KeAi
CHINESE ROOTS
GLOBAL IMPACT

Research Article

Cladophora as ecological engineer: A new test from the largest lake of Qinghai-Tibet plateau with filamentous algal blooms

Zhihua Wu [a,b], Xigong Yuan [c], Xiong Xiong [a], Hongyi Ao [a], Chenxi Wu [a], Guoxiang Liu [a], Huan Zhu [a,*]

[a] *Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, 430072, China*
[b] *College of Science, Tibet University, Lhasa, 850001, China*
[c] *Huaihe River Commission of the Ministry of Water Resources, Bengbu, 233001, China*

ARTICLE INFO

ABSTRACT

Filamentous algae blooms (FABs) have been increasing globally in recent years, and their presence can have both harmful and beneficial effects on aquatic ecosystems. As one of the most common FABs, *Cladophora* blooms have been reported in the lakes of the Qinghai-Tibet Plateau during the past few years. However, there have been few studies focused on how FABs impact other aquatic organisms, especially in alpine lakes since these are at the forefront of responding to global climate change. In this study, the phytoplankton communities in different regions of Qinghai Lake were profiled in different seasons using meta-barcode sequencing. The phytoplankton assemblages in areas with *Cladophora* blooms were compared to those without *Cladophora*. The phytoplankton community structure correlated with physicochemical properties including water temperature, electrical conductivity, nitrate, and the presence or absence of *Cladophora* blooms. The relative abundance of Bacillariophytes was found to be higher in zones with *Cladophora* blooms than in other regions. Significant seasonal changes in phytoplankton biomass and β diversity were observed in zones with *Cladophora* blooms. Growth and microbial degradation of *Cladophora* can change the pH, dissolved oxygen, secchi depth, and nitrate. Together with seasonal temperature and electrical conductivity changes, *Cladophora* growth can significantly impact the phytoplankton biomass, community dissimilarity and assembly process. These results showed that *Cladophora* plays a key role in littoral aquatic ecosystem ecology.

1. Introduction

Excessive algae growth has become a global concern, posing a serious challenge to the management of lakes, rivers, and reservoirs (Vadeboncoeur et al., 2021). While many studies have focused on micro-algal blooms, there is still only limited research on filamentous algal blooms (FABs). In recent years, FABs have been reported in streams, oceans and lakes such as Lake Baikal, and eutrophic waters such as Great Lakes of North America. The apparent increase of FABs was mainly found in global littoral zones which harbor most of the biodiversity and are an essential energy source for lake food webs (Vadeboncoeur et al., 2011). However, there is still a need for scientific efforts to understand the impact of those green filamentous growths on other organisms.

FABs usually refer to the proliferation of long, filamentous algae such as the green macroalgae *Ulva prolifera*, and *Cladophora* that commonly occur in the littoral zones of lakes and rivers. It is traditionally believed

that filamentous algae have an absolute advantage in nutrient uptake in littoral zones due to their complex constructures, which contributes to their capacity for rapid growth and biomass accumulation. FABs can drive changes in the physicochemical properties of water through biogeochemical cycling which can then affect growth of other plankton and benthos. Due to nutrient competition, nearshore *Cladophora* mats can also reshape the epi-biotic microalgae through high spatial and temporal variability (Prazukin et al., 2021). Decomposition of *Cladophora* accumulations in the Gulf of Finland led to an abrupt decline in abundance of macroinvertebrates (Gubelit and Berezina, 2010). In summary, FABs can lead to oxygen depletion, noxious and toxic odors, allelochemical effects, alteration of biogeochemical cycles, which consequently affect other microorganisms. Additionally, these littoral filamentous algae could also provide more micro-habitats, yet still result in habitat loss for periphyton and other benthos. Previous studies on the effects of FABs have primarily focused on the impacts on bacteria or macroinvertebrates, with little

---

attention being given to the impact on phytoplankton. Phytoplankton are a complex and diverse group of microorganisms that play a fundamental role in aquatic systems as primary producers (Borics et al., 2021; Tranvik et al., 2009). The biomass and diversity of phytoplankton in areas with FABs is often lower than in areas without FABs. However, the specifics of FAB effects on phytoplankton communities has not been studied in detail. In fact, it is still unclear how FABs affect the biomass and biodiversity of phytoplankton.

Cladophora is a filamentous green alga, and is widely distributed in both marine and freshwater habitats (Dodds and Gudder, 1992). It is often attached to substrates, and occasionally found floating in the pelagic zone. It is often referred to as an "ecological engineer" because it provides microhabitats and food for aquatic organisms (Zulkifly et al., 2013). As one of the most common FABs, however, *Cladophora* blooms can also adversely impact growth of submerged plants in near-shore landscapes (Whitton, 1970), as has been reported in many lakes, including Great Lake, Caohai Lake and Qinghai Lake and as well as shallow marine environments (Auer et al., 2010; Gubelit and Berezina, 2010; Zhu et al., 2020; Guo et al., 2022).

Many highland lakes such as Qinghai Lake are generally considered oligotrophic, characterized by low phytoplankton abundance, and a stable zooplankton and benthic community structure (Meng et al., 2016). However, due to an increase in water levels caused by a warmer and moister climate, the newly inundated littoral zone has provided a suitable substrate for the growth of *Cladophora*. Abundant bird droppings near Bird Island provide phosphorus for growth. This has led to a recurrence of *Cladophora* blooms after half a century (Zhu et al., 2020). The excessive growth has negatively impacted the wetland ecosystem and surrounding landscape. Several studies have focused on the use of remote sensing to monitor the causes of the *Cladophora* blooms in Qinghai Lake (Duan et al., 2022; Wang et al., 2022; Zhu et al., 2020). However, the impact of *Cladophora* meadows on phytoplankton is still unclear and has been studied less, especially in alpine lakes. To comprehensively assess the effects of *Cladophora* blooms on phytoplankton diversity, the phytoplankton assemblages were profiled in this study using meta-barcode sequencing. Species diversity, community dissimilarity, and assembly processes of phytoplankton in different lake areas and seasons were analyzed. The aim of this study was to test the hypothesis that *Cladophora* as an ecological engineer in the riparian zone, changed the phytoplankton biomass, diversity and community assembly

process. This study provides new evidence for understanding the impacts of FABs on aquatic ecosystems.

2. Materials & methods

2.1. Field sampling

Qinghai Lake is the largest lake in China and is located in the northeast part of the Tibet Plateau between $36°32'–37°15'N$ and $99°36'–100°16'E$. It has a surface area of approximately 4472 km^2 (as in 2018) (Fan et al., 2021). A total of 18 sampling sites were selected in four different regions, i.e., the *Cladophora* Blooming zone (CBZ), the estuary area of the Baha River (BRE), the Nearshore where the *Cladophora* blooms did not occur (NS), and the Pelagic zone of Qinghai Lake (PZ) (Fig. 1). *Cladophora* usually starts to accumulate in May–June and reaches peak biomass in August–September. We collected phytoplankton samples from four different ecological regions of Qinghai Lake in May (bloom development period) and August (when the bloom had peaked) in 2021.

2.2. Phytoplankton collection and processing

Water samples were collected and pre-filtered using a plankton net (0.112 mm in diameter) to remove large zooplankton and floating *Cladophora* filaments. Five hundred milliliters of filtered water was then collected for environmental DNA analysis and filtered onto 0.22 μm Durapore membranes (Millipore). All membranes were immediately frozen and stored in liquid nitrogen. DNA extraction was performed using OMEGA water DNA kit (D5525-01, OMEGA biotech). The quality of extracted total DNA was tested using an ultra-micro spectrophotometer (Nanodrop 8000, Thermo). The V4 region of 18S rDNA was amplified using universal eukaryotic V4 region primers (forward primer CCAGCASCYGCGGTAATTCC, reverse primer ACTTTCGTTCTTGATYRA) (STOECK et al., 2010). Gel Extraction Kit (Omega, USA) was used to purify the PCR products after they were electrophoresed. The purified PCR products were used for library construction using SolexaPCR, and the constructed libraries were tested by Qsep-400 and sequenced on Hiseq 2500 (Illumina). All sequencing raw data were uploaded to the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under the biological project number PRJNA865045.
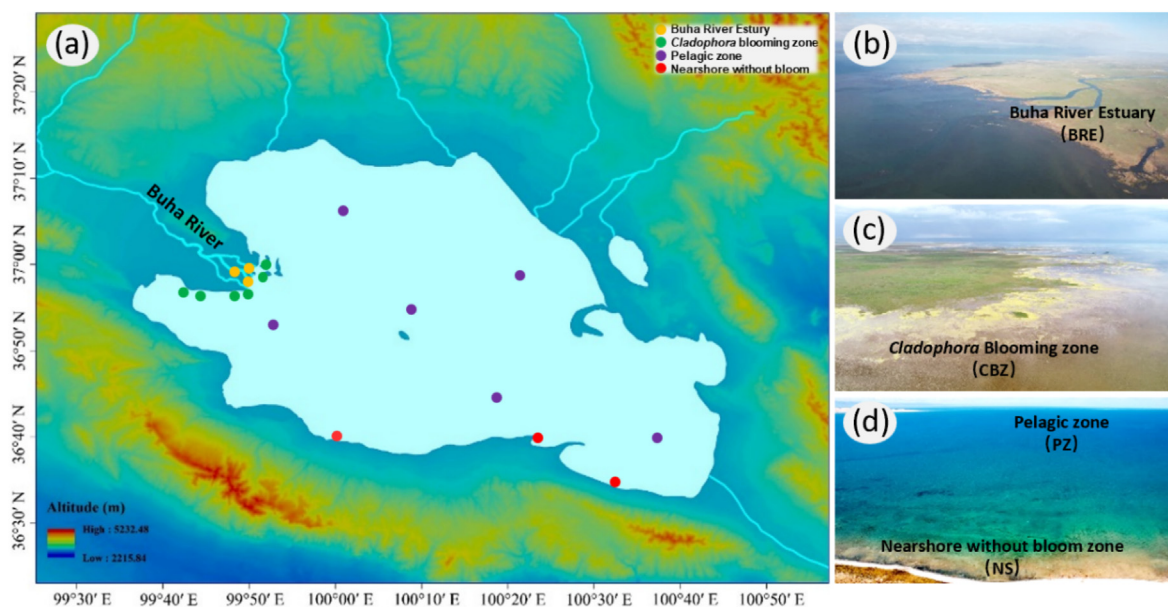
Fig. 1. Distribution of sampling sites and representative habitat areas in Qinghai Lake. (**a**) Distribution of sampling sites. (**b–d**) aerial views of habitat areas of the Buha River Estuary (BRE), *Cladophora* Blooming zone (CBZ), Nearshore without bloom zone (NS), and Pelagic zone (PZ), respectively.

2.3. Determination of environmental factors

Water temperature (Temp), electrical conductivity (EC), pH, and dissolved oxygen concentration (DO) were measured in the field using a Hydrolab Hash (Austin, TX, USA). We used concentration of chlorophyll *a* (Chla) to estimate the biomass of phytoplankton. The concentrations of total nitrogen (TN), ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), secchi depth (SD), total phosphorus (TP), soluble reactive phosphate (SRP) and chlorophyll *a* (Chla) were determined as described previously (Ao et al., 2014).

2.4. Data processing and analysis

The raw data were primarily filtered and merged, and removal of primer base pairs was performed using USEARCH (Edgar and Flyvbjerg, 2015). The high-quality reads generated from the above-mentioned steps were used in the following analysis. Sequences with similarity ≥97% were clustered into the same operational taxonomic unit (OTU) by USEARCH (v10.0), and OTU's with abundance lower than 0.005% were filtered, followed by chimera removal using UCHIME (version 8.1) (Edgar et al., 2011). The representative sequences of each OTU were annotated by USEARCH (v10.0), and only eukaryotic algal OTU's were subsequently processed (Edgar, 2010). The sequence matrix was aligned using the Mafft online service (Katoh et al., 2019), and then trimmed using TrimAl (Capella-Gutierrez et al., 2009). The phylogenetic tree was constructed using IQtree (Nguyen et al., 2015), and the consensus tree that was obtained was used for calculating phylogenetic diversity and assembly process. To explore the differences between phytoplankton

communities, principal coordinate analysis (PCoA) based on Bray-Curtis distance was performed. The richness, Shannon–Wiener diversity, and phylogenetic diversity indices were used to measure alpha diversity, while the community dissimilarity (based on Bray-Curtis, Jaccard, and Morisita distances) was calculated to determine beta diversity (Amorim and Moura, 2021). All these indices were computed and compared using VEGAN and PICANTE packages (Kembel et al., 2010; Oksanen et al., 2017). To identify the key environmental drivers, redundancy analysis (RDA), and variance partitioning analysis (VPA) were performed using VEGAN packages. To explore the mechanism of community assembly in different lake groups, the ecological processes affecting phytoplankton assemblages were quantified using Picante, iCAMP and NST packages (Stegen et al., 2013). Structural equation models (SEM) were constructed to summarize the effects of *Cladophora* biomass and physicochemical properties on the community and biomass of phytoplankton using PIECEWISESEM (Lefcheck, 2016). All numerical ecological analyses were performed in R (Team, 2017).

3. Results

The phytoplankton communities in Qinghai Lake showed significant temporal ($R^2 = 0.17$, $p < 0.001$) and spatial ($R^2 = 0.39$, $p < 0.001$) differences (Fig. 2a). The PZ and NS sites were clustered together in either spring or summer. There was a significant difference between spring and summer in phytoplankton communities for all lakes areas except BRE. The richness and relative abundances of phytoplankton also exhibited strong temporal and spatial variation. Bacillariophytes (diatoms) was the most species-rich algal group in Qinghai Lake during both
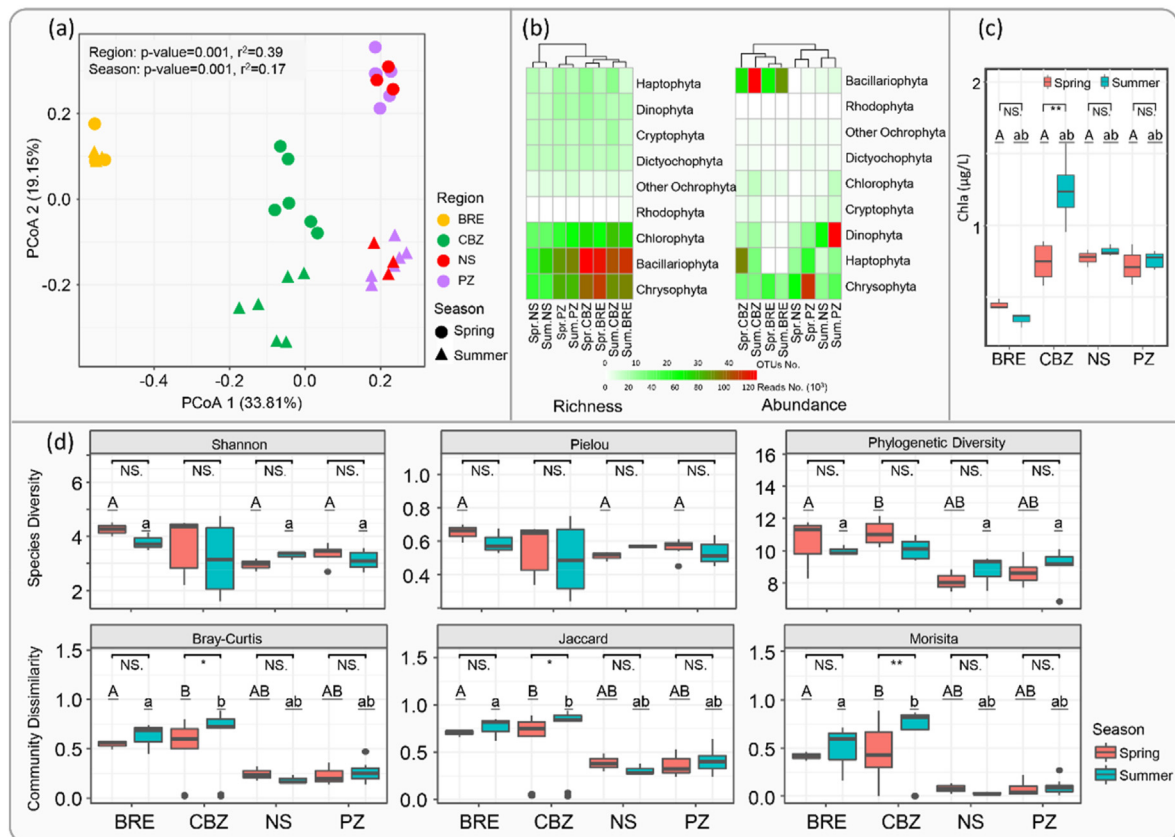
Fig. 2. (**a**) PCoA ranking based on Bray-Cruti distance of the phytoplankton community. (**b**) the richness (number of OTU's) and abundance (number of reads) of phytoplankton in each lake area of Qinghai Lake in spring (Spr.) and summer (Sum.). (**c**) The box plot and comparison of phytoplankton biomass (concentration of chlorophyll *a*) difference in spring and summer in each lake area. (**d**) Box plot and comparison of species diversity differences in different periods and different lake areas based on Shannon's-Wiener index, Pielou's evenness index, Phylogenetic diversity index; and comparisons of phytoplankton community dissimilarity in different lake areas and seasons based on Bray-Curtis distance, Jaccard distance and Morisita distance. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Different letters for the same season represent significant differences among the four habitats (P < 0.05).

spring and summer, followed by Chrysophytes and Chlorophytes. The relative abundance and richness of Bacillariophytes in the BRE and CBZ regions were significantly higher than in the PZ and NS regions (Fig. 2b). The phytoplankton biomass of CBZ in spring was significantly lower than in summer, and the other regions did not display significant seasonal difference (Fig. 2c). The phytoplankton biomass of CBZ is also significantly higher than in other regions in the same season. The alpha diversity (Shannon-Wiener, Pielou and phylogenetic diversity) did not show any significant difference between spring and summer in all lake regions (Fig. 2d). The Shannon and Pielou indices of CBZ were not significantly different from those of NS and PZ, but the phylogenetic diversity of CBZ was higher. In terms of community dissimilarity, there was no significant difference between spring and summer in all regions except CBZ, where the community dissimilarity was higher in summer than in spring (Fig. 2d). In the same season, the dissimilarity was significantly higher in BRE and CBZ than in the other two regions. Overall, there was little seasonal variation in alpha diversity among different lake regions, but their community assembly and dissimilarity were more variable. Excessive *Cladophora* growth increased the phytoplankton biomass and community dissimilarity, especially in summer.

Together, stochastic and deterministic ecological processes based on neutral process theory and ecological niche theory respectively, have shaped the microbial community assembly, and are increasingly becoming an important part of our understanding of phytoplankton community structure. The assembly process of phytoplankton communities across all regions of Qinghai Lake during Spring and Summer was dominated by stochastic processes (Fig. 3). The ecological drift was the main determinant of the assembly process of NS and PZ in spring and summer with a relative contribution of 100% and 80%, respectively. Stochastic processes contributed to the spring and summer phytoplankton assembly respectively with 66% and 100% in the BRE. The proportion of deterministic processes was higher in the CBZ region (33%) than other regions in summer.

There were 12 environmental factors remaining after calculating a variance inflation factor (Fig. 4a). The results of RDA analysis between phytoplankton assemblages and environmental factors revealed that the eigenvalues of the two ranking axes were 29.8% and 25.9%, respectively. The significant environmental variables affecting the phytoplankton community were Temp, pH, EC, SD, DO, NO_3^- and *Cladophora* biomass (Fig. 4a). The VPA results showed that PCI (physicochemical properties, including SD, EC, pH, Temp, and DO) alone contributed 11% variance ($p < 0.001$), followed by nitrogen nutrition (6%, $p < 0.030$) and *Cladophora* biomass (4%, $p < 0.040$). Even still 45% of the variance remained unexplained.

The results of the SEM analyses were similar to the RDA and VPA analyses. Alpha diversity is only correlated with Temp. There were 6 environmental drivers, (Temp, pH, EC, SD, DO, and nitrate) that were

significantly corelated with community dissimilarity. Phytoplankton biomass was correlated with Temp, pH and EC (Montes-Hugo et al., 2009). Assembly process showed a strong relationship with pH, EC and nitrate. The spatial change of EC affects phytoplankton growth, community dissimilarity, and assembly process. In conclusion, phosphorus and water temperature play crucial roles in the recurrence of *Cladophora* blooms in Qinghai Lake. Excessive *Cladophora* growth affected the concentration of nitrate and DO, pH, and SD. These factors, in combination with EC and Temp, further affected the phytoplankton assemblage, assembly process, and phytoplankton biomass (Fig. 5).

4. Discussion

Cladophora is often considered to be an ecological engineer, that provides a unique habitat for microorganisms that can affect biogeochemical cycling in coastal regions, and thus it can impact on the phytoplankton community (Jones et al., 1994; Zulkifly et al., 2013). These FABs alter ecological processes within the littoral zone, which in turn indirectly influences the composition of the phytoplankton community (Dodds and Gudder, 1992; Lyons et al., 2014). However, the mechanisms underlying these indirect effects are still not well understood. The results of this study show the community dissimilarity of CBZ was significantly higher than in other regions and had obvious seasonal differences. This shows that FABs can provide beneficial effects and enhance the biodiversity in some ecosystems (Bolam and Fernandes, 2002; Dolbeth et al., 2003; Holmquist, 1997). *Cladophora* blooms provided a growth substratum for a diverse range of microbial epiphytes (mainly diatoms such as *Cocconeis*, *Rhoicosphenia*, and *Gomphonema*) due to its biomass and high surface area (Bergey et al., 1995; Young et al., 2010; Zulkifly et al., 2013). Wave disturbance and other forces contribute to a shift of these epiphytes from an attached to a planktonic state. This study showed that diatom species richness and relative abundance in the CBZ were significantly higher than in the PZ and NS, which is consistent with our hypothesis. Just like Lake Huron, diatom abundance was higher in CBZ in summer than in spring, and this may be related to the increased biomass of *Cladophora* in summer, and frequent weather changes such as strong wind and wave disturbances (Stevenson and Stoermer, 1982).

The phytoplankton communities are primarily driven by physicochemical properties and nitrogen nutrition, with phosphorus having little effect, as observed in other plateau lakes (Tang et al., 2021; Wu et al., 2006), which suggest that nitrogen may be the limiting nutrient to phytoplankton. Physicochemical properties and nitrogen nutrition mainly affected phytoplankton community dissimilarity and assembly processes, while the effects on alpha diversity and phytoplankton biomass were weak. EC was the dominant factor affecting phytoplankton biomass, as confirmed by most plateau lake studies (Zhang et al., 2022). Photosynthesis by excessive *Cladophora* growth produces lots of
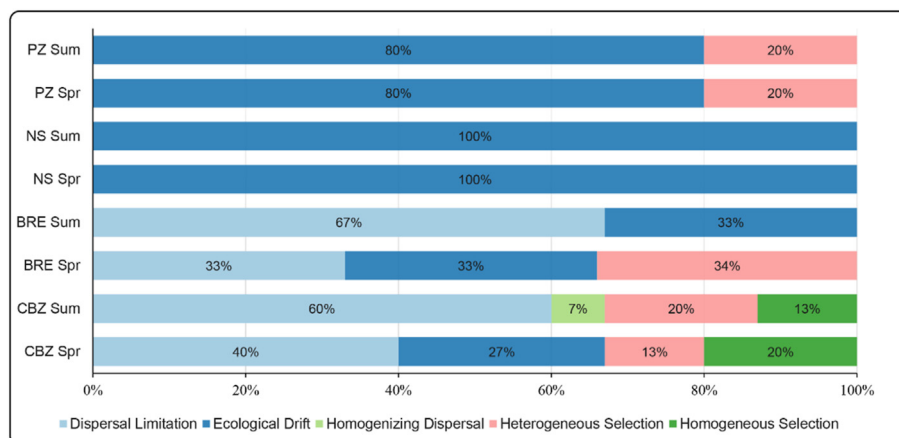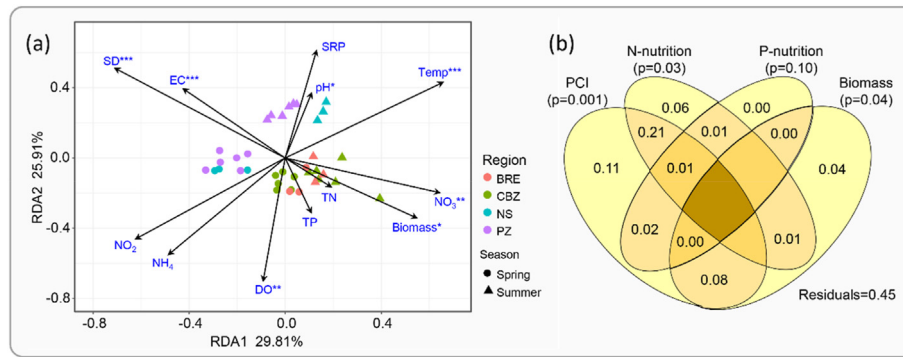

Fig. 3. Phytoplankton assembly process quantification in spring and summer of different lake areas.

Fig. 4. (**a**) Biplot (samples and environmental variables) of the redundancy analysis based on phytoplankton abundance matrix. (**b**) Variation partitioning analysis based Venn diagrams showing variation according to Bray-Curtis community distance explained by unique and joint effects of physiochemical index (PCI), phosphorus nutrition (P-nutrition), nitrogen nutrition (N-nutrition), and Cladophora Biomass (Biomass). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.
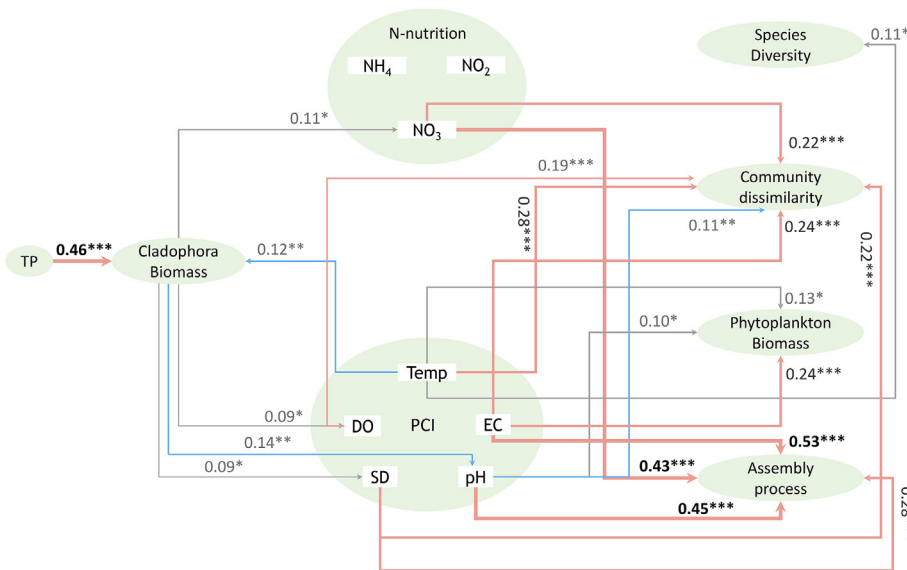
Fig. 5. Correlation among *Cladophora* biomass, phosphorus, nitrogen, physicochemical properties, phytoplankton species diversity, community dissimilarity, phytoplankton biomass, and assembly processes. Species diversity, community dissimilarity, phytoplankton biomass, and assembly processes were measured using the Shannon diversity index, Bray-Curtis distances, concentration of Chlorophyll *a*, and βNTi respectively. The width of arrows indicates the Spearman's correlation coefficient, while the color of arrows represents significant correlations. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Abbreviations: Temp, temperature; DO, dissolved oxygen; SD, secchi depth; EC, electrical conductivity; TP, total phosphorus; NH_4^+, ammonia; NO_3^-, nitrate; NO_2^-, nitrite.

dissolved oxygen, and increases the pH through removal of dissolved inorganic carbon. Conversely, microbial degradation of *Cladophora* consumes DO (generates a biological oxygen demand), and decreases pH (Zhang et al., 2021). Thus, *Cladophora* biomass dynamics will be directly correlated with changes in DO and pH, which in turn will also affect assemblages of other aquatic organisms. Increased DO and decreased pH could benefit most phytoplankton and benthos, while decreased DO will impair the survival of planktonic and benthic fauna. It has been shown that *Cladophora* can exude allelochemicals that can control planktonic and epiphytic (Cheney and Hough, 1983) organisms. These compounds together with other plankton can change the SD, which changes the depth of phytoplankton photosynthesis by changing the depth of the euphotic zone. The results of this study proved that growth of FABs changed the pH, DO and the SD, and consequently affected community dissimilarity and assembly processes. Moreover, *Cladophora* provides plenty of micro-habitat for microorganisms especially some bacteria and cyanobacteria involved in geochemical cycling of some biogenic elements including nitrogen and sulfate (Lewis and Wurtsbaugh, 2008; Zhang et al., 2021). Since nitrogen is often the main limiting element in oligotrophic aquatic ecosystems (Zulkifly et al., 2012), *Cladophora* blooms can help phytoplankton to overcome nitrogen limitation by hosting epiphytic nitrogen-fixers. Nitrogen-fixing planktonic cyanobacteria were found associated with *Cladophora* in Mendota Lake, suggesting that phytoplankton might not often be limited by nitrogen. This is

consistent with the results of this study which showed that *Cladophora* has a significant effect on nitrate availability (Zulkifly et al., 2012).

Previous studies have indicated that stochastic processes dominate the assembly of phytoplankton communities in highland lakes, primarily driven by seasonality and salinity (or EC) (Zhang et al., 2022). This study showed that this is also the case in Qinghai Lake. The species pool hypothesis can explain why stochastic processes dominated the community assembly process. The hypothesis holds that macroevolution, and historical and geographical factors were the determinants of regional species pool sizes (Taylor et al., 1990; Zobel, 1992). Due to the harsh plateau climate (cold, hypoxia, strong ultraviolet radiation) and poor species pool in Qinghai Lake, the dominant role of stochastic process was similar to the dominance of random processes in the large invertebrate community of the lake (Ge et al., 2021). Notably, in contrast with the other lake regions, deterministic processes consistently contributed 33% of the assembly process in the CBZ, which were not seasonally variable. *Cladophora* plays a key role in maintaining microhabitats, and shaping the spatial hydrological environment, thus indirectly influencing the coastal biogeochemical cycle and mitigating the effects of ultraviolet radiation (Dodds and Gudder, 1992; Higgins et al., 2008b; Zulkifly et al., 2013). This may be the primary reason for the existence of deterministic processes. In summary, *Cladophora* meadows function as an ecological engineer by creating, modifying and maintaining habitats, and these meadows also provide the main species pool for a diverse range of microorganisms in lake littoral zones.

5. Conclusion

In this paper, the phytoplankton community of Qinghai Lake was comprehensively profiled using amplicon sequencing, leading to the subsequent characterization of its key drivers. This study showed that FABs could impact key aspects of the phytoplankton community structure. Although our results could not comprehensively show the underlying mechanisms by which FABs drive phytoplankton communities, we hypothesize that FABs in alpine lake ecosystems may influence phytoplankton communities in the following ways. FABs could alter the assemblage and assembly process by providing more microhabitats for algae. It could also lead to shifts in the nitrogen level particularly nitrate, possibly through interactions with other nitrogen-fixing organisms. Both FABs and phytoplankton are affected by the physicochemical properties. The presence of FABs and its degradation may lead to changes in physicochemical properties, particularly pH, DO, SD, which can in turn affect phytoplankton community structure. Overall, in the alpine lake ecosystems, the FABs do not appear to strongly inhibit phytoplankton but instead promote their growth as well as α and β diversity. This suggests that *Cladophora* indeed functions as an ecological engineer in the lake littoral zone. Further studies could better focus on mechanisms by which FABs change physicochemical properties and nitrate levels.

Author contributions

Conceptualization, Z.W. and H.Z.; methodology, Z.W., X.Y., X.X. H. A. and H.Z.; writing, original draft preparation, Z.W. and H.Z.; writing, review and editing, H.Z. Z.W., X.X., C.W. and G.L.; supervision, H.Z.; and funding acquisition, H.Z. All authors have read and agreed to the published version of the manuscript.

Funding

Declaration of competing interest

The authors declare no potential conflicts of interest. C.W. is an editorial board member for *Water Biology and Security* and was not involved in the editorial review or the decision to publish this article.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.watbs.2023.100210.

References

Ao, H.Y., Wu, C.X., Xiong, X., Jing, L.D., Huang, X.L., Zhang, K., Liu, J.T., 2014. Water and sediment quality in Qinghai Lake, China: a revisit after half a century. Environ. Monit. Assess. 186 (4), 2121–2133. https://doi.org/10.1007/s10661-013-3522-7.

Amorim, C.A., Moura, A.d.N., 2021. Ecological impacts of freshwater algal blooms on water quality, plankton biodiversity, structure, and ecosystem functioning. Sci. Total Environ. 758, 143605. https://doi.org/10.1016/j.scitotenv.2020.143605.

Auer, M.T., Tomlinson, L.M., Higgins, S.N., Malkin, S.Y., Howell, E.T., Bootsma, H.A., 2010. Great Lakes Cladophora in the 21st century: same algae-different ecosystem. J. Great Lake. Res. 36 (2), 248–255. https://doi.org/10.1016/j.jglr.2010.03.001.

Bergey, E.A., Boettiger, C.A., Resh, V.H., 1995. Effects of water velocity on the architecture and epiphytes of Cladophora-glomerata (Chlorophyta). J. Phycol. 31 (2), 264–271. https://doi.org/10.1111/j.0022-3646.1995.00264.x.

Bolam, S.G., Fernandes, T.F., 2002. The effects of macroalgal cover on the spatial distribution of macrobenthic invertebrates: the effect of macroalgal morphology. Hydrobiologia 475 (1), 437–448. https://doi.org/10.1023/A:1020307929624.

Borics, G., Abonyi, A., Salmaso, N., Ptacnik, R., 2021. Freshwater phytoplankton diversity: models, drivers and implications for ecosystem properties. Hydrobiologia 848 (1), 53–75. https://doi.org/10.1007/s10750-020-04332-9.

Capella-Gutierrez, S., Silla-Martinez, J.M., Gabaldon, T., 2009. trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25 (15), 1972–1973. https://doi.org/10.1093/bioinformatics/btp348.

Cheney, C., Hough, R.A., 1983. Factors controlling photosynthetic productivity in a population of Cladophora fracta (chlorophyta). Ecology 64 (1), 68–77. https://doi.org/10.2307/1937330.

Dodds, W.K., Gudder, D.A., 1992. The ecology of Cladophora. J. Phycol. 28 (4), 415–427. https://doi.org/10.1111/j.0022-3646.1992.00415.x.

Dolbeth, M., Pardal, M.A., Lillebo, A.I., Azeiteiro, U., Marques, J.C., 2003. Short- and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. Mar. Biol. 143 (6), 1229–1238. https://doi.org/10.1007/s00227-003-1133-5.

Duan, H.Y., Yao, X.J., Zhang, D.H., Jin, H.A., Wei, Q.X., 2022. Long-Term temporal and spatial monitoring of Cladophora blooms in Qinghai Lake based on multi-source remote sensing images. Rem. Sens. 14 (4). https://doi.org/10.3390/rs14040853.

Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26 (19), 2460–2461. https://doi.org/10.1093/bioinformatics/btq461.

Edgar, R.C., Flyvbjerg, H., 2015. Error filtering, pair assembly and error correction for next-generation sequencing reads. Bioinformatics 31 (21), 3476–3482. https://doi.org/10.1093/bioinformatics/btv401.

Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27 (16), 2194–2200. https://doi.org/10.1093/bioinformatics/btr381.

Fan, C.Y., Song, C.Q., Li, W.K., Liu, K., Cheng, J., Fu, C.S., Chen, T., Ke, L.H., Wang, J.D., 2021. What drives the rapid water-level recovery of the largest lake (Qinghai Lake) of China over the past half century? J. Hydrol. 593. https://doi.org/10.1016/j.jhydrol.2020.125921.

Ge, Y., Meng, X., Heino, J., García-Girón, J., Liu, Y., Li, Z., Xie, Z., 2021. Stochasticity overrides deterministic processes in structuring macroinvertebrate communities in a plateau aquatic system. Ecosphere 12 (7), e03675. https://doi.org/10.1002/ecs2.3675.

Gubelit, Y.I., Berezina, N.A., 2010. The causes and consequences of algal blooms: the Cladophora glomerata bloom and the Neva estuary (eastern Baltic Sea). Mar. Pollut. Bull. 61 (4–6), 183–188. https://doi.org/10.1016/j.marpolbul.2010.02.013.

Guo, L.L., Dai, L.L., Zheng, J.L., Zhou, W.C., Peng, C.R., Li, D.H., Li, G.B., 2022. Environmental factors associated with the filamentous green algae Cladophora blooms: a mesocosm experiment in a shallow eutrophic lake. J. Environ. Manag. 313, 114977. https://doi.org/10.1016/j.jenvman.2022.114977.

Higgins, S.N., Malkin, S.Y., Todd Howell, E., Guildford, S.J., Campbell, L., Hiriart-Baer, V., Hecky, R.E., 2008. An ecological review of Cladophora glomerata (chlorophyta) in the laurentian Great Lakes1. J. Phycol. 44 (4), 839–854. https://doi.org/10.1111/j.1529-8817.2008.00538.x.

Holmquist, J.G., 1997. Disturbance and gap formation in a marine benthic mosaic: influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. Mar. Ecol. Prog. Ser. 158, 121–130. https://doi.org/10.3354/meps158121.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69 (3), 373–386. https://doi.org/10.2307/3545850.

Katoh, K., Rozewicki, J., Yamada, K.D., 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings Bioinf. 20 (4), 1160–1166. https://doi.org/10.1093/bib/bbx108.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26 (11), 1463–1464. https://doi.org/10.1093/bioinformatics/btq166.

Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7 (5), 573–579. https://doi.org/10.1111/2041-210X.12512.

Lewis Jr., W.M., Wurtsbaugh, W.A., 2008. Control of lacustrine phytoplankton by nutrients: erosion of the phosphorus paradigm. Int. Rev. Hydrobiol. 93 (4–5), 446–465. https://doi.org/10.1002/iroh.200811065.

Lyons, D.A., Arvanitidis, C., Blight, A.J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-Kotta, H., Queirós, A.M., Rilov, G., Somerfield, P.J., Crowe, T.P., 2014. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. Global Change Biol. 20 (9), 2712–2724. https://doi.org/10.1111/gcb.12644.

Meng, X.L., Jiang, X.M., Xiong, X., Wu, C.X., Xie, Z.C., 2016. Mediated spatio-temporal patterns of macroinvertebrate assemblage associated with key environmental factors in the Qinghai Lake area, China. Limnologica 56, 14–22. https://doi.org/10.1016/j.limno.2015.11.005.

Montes-Hugo, M., Doney, S.C., Ducklow, H.W., Fraser, W., Martinson, D., Stammerjohn, S.E., Schofield, O., 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the western antarctic peninsula. Science 323 (5920), 1470–1473. https://doi.org/10.1126/science.1164533.

Nguyen, L.T., Schmidt, H.A., von Haeseler, A., Minh, B.Q., 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol. Biol. Evol. 32 (1), 268–274. https://doi.org/10.1093/molbev/msu300.

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Simpson, G., Solymos, P., Stevens, M., Wagner, H., 2017. Vegan: Community Ecology Package. R Package Version 2, pp. 3–5, 2016.

Prazukin, A., Shadrin, N., Balycheva, D., Firsov, Y., Lee, R., Anufriieva, E., 2021. Cladophoraspp. (Chlorophyta) modulate environment and create a habitat for microalgae in hypersaline waters. Eur. J. Phycol. 56 (3), 231–243. https://doi.org/10.1080/09670262.2020.1814423.

Stegen, J.C., Lin, X.J., Fredrickson, J.K., Chen, X.Y., Kennedy, D.W., Murray, C.J., Rockhold, M.L., Konopka, A., 2013. Quantifying community assembly processes and identifying features that impose them. ISME J. 7 (11), 2069–2079. https://doi.org/10.1038/ismej.2013.93.

Stevenson, R.J., Stoermer, E.F., 1982. Seasonal abundance patterns of diatoms on Cladophora in lake Huron. J. Great Lake. Res. 8 (1), 169–183. https://doi.org/10.1016/S0380-1330(82)71955-0.

STOECK, T., Bass, D., Nebel, M., Christen, R., Jones, M.D.M., Breiner, H.-W., Richards, T.A., 2010. Multiple marker parallel tag environmental DNA sequencing reveals a highly complex eukaryotic community in marine anoxic water. Mol. Ecol. 19 (s1), 21–31. https://doi.org/10.1111/j.1365-294X.2009.04480.x.

Tang, X., Xie, G., Shao, K., Tian, W., Gao, G., Qin, B., 2021. Aquatic bacterial diversity, community composition and assembly in the semi-arid inner Mongolia plateau: combined effects of salinity and nutrient levels. Microorganisms 9 (2), 208. https://www.mdpi.com/2076-2607/9/2/208.

Taylor, D.R., Aarssen, L.W., Loehle, C., 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. Oikos 58 (2), 239–250. https://doi.org/10.2307/3545432.

Team, R.C., 2017. Changes in R From version 3.4.2 to version 3.4.3. R Journal 9 (2), 568–570.

Tranvik, L.J., Downing, J.A., Cotner, J.B., Loiselle, S.A., Striegl, R.G., Ballatore, T.J., Dillon, P., Finlay, K., Fortino, K., Knoll, L.B., Kortelainen, P.L., Kutser, T., Larsen, S., Laurion, I., Leech, D.M., McCallister, S.L., McKnight, D.M., Melack, J.M., Overholt, E., Porter, J.A., Prairie, Y., Renwick, W.H., Roland, F., Sherman, B.S., Schindler, D.W., Sobek, S., Tremblay, A., Vanni, M.J., Verschoor, A.M., von Wachenfeldt, E., Weyhenmeyer, G.A., 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnol. Oceanogr. 54 (6), 2298–2314. https://doi.org/10.4319/lo.2009.54.6_part_2.2298.

Vadeboncoeur, Y., McIntyre, P.B., Vander Zanden, M.J., 2011. Borders of biodiversity: life at the edge of the world's large lakes. Bioscience 61 (7), 526–537. https://doi.org/10.1525/bio.2011.61.7.7.

Vadeboncoeur, Y., Moore, M.V., Stewart, S.D., Chandra, S., Atkins, K.S., Baron, J.S., Bouma-Gregson, K., Brothers, S., Francoeur, S.N., Genzoli, L., Higgins, S.N., Hilt, S., Katona, L.R., Kelly, D., Oleksy, I.A., Ozersky, T., Power, M.E., Roberts, D., Smits, A.P., Timoshkin, O., Tromboni, F., Vander Zanden, M.J., Volkova, E.A., Waters, S., Wood, S.A., Yamamuro, M., 2021. Blue waters, green bottoms: benthic filamentous algal blooms are an emerging threat to clear lakes worldwide. Bioscience 71 (10), 1011–1027. https://doi.org/10.1093/biosci/biab049.

Wang, K., Zhao, K., Xiong, X., Zhu, H., Ao, H., Ma, K., Xie, Z., Wu, C., Wang, H., Zhang, H., Zhang, P., Xu, J., 2022. Altered energy mobilization within the littoral food web in new habitat created by climate-induced changes in lake water level. Frontiers in Ecol. Evol. 10. https://doi.org/10.3389/fevo.2022.886372.

Whitton, B.A., 1970. Biology of Cladophora in freshwaters. Water Res. 4 (7), 457–476. https://doi.org/10.1016/0043-1354(70)90061-8.

Wu, Q.L., Zwart, G., Schauer, M., Agterveld, M.P.K.-v., Hahn, M.W., 2006. Bacterioplankton community composition along a salinity gradient of sixteen high-mountain lakes located on the Tibetan plateau, China. Appl. Environ. Microbiol. 72 (8), 5478–5485. https://doi.org/10.1128/AEM.00767-06.

Young, E.B., Tucker, R.C., Pansch, L.A., 2010. Alkaline phosphatase in freshwater Cladophora-epiphyte assemblages: regulation in response to phosphorus supply and localization1. J. Phycol. 46 (1), 93–101. https://doi.org/10.1111/j.1529-8817.2009.00782.x.

Zhang, J., Shen, H., Wang, H., Zhang, W., Deng, X., Gao, Q., Yang, X., Chen, J., Xie, P., 2022. Salinity and seasonality shaping free-living and particle-associated bacterioplankton community assembly in lakeshores of the northeastern Qinghai-Tibet Plateau. Environ. Res. 214, 113717. https://doi.org/10.1016/j.envres.2022.113717.

Zhang, L., Huang, S., Peng, X., Liu, B., Zhang, X., Ge, F., Zhou, Q., Wu, Z., 2021. Potential ecological implication of Cladophora oligoclora decomposition: characteristics of nutrient migration, transformation, and response of bacterial community structure. Water Res. 190, 116741. https://doi.org/10.1016/j.watres.2020.116741.

Zhu, H., Xiong, X., Ao, H., Wu, C., He, Y., Hu, Z., Liu, G., 2020. Cladophora reblooming after half a century: effect of climate change-induced increases in the water level of the largest lake in Tibetan Plateau. Environ. Sci. Pollut. Control Ser. 27 (33), 42175–42181. https://doi.org/10.1007/s11356-020-10386-y.

Zobel, M., 1992. Plant species coexistence: the role of historical, evolutionary and ecological factors. Oikos 65 (2), 314–320. https://doi.org/10.2307/3545024.

Zulkifly, S., Hanshew, A., Young, E.B., Lee, P., Graham, M.E., Graham, M.E., Piotrowski, M., Graham, L.E., 2012. The epiphytic microbiota of the globally widespread macroalga Cladophora glomerata (Chlorophyta, Cladophorales). Am. J. Bot. 99 (9), 1541–1552. https://doi.org/10.3732/ajb.1200161.

Zulkifly, S.B., Graham, J.M., Young, E.B., Mayer, R.J., Piotrowski, M.J., Smith, I., Graham, L.E., 2013. The genus Cladophora kützing (ulvophyceae) as a globally distributed ecological engineer. J. Phycol. 49 (1), 1–17. https://doi.org/10.1111/jpy.12025.