on identifying the potential risks and drivers of harmful algal blooms but also on understanding the patterns of algal succession if we wish to mitigate their adverse effects. Our findings offer novel insights for aquatic ecological restoration and seasonal algal bloom management, thereby boosting the precision and efficiency of urban water environmental stewardship.

CRedit authorship contribution statement

Xinyue Jv: Writing – original draft, Validation, Methodology, Conceptualization. **Gaofang Yin:** Writing – review & editing, Methodology. **Nanjing Zhao:** Conceptualization. **Jiajia Xu:** Writing – review & editing. **Zhiyong Zhai:** Supervision. **Yao Chen:** Investigation. **Tiannan Huang:** Investigation. **Hengxiang Zhu:** Investigation. **Peng Huang:** Investigation. **Jingze Zhang:** Investigation, Conceptualization. **Li Hu:**

Supervision. **Qun Ye:** Investigation. **Xiang Wang:** Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.watcyc.2025.09.001>.

Data availability

Data will be available on request.

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