Review

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Review

A Review of the Effects of Water Environment on Phytoplankton Growth Competition in Seasonally Ice-Covered Lakes

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Abstract: Phytoplankton under the ice of seasonally ice-covered lakes is a key indicator species for maintaining the health of lake ecosystems. However, there is a lack of a unified definition of cold lakes internationally. In addition, there are few studies on the distribution, driving mechanism and simulation prediction of phytoplankton under the ice, which have limited the development of winter limnology and the prevention and control of spring algal blooms. The average temperature of the coldest month, the duration of the ice period and the average annual water temperature were the main indicators for defining cold lakes based on the literatures review. The cross-action of subglacial hydrodynamics and biogeochemistry during the ice period and freeze-thaw period is the key to promoting the phytoplankton growth. The migration and transformation of nutrients and the formation of hypoxic zones of subglacial were driven by physical factors such as available light and water temperature. Cyanobacteria got advantages in the ice period and above the water column through their own gas vesicles and strong adaptation to low temperature and low oxygen. Diatoms are able to multiply rapidly with the increasing of available light and the water temperature in spring. However, the migration and transformation of nutrients induced by physical factors during the freezing-freezing-thawing process, the role of microorganisms in biogeochemical reactions, and the extent and direction of the combined effects of multiple environmental factors on phytoplankton functional groups are still unclear. At present, lake algal blooms have gradually expanded to higher latitudes under the climate change. How to accurately predict the development and response mechanism of algal blooms in cold lakes under the climate change has become a key direction in the development of winter limnology. This review explains the unique physical and chemical processes of phytoplankton growth competition in cold lakes from the perspectives of bibliometrics, mechanism analysis, method construction and future prospects. These findings would provide new insights into the field of winter limnology and provide theoretical support for the future management of spring algal blooms in cold lakes.

Keywords: phytoplankton growth and competition; algal blooms; subglacial hydrodynamics; climate change; seasonally ice-covered lakes

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1. Introduction

68% of lakes worldwide are experiencing an increasing trend in the scale, frequency, and duration of algal blooms, which seriously serious threat to the health and sustainability of freshwater ecosystems [1]. Algal blooms, especially cyanobacterial blooms, not only reduced the survival space of other aquatic species by competing for dissolved oxygen, nutrients, and available light in the lake, but also produced harmful algal toxins that harm terrestrial organisms and humans [2,3]. In addition, the economic value of surface freshwater will also be reduced due to the turbidity and odorous gases caused by algal blooms [4,5]. Therefore, preventing, controlling and managing algal blooms in lakes is a key and challenge for aquatic ecological management.

The water temperature and nutrient concentration of lakes continue to rise with climate warming and intensified human activities, leading to eutrophication of lakes and the expansion of algal blooms to mid to high latitudes [6]. Relative to mid-low latitude lakes, there was evidence that algal blooms have been found in lakes with low water temperatures, especially cyanobacterial blooms [7]. Cyanobacteria have stronger adaptability to low temperatures than other algae species, which also causesd cyanobacterial blooms to be more frequently in lakes with low water temperatures than other algae [8,9]. Therefore, cyanobacterial blooms may also like cold water based on the area, frequency, physiological shape, and abiotic factors of cyanobacterial blooms [8–11]. Cyanobacterial blooms were defined as the accumulation of cyanobacteria in the water column or edges, resulting discoloration of the water body or a maximum chlorophyll-a concentrations in the thermocline [36]. Relatively, the definition of cyanobacterial blooms in cold lakes is not clear. Recently, cyanobacterial blooms in cold lakes have been defined as those that occur in lakes with water temperatures below 15°C [12]. According to the above definition, cold lakes included not only mid-high latitude lakes, but also included high-altitude lakes. However, there were few studies on the mechanisms of algal blooms in cold lakes, which have limited the effective prevention and control of algal blooms

The unique water environment with low water temperature, subglacial hydrodynamics, and biogeochemical processes for the survival of phytoplankton in cold lakes was created. [13,14]. However, there was a lack of systematic research on the impact of various environmental factors on the growth of phytoplankton under ice, which made it difficult to support a deeper understanding of the mechanisms of phytoplankton succession [14]. Winter limnology originated in 1963, when the study of phytoplankton ecology in ice-covered lakes was proposed by Wright's [15]. At present, the nutrient migration pathways and transformation mechanisms of cold lakes during the freezing period, as well as their understanding of lake ecological functions, are limited due to the lack of research data [16]. Since 2016, winter limnology has been developing rapidly abroad. Lake ice dynamics, subglacial biogeochemical reaction processes and subglacial hydrothermal evolution has accelerated the understanding of subglacial environmental factors on phytoplankton [17]. However, the contribution of these processes such as freezing, ice melting, and snowmelt to water circulation, phytoplankton competition, and algal blooms in cold lakes is not yet clear. The biogeochemical processes under the variations in hydrothermal structure of cold lakes have become more complex and variable with the intensification of climate warming [18]. Therefore, in order to enrich the theoretical basis of winter limnology, it is urgent to reveal the definition and mechanisms of algal blooms in cold lakes, and aim to propose adaptive strategies for future climate change [19,20].

Our study summarized domestic and foreign papers of phytoplankton in cold lakes in the past 60 years, which conducted a more detailed analysis related to phytoplankton in ice periods from 1963 to 2023 in the Web of science (WoS) database. Clarifying the development history and current research hotspots based on the visual analysis. Sort out the definition of cold lakes. The focus was on revealing the effects of subglacial fluid dynamics and biogeochemistry on the phytoplankton growth during freezing periods, as well as their responsed to climate change. In view of the problem that current winter limnology research was not systematic, emerging methods for future winter limnology have been proposed to enrich the development of winter limnology theory and control the algal blooms in cold lakes.

2. Data and Hot Spot Analysis

CiteSpace was used to analyze historical documents on the impact of lake subglacial water environment on phytoplankton growth and competition from 1963 to 2023. Research hot spots and trends will be further revealed in our study. The advantage of CiteSpace is the in-depth exploration of literature through mathematical and statistical methods, as well as the visualization of data structures and hotspot relationships [21]. This study mainly used time slicing technology to construct a time-varying model of time series and integrated a single network into an overview network. In addition, this study achieved document visualization through dynamic time series mapping, including keyword identification, research hotspot extraction, correlation between publishing units [6].

2.1. Data Sources

The database for literature search was mainly web of science, and the search period was 60 years of relevant literature from 1963 to 2023. The search keywords were "phytoplankton", "cold region lakes", "cyanobacterial blooms", "ice-covered Lake", "phytoplankton dynamics", "winter", "winter limnology", "winter convection" and "phytoplankton dynamics". The "phytoplankton" must be included, which included a total of 8919 papers.

2.2. Hot Spot Analyze

Based on a total of 60 years from 1963 to 2023, the top five countries that have published research on the competitive mechanism of phytoplankton growth in cold lakes were the United States (2,084), China (1654), Canada (747), the United Kingdom (665), and Germany (663) (Figure 1). The number of published articles has increased significantly, especially in the United States and China after 2007. The number of publications in the UK, France, and Canada has remained relatively stable. The number of publications in the United States peaked at 158 in 2019.

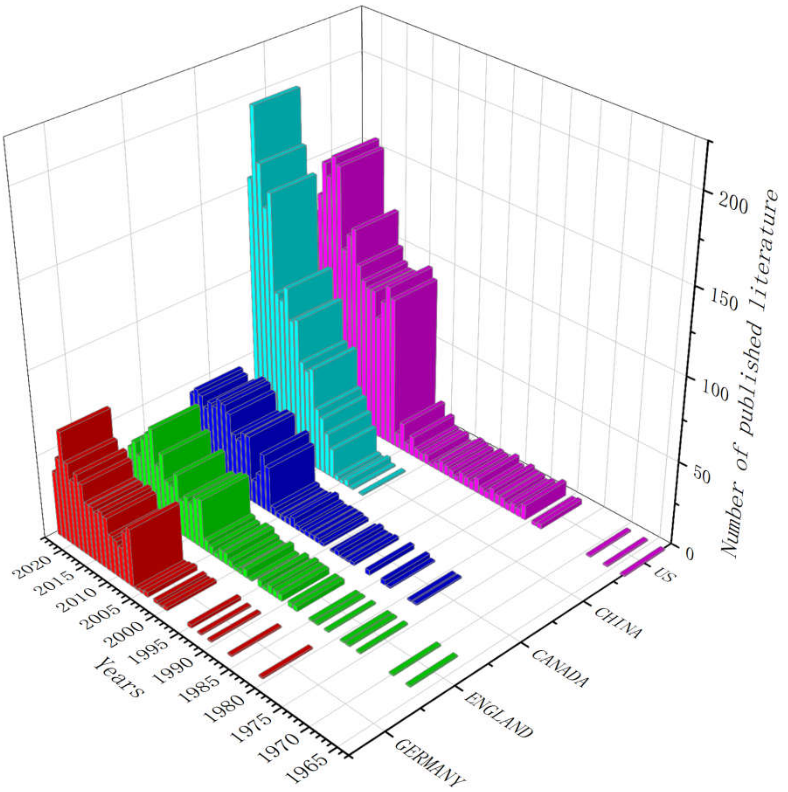

Figure 1. Statistical chart of the top five countries with the most publications on lakes in cold regions, 1963-2023.

In recent years, the number of publications in China has significantly increased, especially since 2018, from 96 to the current 198. In contrast, the number of published articles in the United States has shown a slow downward trend since reaching its peak in 2010. The number of publications in Canada, the United Kingdom, and Germany has been relatively stable in the past few years. Although there have been some fluctuations, the overall change is not significant. 280 hot keywords extracted from 1963 to 2013 based on WOS database for hot spot analysis (Figure 2). The 280 keywords with high frequency were climate change (3359), phytoplankton (1346), temperature (1098), Nitrogen (1095) and ice (1008).

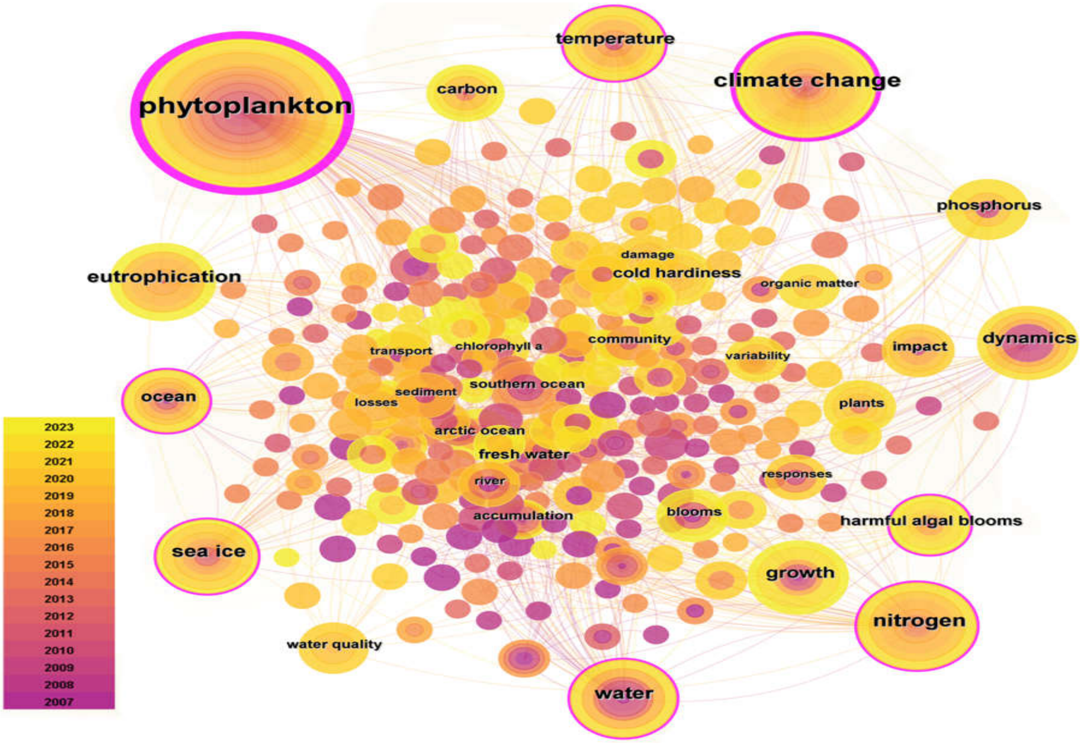

Figure 2. Keyword co-occurrence analysis diagram.

Table 1. Mapping of keyword frequency, centrality and high-frequency burst.

order	Sort by frequency of occurrence		Centrality sorting		Emergent analysis				
	Key words	frequency	Key words	Centrality	Key words	Emergence rate	Start	Over	1963-2023
1	Phytoplankton	3359	Phytoplankton	0.11	Carbon	0.87	2007	2012	
2	Climate change	1346	Water	0.09	Plankton	0.09	2007	2010	
3	Temperature	1098	Great lakes	0.09	Dynamics	0.12	2009	2015	
4	Nitrogen	1095	impacts	0.08	Sea ice	0.85	2010	2014	
5	ice	1008	ecology	0.07	Nitrogen	0.5	2013	2016	
6	Phosphorus	970	ice	0.06	diversity	0.69	2014	2017	
7	Constructed wetland	969	dynamics	0.06	winter	0.88	2014	2019	
8	Denitrification	823	climate	0.05	tibetan plateau	0.55	2019	2023	
9	Waste water treatment	762	trends	0.05	northern hemisphere	0.1	2020	2023	
10	Dynamics	707	diversity	0.05	lake ice phenology	0.66	2020	2023	

analysis in the WoS database.

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3. Definition and Driving Mechanism

3.1. Definition of Algal Blooms in Cold Lake

There were differences in the definitions of cold lakes among international scholars. They defined cold lakes based on indicators such as the average temperature of the coldest month, the duration of the freezing period, and the average annual water temperature (Table 2). In 1966, American scholars defined cold lakes based on their average freezing period exceeding 100 days per year and ice depth exceeding 0.3 meters for at least one year every 10 years [22]. In 1997, Yang defined China's cold lakes based on the fact that the coldest month had a temperature below -3 ° C, the number of months with an average monthly temperature above 10 ° C did not exceed 4 months, the freezing period of lakes exceeded 100 days, and the proportion of solid precipitation received exceeded 50% [22]. In 2000, Yang added accumulated temperature and annual average snowfall days to define cold lakes [107]. In 2013, lakes with an annual average water temperature below 15 ° C were defined as cold lakes by Lurling [22]. Cyanobacterial blooms that occured in lakes with water temperatures well below optimal growth temperatures were defined as cold water cyanobacterial blooms [23].

Table 2. Definitions of lakes in cold regions.

Name	Country	Identify	References
Bates, R. E. And Bilello	US	The maximum snow depth observed on the ground is greater than 0.3m, the average freezing period of rivers and lakes is greater than 100 days per year, and the ice depth is greater than 0.3m in at least one year every 10 years.	Bates, R. E. And Bilello et al. (1966)
Yang, Z	China	Yang proposed the criteria for the division of China's cold regions, including the coldest month temperature below -3°C, the average monthly temperature above 10°C for no more than 4 months, the freezing period of rivers and lakes for more than 100 days, and the proportion of precipitation received in the form of frozen ice exceeding 50%. Yang et al. added the accumulated temperature between 500 and 1000°C and the average number of snow days per year of 30 days to calculate China's cold regions.	Yang, Z et al. 2000
Paerland and huisman 2008;Lurling et al. 2013	US	When the annual average water temperature is below 15°C, which is far below the optimal temperature for cyanobacteria to grow, cyanobacterial blooms are observed, which are called cold water cyanobacterial blooms.	Paerland and huisman 2008;Lurling et al. 2013
Maartje 2024	US	Lake surface ice is defined as cold region lakes	Maartje et al. 2024

The United States has conducted a lot of research on phytoplankton in cold lakes at high latitudes. Cyanobacteria (Microcystis, Anabaena, Aphanizomenon, Asterix, Chromococcus, etc.) and diatoms (Icelandic Streptocystis, filamentous diatoms, Baikal Streptocystis, Navicula gracilis, Glacier Navicula, Antarctic Thalassiocystis, Nitzschia fragmenta, etc.) were the dominant algae species in typical cold lakes. The driving factors of dominant cyanobacteria included TP, TN, WT and BOD_5, among which nutrients were the main driving factors.

Table 3. Dominant phytoplankton species and driving factors in typical cold region lakes.

Lake/country	Representative dominant species	Impact factor
Alte Donau/(US)	Raphidiopsis and raciborskii	TN TP
Bethel Lake/Canada	Dolichospermum affinis	TN TP BOD_5
Brandy Lake/Canada	Aphanizomenonspp. And Dolichospermum	TN TP BOD_5 WT
Suya Lake Reservoir/China	Cyanobacteria: Microcystis and Anabaena	TN TP
Lake Baikal/Russia	Diatom Melosomum baikalense (Russia)	WT TN
Lake Erie/North America	Cyanobacteria: Anabaena and Aphanizomenon and MicrocystisDiatoms and Melosceles Icelandica and filamentous diatoms	TN TP
Balkan Lakes/Albania	Diatoms and Cyclotella menifolia and Golden algae and Yellow algae	TN TP
Lake Luboszki / Latvia	Cyanobacteria	TN TP BOD_5 WT
Antarctica	Diatoms and Navicula gracilis and Navicula glacierica and Thalassiosira and Nitzschia fragmenta	TN TP NO_3^-
Hulun Lake/China	Cyanobacteria and Chromococcus Chlorella and Fibrous algae and Chlorella and Chlamydomonas	NH_3-N TP TN
Lake Khanka/China	Cyanobacteria Microcystis and Anabaena	TN TP BOD_5 WT
Xidayang Reservoir/China	Cyanobacteria Microcystis	BOD_5 TN TP
Devil's Lake/US	Dolichospermum circinalis and Aphanizomenon flos-aquae	BOD_5
Fernan Lake/US	Microcystis spp and Dolichospermum spp and Gloeotrichia spp.	TN TP
LakeStechlin/Germany	Dolichospermum(primary)and Aphanizomenon, and Planktothrix	BOD_5 WT
Lough Neagh/Northern Ireland	Planktothrix agardhii and Pseudanabaena spp.	TN TP BOD_5 WT
Neusiedler see/Austria	Aphanocapsa incerta and Oscillatoria and Dolichospermum	TN TP WT chl-a
Three Mile Lake/Canada	Aphanizomenonspp.and Dolichospermum spp.	TP BOD_5 WT
VänernWeyhenmeyer/Sweden	Aphanizomenon sp.	TN BOD_5 WT

3.2. Hydrothermal and Hydrodynamic Conditions

Hydrodynamics and thermal stratification under lake ice were the key physical factors that trigger the spatiotemporal heterogeneity of subglacial phytoplankton [24]. The difference of hydrodynamic processes between ice- period and freeze-thaw period leads to the different migration and transformation of nutrients from other lakes, which further provided an explanation for the competitive mechanism of phytoplankton growth in cold lakes from the perspective of physical environment (Figure 3) [25,26]. Notably, snow on the ice also affected the vertical distribution of physical and chemical properties in the lake by limiting the amount of solar radiation available under the ice [25]. The physical processes of lakes during the freeze-thaw and ice-covered periods are as follows:

(1) Freeze-thaw period (Figure 3c): It mainly occured in early winter and early spring. During this period, there were significant temperature variations and lakes were in a state of both freezing and thawing. In early winter, the freezing process caused nutrients from ice to be released into the water, which triggerred osmotic convection and stratification of the water column [16]. This caused the water quality factors to slow down and formed a stable stratified state [26]. During melting, solar radiation (higher than in winter) penetrating the ice will cause hydrodynamic processes to become more intensity [27]. Radiation-driven (RDC) convection driven vertical convective circulation, which penetrates from the surface boundary layer to the stratified water column below [28]. How water quality factors were affected by increasing water temperature, increasing convection and increasing resussuspension are worthy of further discussion. The melting of ice and snow in early spring can lead to a large amount of freshwater flowing into lakes, exacerbating the resuspension of sediment at the bottom of the lake and carrying a large amount of pollutions into the lake [26]. Wind-induced waves can also cause sediment re-suspension, which induces the release of nutrients (such as nitrogen and phosphorus) from the sediment into the water body [29].

(2) Ice-covered period (Figure 3a-b): mainly occured in midwinter. The presence of snow and ice reduced the available solar radiation under the ice, and the radiation-driven convection has little affected on the hydrodynamic force under the ice (Figure 3a) [26]. Lake convective circulation continued to occur slowly when there was no snow on the ice (Figure 3b) [24].

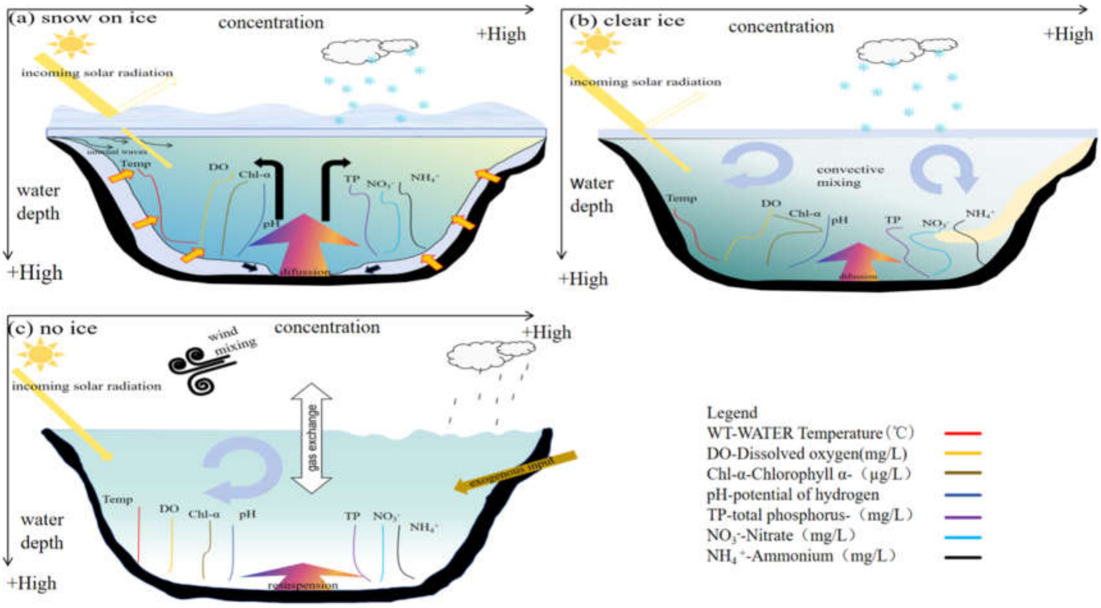

Figure 3. Schematic diagram of the changes in water heat, hydrodynamics and physical and chemical forms of cold region lakes with water depth (lake ice cover stage diagram). The thermal-hydrodynamic and physicochemical properties of lake water change with water depth when ice and snow coexist in the lake in winter; (b) The thermal-hydrodynamic and physicochemical properties of lake water change with water depth when there is only ice in the lake in winter; (c) Schematic diagram of the thermal-hydrodynamic and physicochemical properties of lake water change with water depth after the early spring ice and snow melt.

The variation of hydrodynamic circulation under ice also triggerred vertical variations in water quality indicators (Figure 3). Total phosphorus (TP), nitrate (NO_3^-), and ammonium (NH_4^+) concentrations all increased with increasing water depth. Under different conditions, light and temperature have a significant effect on the concentration and distribution of various chemical substances in the water body. The presence of ice will reduce the surface water temperature and dissolved oxygen content, while the concentration of chemical substances at the bottom was generally higher [31]. The increasing of available light underwater would increased the surface temperature, chlorophyll-a concentration, and dissolved oxygen, when the surface of the lake was free of ice and snow [32]. Understanding these impacts will help us better understand and predict the ecological processes and ecosystem functions of phytoplankton. The impact of subglacial hydrodynamics on phytoplankton was multifaceted, including nutrient transport, dissolved oxygen levels, and the special environment of the ice-covered period [33]. These processes controlled subglacial phytoplankton growth by influencing the migration and transformation of N and P between water and sediment [34]. High concentrations of nutrients and low nitrogen-phosphorus ratios can maintain the growth rate of phytoplankton during the ice-covered period, promoting phytoplankton more adaptable to the light conditions during the ice-covered period [35]. Light, temperature, and nutrients work synergistically to maintain the growth of phytoplankton under the ice.

3.3. Nutrient Migration and Transformation During Freezing

The multi-media migration and transformation of nutrients during the freezing-ice-thaw process was the key to affecting the growth competition of phytoplankton under the ice (Figure 4). The ice-covered period changed the physical and chemical processes of the lake, resulting in different nutrient migration and transformation from other seasons [36]. In early winter, the lake has a strong repulsive effect on nutrients during the ice-covered period, resulting in higher nutrient concentrations in the lake water than in the ice [34]. Nutrients continued to migrate and concentrate in the water with lake ice crystals gradually precipitate [37]. During the ice-covered period, the dynamic balance of nutrients between water and sediments was broken, and the nutrients in the water migrates to the sediment under the driving force of the concentrations gradient [38]. Sediments accept a large amount of nutrients and become endogenous pollutants [39]. However, dissolved nitrogen and phosphorus in the interstitial water of endogenous sediments tended to be released into the subglacial water during the ice-covered period, which will also lead to an nutrients increasing in the water [40]. In addition to the uncertainty of the migration direction and process of nutrients, their transformation process was also more complicated. Organic nitrogen in sediments formed ammonium through ammonification, and ammonium salts formed nitrates under nitrification and denitrification (Figure 4). Organic phosphorus in sediments formed phosphates under mineralization [41]. Phytoplankton mainly absorbed carbon dioxide and other nutrients from water through photosynthesis. These nutrients can contribute to the nitrogen fixation activity of nitrogen fixing cyanobacteria [6–9]. In addition, phytoplankton residues were also the main source of organic nitrogen and phosphorus in sediments [42]. External inputs such as factory wastewater and agricultural wastewater directly provided phosphates and nitrates to phytoplankton. In a word, the direction and amount of multi-media migration and transformation of nutrients in the freezing-thawing process are uncertain, which would increase the difficulty of studying the nutrient driving mechanism of algal blooms in cold lakes.

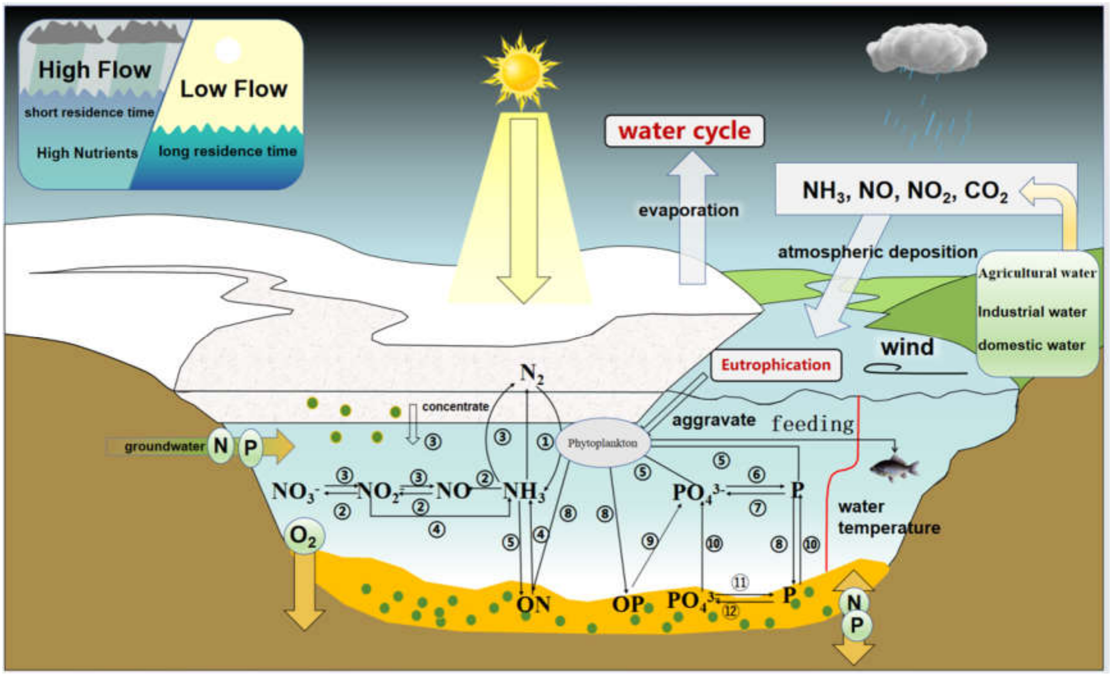

Figure 4. Schematic diagram of the mechanism of the impact of nutrient migration and transformation on phytoplankton. Note: 1-12 represent ① Nitrogen fixation, ② Nitrification, ③ Denitrification, ④ Amination, ⑤ Assimilation, ⑥ Adsorption, ⑦ Desorption, ⑧ settlement, ⑨ Mineralization, ⑩ Resuspension, ⑪ Adsorption complexation, ⑫ Dissolve.

3.4. Phytoplankton Characteristics

Phytoplankton is the basis of material circulation and energy flow in lake ecosystems, and plays a very important role in maintaining the balance of lake ecosystems and improving the ecological environment [43,44]. Variations in phytoplankton community structure directly affect water quality. Phytoplankton growth during the ice-covered period was related to the characteristics of phytoplankton cellular structure and the migration and transformation of nutrients [45]. The main reason why cyanobacteria can easily gain an advantage during the ice-covered period was that cyanobacteria have air vesicles and have a stronger ability to adapt to temperature changes [46]. Air vesicles can regulate buoyancy, allowing cyanobacteria to float on the surface of the water body, thereby obtaining more light available under the ice for photosynthesis during the ice-covered period [47]. Therefore, cyanobacteria can survive and reproduce in harsh environments such as low temperature, low oxygen and low nitrogen [35–46]. Diatoms have siliceous cell walls (silica shells) and lack air vesicles. Diatoms usually inhabit the lower and middle layers of the water column, relying on water flow and turbulence to maintain suspension [19]. Therefore, diatoms are more adapted to living in environments with abundant light and rich nutrients [61].

4. Advances in Research Methods

Common research methods for the competition mechanism of phytoplankton in cold lakes included remote sensing, field sampling, indoor simulation and numerical simulation [37]. Among them, the conventional methods were remote sensing, field sampling and indoor simulation. With the development of computer technology, data-driven numerical simulation and mechanism-driven numerical simulation were gradually applied to the prediction and prevention of cyanobacterial blooms in lakes.

4.1. Conventional Technical Means

At present, field monitoring is the basis of all monitoring. The advantage of on-site monitoring was that sample testing is the most accurate [38–102]. However, the monitoring frequency, monitoring cost and monitoring scope all limited the effective prevention and control of lake algal blooms [82]. Remote sensing technology was widely used due to its wide coverage and high real-time performance [36]. However, remote sensing technology has the limitations of discontinuous spatiotemporal monitoring and complex monitoring methods due to the existence of rain and fog [91]. In order to predict the mechanism of multiple environmental factors on phytoplankton growth competition, indoor simulation has became a conventional method [39–57]. Experimental simulation experiments can accurately control variables such as temperature, light, nutrients, etc, and have the advantages of strong repeatability and high reliability. Equipment technology and simulation scale limited the accuracy of prediction.

4.2. Numerical Simulation Model

Numerical simulation includes data-driven machine learning methods and mechanism-driven hydrodynamic-ecological integrated model methods. They have significant advantages in the study of competition mechanisms among phytoplankton in cold lakes [49]. The deeper and more comprehensive understanding of the advantages of numerical simulation for research was provided [93]. Machine learning methods can extract complex patterns and relationships from a large amount of observational data, which were suitable for processing high-dimensional and nonlinear data [49]. This method was suitable for real-time or near-real-time applications. The disadvantage of data-driven numerical simulation was that it was highly data-dependent [95]. The model relied more on statistical relationships in the data rather than physical mechanisms [47].

In order to enhance the accuracy and precision of model simulation, it is necessary to construct a numerical simulation model for mechanism characterization [94]. The mechanism model was based on physical and ecological principles, can provide a physical explanation of the system behavior. These models were applicable to lakes of different types and sizes, and has strong extrapolation capabilities [48,100]. Most numerical simulations focused on the characterization of the non-ice-covered period, and lack of the construction of all-season model [Powers et al. 2016]. There were few studies and data on ice-covered lakes, lacking systematicity and in-depthness [44–63]. Therefore, it is urgent to improve the hydrodynamic-algal bloom module based on the principles of lake ice dynamics, mass balance principle and algal competition mechanism, and construct all-season hydrodynamic-water quality-water ecology coupling model (Figure 5). Among them, the hydrodynamic module mainly corrected the hydraulic and thermal elements during the ice-covered period. During the ice-covered period, the lake surface water level used a water gauge and an automatic flow monitor to measure ice thickness (Hi), water depth under ice (d), water level (L), flow velocity (v), and the water level are corrected using the density difference between ice and water and the ice body pressure. Net solar radiation (I), atmospheric radiation (a), convective heat flux (QS), evaporative heat flux (QE), reflectivity (β), and initial temperature (T) are also obtained based on empirical formulas or measurement methods. On the basis of the traditional lake hydrodynamics-water quality-water ecology coupling model, the algal bloom module (BLOOM) is nested to reflect the growth and competition process of algae at the level of phenotypic characteristics. Hydrodynamic, water quality and algal bloom modules are modified as Equation (1)–(6).

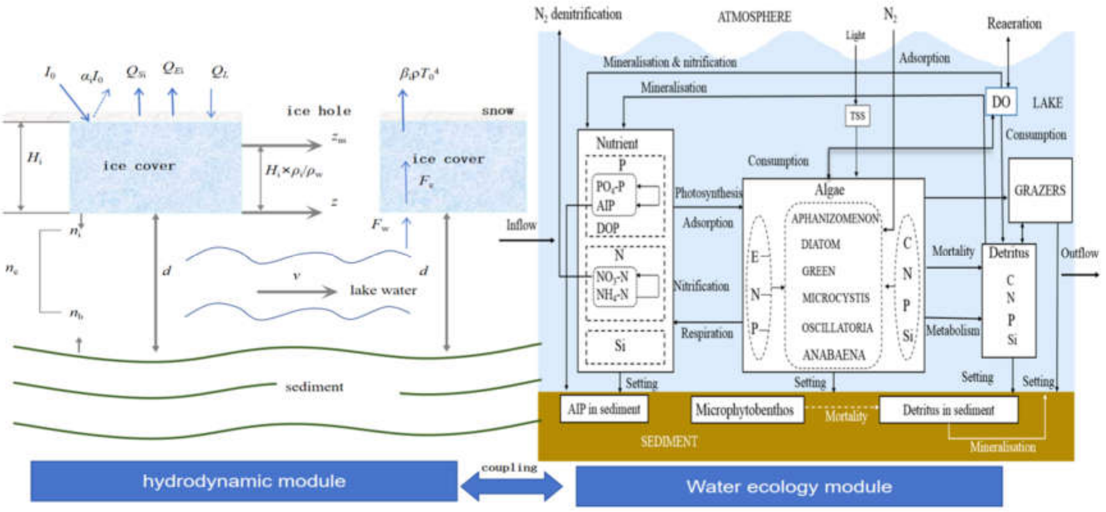

Figure 5. Schematic diagram of the improved cold region lake hydrodynamic-water ecology model.

The roughness coefficient during the ice-covered period is n_c, and the expression is:

$$n_c = \left[\frac{n_b^{3/2} + n_i^{3/2}}{2} \right]^{2/3} \tag{1}$$

n_b is the lake basin roughness; ni is the ice cover roughness value.

The expression of the actual water level is:

$$z = z_m - H_i \times \rho_i / \rho_w \tag{2}$$

z is the actual water level, z_m is the monitored water level, H_i is the ice thickness, ρ_i and ρ_w are the densities of ice and water respectively.

The total heat flux expression of the ice surface is:

$$Q_{\mathrm{tot}} = I_0 + Q_{ai} - Q_{ei} - Q_{si} \tag{3}$$

where I_0 is the net solar radiation (short wave), Q_{ai} is the net atmospheric radiation (long wave), Q_{br} is the reflection (long wave), Q_{ii} is the evaporation heat flux (latent heat flux), and Q_{si} is the convective heat flux (sensible heat flux).

Based on the traditional lake hydrodynamic-water quality-water ecology model, the algal bloom module (BLOOM) is nested to reflect the growth and competition process of algae at the level of algal representation.

Mass balance equation:

$$\frac{\partial C}{\partial t} + \frac{\partial (uC)}{\partial x} + \frac{\partial (vC)}{\partial y} + \frac{\partial (wC)}{\partial z} = \frac{\partial}{\partial x}\left(K_x \frac{\partial C}{\partial x} \right) + \frac{\partial}{\partial y}\left(K_y \frac{\partial C}{\partial y} \right) + \frac{\partial}{\partial z}\left(K_z \frac{\partial C}{\partial z} \right) + Sc \tag{4}$$

C is the concentration of water quality parameters; t is the simulation time; u, v, w represent the flow velocity in the x, y, and z directions respectively; K_x, K_y, K_z represent the turbulent diffusion coefficients in the x, y, and z directions respectively; S_c represents the biochemical transformation of nutrients.

Algae growth and characterization equations:

Nitrogen limitation
$$\sum_{i=1}^{n}(S_{\mathrm{N},i}\times Phy_{i,new})\leq\sum_{i=1}^{n}(S_{\mathrm{N},i}\times Phy_{i})+\mathrm{NO_3}+\mathrm{NH_4} \tag{5}$$

Phosphorus limitation
$$\sum_{i=1}^{n}(S_{\mathrm{P},i}\times Phy_{i,new})\leq\sum_{i=1}^{n}(S_{\mathrm{P},i}\times Phy_{i})+\mathrm{PO_4} \tag{6}$$

Phy_i is the phytoplankton type, k_d is the total extinction coefficient, $S_{N,i}$ is the stoichiometry of nitrogen in type *i* phytoplankton, and $S_{P,i}$ is the stoichiometry of phosphorus in type *i* phytoplankton.

5. Response to Climate Change

Global warming has led to rising temperatures, shortening the ice-covered time of cold lakes and advancing the melting time [43]. Phytoplankton is sensitive to environmental changes. Physical and biogeochemical changed during the ice-covered period (such as subglacial solar radiation, temperature, subglacial hydrodynamics, nutrient migration and transformation, nutrient migration and concentration, and dominant phytoplankton species) will affect the structure and function of phytoplankton communities [31–63]. This variations not only affected the seasonal dynamics of lakes, but also had a profound impact on lake ecosystems. The shortening of ice-covered time and the advancement of melting time provide a longer growing season for algae, resulting in the expansion of the range of algal blooms to high-latitude ice-covered lakes [58]. High-latitude regions may not have had algal blooms before, but these areas are also suitable for algal growth with climate warming. Rising water temperatures speed up the circulation of nutrients in the lake, which increases the intensity and frequency of algal blooms [29]. Algal blooms frequently occur in early spring, causing serious impacts on lake water quality, leading to eutrophication of water bodies and destroying the ecological balance of lakes [45–84].

Subglacial physical effected influence subglacial phytoplankton competition by influencing biogeochemistry. The most important physical effects were the dynamic changes of underwater light, lake ice sheet thickness and lake temperature [25,64]. The intensification of fluid dynamics, nutrient migration and transformation under the ice led to the early end of the freezing period due to the rising temperature [102]. The reduction of lake ice cover and the shortening of ice age may lead to increased light intensity and longer photoperiods in subglacial waters [18–22]. This was conducive to the photosynthesis of subglacial phytoplankton, which may lead to an increase in its abundance and productivity.

The melting of lake ice may change the distribution and supply of oxygen, affecting the respiratory process of plankton [97]. The increasing of temperature in subglacial water environment may affect the growth, reproduction and metabolic processes of plankton, thereby affecting its ecological function and survival ability [58]. The reduction of ice cover and the increase in water temperature led to more intense and earlier algal blooms [73–93]. The ice-covered period changed the chemical processes of the lake, resulting in nutrient migration and transformation that were different from other seasons. The nutrient concentrations affected in the water during the ice-covered period may be more significant under global warming. Nutrient may migrate faster from the subglacial water body to the interstitial water, changing the dynamic balance of salt between the water body and the sediment with decreasing ice layer [93]. Variation in nutrient concentrations affected the diffusion and transformation of nutrients. The increasing endogenous nitrogen and phosphorus would lead to lake eutrophication, providing abundant nutrients and promoting the rapid growth and reproduction of phytoplankton [41].

6. Conclusion and Outlook

Understanding the mechanism of algal blooms in cold lakes is an important part of enriching and developing winter limnology, and is also the basis of environmental management and water ecological protection of cold lakes. Based on a literature review of nearly 60 years, this study has summarized the current hot spots and future development directions of phytoplankton growth in cold lakes. Elucidated the mechanisms by which lake ice induced hydrodynamics, nutrient migration and transformation, and the inherent characteristics of phytoplankton compete for growth in cold lakes. The main factors for the frequent occurrence of algal blooms in early spring after ice-melting are analyzed. The existence of ice-melting-ice-covering further made the response of phytoplankton in cold lakes more sensitive to climate change. Variations in lake ice phenology (shortened ice-covered time, early ice-melting time, and increased water temperature) have led to the expansion of the scale, increase in frequency, and prolonged duration of algal blooms in cold lakes. Existing technical such as field monitoring, remote sensing inversion, and indoor simulation can no longer meet the real-time monitoring of algal blooms in cold lakes and effective predictions for future climate change. It is urgent to build a hydrodynamics-water quality-water ecology comprehensive model for cold lakes in all-seasons to provide technological for the effective prevention and control of algal blooms in cold lakes. Based on the existing conclusions, the following prospects are proposed for the study of algal blooms in cold lakes:

(1) Provide a definition of the validity of cold lakes with physical and ecological significance;
(2) Accurately characterize the subglacial hydrodynamics and biogeochemical processes under the action of ice sheet formation and decline, so as to reveal the internal mechanism of algal blooms in cold lakes;
(3) Build a comprehensive simulation technology of hydrodynamics, water quality and water ecology for cold lakes in all seasons, so as to provide technical means for the precise prevention and control of algal blooms in cold lakes;
(4) Strengthen the in-depth understanding of the response of algal blooms in cold lakes to climate change, so as to propose adaptive prevention and control strategies to cope with future climate change.

Data Availability Statement: Some or all data, models, or code generated or used during the study are available from the corresponding author by request.

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References

1. Huisman J, Codd G A, Paerl H W, et al. Cyanobacterial blooms[J]. NatureReviews Microbiology, 2018, 16(8): 471-483
2. Merel S, Walker D, Chicana R, et al. State of knowledge and concerns on cyanobacterial blooms and cyanotoxins[J]. Environment international, 2013, 59: 303-327.
3. Sellner K G. Physiology, ecology, and toxic properties of marine cyanobacteria blooms[J]. Limnology and oceanography, 1997, 42(5part2): 1089-1104.
4. Falconer I R. Toxic cyanobacterial bloom problems in Australian waters: risks and impacts on human health[J]. Phycologia, 2001, 40(3): 228-233.
5. O’Neil J M, Davis T W, Burford M A, et al. The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change[J]. Harmful algae, 2012, 14: 313-334.
6. Vincent W F, Hobbie J E, Laybourn-Parry J. Introduction to the limnology of high-latitude lake and river ecosystems[J]. Polar lakes and rivers: limnology of Arctic and Antarctic aquatic ecosystems, 2008: 1-24.
7. Przytulska A, Bartosiewicz M, Vincent WF. Increased risk of cyanobacterialblooms in northern high-latitude lakes through climate warming and phosphorusenrichment[J]. Freshwater Biology, 2017, 62(12): 1986-1996.
8. Vincent W F. Cold tolerance in cyanobacteria and life in the cryosphere[M]//Algae and cyanobacteria in extreme environments. Dordrecht: Springer Netherlands, 2007: 287-301.
9. Pandey K D, Shukla S P, Shukla P N, et al. Cyanobacteria in Antarctica: ecology, physiology and cold adaptation[J]. CELLULAR AND MOLECULAR BIOLOGY-PARIS-WEGMANN-, 2004, 50(5): 575-584.
10. Salmaso N, Capelli C, Shams S, et al. Expansion of bloom-forming Dolichospermum lemmermannii (Nostocales, Cyanobacteria) to the deep lakes south of the Alps: colonization patterns, driving forces and implications for water use[J]. Harmful Algae, 2015, 50: 76-87.
11. Babanazarova O, Sidelev S, Schischeleva S. The structure of winter phytoplankton in Lake Nero, Russia, a hypertrophic lake dominated by Planktothrix-like Cyanobacteria[J]. Aquatic Biosystems, 2013, 9: 1-11.

12. Reinl K L, Harris T D, North R L, et al. Blooms also like it cold[J]. Limnology and Oceanography Letters, 2023, 8(4): 546-564.
13. Özkundakci D, Gsell A S, Hintze T, et al. Winter severity determines functional trait composition of phytoplankton in seasonally ice-covered lakes[J].Global change biology, 2016, 22(1): 284-298.
14. Hampton S E, Moore M V, Ozersky T, et al. Heating up a cold subject: prospects for under-ice plankton research in lakes[J]. Journal of plankton research, 2015, 37(2): 277-284.
15. Wright R T. The Ecology of Phytoplankton in an Ice-covered Lake[D]. Harvard University, 1963.
16. Jansen J, MacIntyre S, Barrett D C, et al. Winter limnology: How do hydrodynamics and biogeochemistry shape ecosystems under ice?[J]. Journal of Geophysical Research: Biogeosciences, 2021, 126(6): e2020JG006237.
17. Powers S M, Hampton S E. Winter limnology as a new frontier[J]. Limnology and Oceanography Bulletin, 2016, 25(4): 103-108.
18. Favot E J, Rühland K M, DeSellas A M, et al. Climate variability promotes unprecedented cyanobacterial blooms in a remote, oligotrophic Ontario lake: evidence from paleolimnology[J]. Journal of Paleolimnology, 2019, 62(1): 31-52.
19. Favot E J, Rühland K M, DeSellas A M, et al. Climate variability promotes unprecedented cyanobacterial blooms in a remote, oligotrophic Ontario lake: evidence from paleolimnology[J]. Journal of Paleolimnology, 2019, 62(1): 31-52.
20. Klanten Y, MacIntyre S, Fitzpatrick C, et al. Regime shifts in lake oxygen and temperature in the rapidly warming high Arctic[J]. Geophysical Research Letters, 2024, 51(6): e2023GL106985.
21. Salonen K, Leppäranta M, Viljanen M, et al. Perspectives in winter limnology: closing the annual cycle of freezing lakes[J]. Aquatic Ecology, 2009,43: 609-616.
22. Chen C. CiteSpace II: Detecting and visualizing emerging trends and transient patterns in scientific literature[J]. Journal of the American Society for information Science and Technology, 2006, 57(3): 359-377.
23. Huang Y, Zhang L, Li Y, et al. Characteristics of the Northern Hemisphere cold regions changes from 1901 to 2019[J]. Scientific Reports, 2023, 13(1): 3879.
24. Leppäranta M. Freezing of lakes[M]//Freezing of Lakes and the Evolution of their Ice Cover. Cham: Springer International Publishing, 2023: 17-62.
25. Bouffard D, Zdorovennova G, Bogdanov S, et al. Under-ice convection dynamics in a boreal lake[J]. Inland Waters, 2019, 9(2): 142-161.
26. Zhao W, Huang W, Li R, et al. Solar radiation transfer in an ice-covered lake at different snow thicknesses[J]. Hydrological Sciences Journal,2024: 1-12.
27. Yang B, Wells M G, McMeans B C, et al. A new thermal categorization of ice-covered lakes[J]. Geophysical Research Letters, 2021, 48(3): e2020GL091374.
28. Jonas T, Terzhevik A Y, Mironov D V, et al. Radiatively driven convection in an ice-covered lake investigated by using temperature microstructure technique[J]. Journal of Geophysical Research: Oceans, 2003, 108(C6).
29. Talling J F. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation[J]. The New Phytologist, 1957, 56(1): 29-50.
30. Rosa F. Sedimentation and sediment resuspension in Lake Ontario[J].
31. Journal of Great Lakes Research, 1985, 11(1): 13-25.
32. Bengtsson L, Malm J, Terzhevik A, et al. Field investigation of winter thermo-and hydrodynamics in a small Karelian lake[J]. Limnology and oceanography, 1996, 41(7): 1502-1513.
33. Leu E, Søreide J E, Hessen D O, et al. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelfseas: Timing, quantity, and quality[J]. Progress in Oceanography, 2011, 90(1-4): 18-32.
34. Yang T, Hei P, Song J, et al. Nitrogen variations during the ice-on season in the eutrophic lakes[J]. Environmental Pollution, 2019, 247: 1089-1099.
35. Steinberg D K, Goldthwait S A, Hansell D A. Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea[J]. Deep Sea Research Part I: Oceanographic Research Papers, 2002, 49(8): 1445-1461.
36. Zhao W, Huang W, Li R, et al. Solar radiation transfer in an ice-covered lake at different snow thicknesses[J]. Hydrological Sciences Journal,2024: 1-12.
37. Yang B. Physical Processes in Ice-covered Lakes[D]. University of Toronto (Canada), 2022.
38. Whitfield C J, Casson N J, North R L, et al. The effect of freeze-thaw cycles on phosphorus release from riparian macrophytes in cold regions[J]. Canadian Water Resources Journal/Revue Canadienne des Ressources Hydriques,2019, 44(2): 160-173.
39. Fang Y, Changyou L, Leppäranta M, et al. Notable increases in nutrient concentrations in a shallow lake during seasonal ice growth[J]. Water Science and Technology, 2016, 74(12): 2773-2783.
40. Cao X, Wang Y, He J, et al. Phosphorus mobility among sediments, water and cyanobacteria enhanced by cyanobacteria blooms in eutrophic Lake Dianchi[J]. Environmental Pollution, 2016, 219: 580-587.

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41. Vallina S M, Cermeno P, Dutkiewicz S, et al. Phytoplankton functional diversity increases ecosystem productivity and stability[J]. Ecological Modelling, 2017, 361: 184-196.
42. Borics G, Abonyi A, Salmaso N, et al. Freshwater phytoplankton diversity: models, drivers and implications for ecosystem properties[J]. Hydrobiologia, 2021, 848: 53-75.
43. Tanabe Y, Kudoh S, Imura S, et al. Phytoplankton blooms under dim and cold conditions in freshwater lakes of East Antarctica[J]. Polar Biology, 2008, 31: 199-208.
44. Jungblut A D, Lovejoy C, Vincent W F. Global distribution of cyanobacterial ecotypes in the cold biosphere[J]. The ISME Journal, 2010, 4(2): 191-202.
45. Priscu J C, Adams E E, Paerl H W, et al. Perennial Antarctic lake ice: a refuge for cyanobacteria in an extreme environment[J]. Life in ancient ice, 2005: 22-49.
46. Neumann A, Kim D K, Perhar G, et al. Integrative analysis of the Lake Simcoe watershed (Ontario, Canada) as a socio-ecological system[J]. Journal of environmental management, 2017, 188: 308-321.
47. Wilkins D, Yau S, Williams T J, et al. Key microbial drivers in Antarctic aquatic environments[J]. FEMS Microbiology Reviews, 2013, 37(3): 303-335.
48. Sridhar R, Thangaradjou T, Kumar S S, et al. Water quality and phytoplankton characteristics in the Palk Bay, southeast coast of India[J]. Journal of environmental biology, 2006, 27(3): 561-566.
49. Montes-Hugo M, Doney S C, Ducklow H W, et al. Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula[J]. Science, 2009, 323(5920): 1470-1473.
50. Prowse T, Alfredsen K, Beltaos S, et al. Effects of changes in arctic lake and river ice[J]. Ambio, 2011, 40: 63-74.
51. Laybourn-Parry J, Pearce D A. The biodiversity and ecology of Antarctic lakes: models for evolution[J]. Philosophical Transactions of the Royal Society B: Biological Sciences, 2007, 362(1488): 2273-2289.
52. Zepernick B N, Chase E E, Denison E R, et al. Declines in ice cover are accompanied by light limitation responses and community change in freshwater diatoms[J]. The ISME Journal, 2024: wrad015.
53. Twiss M R, McKay R M L, Bourbonniere R A, et al. Diatoms abound in ice-covered Lake Erie: An investigation of offshore winter limnology in Lake Erie over the period 2007 to 2010[J]. Journal of Great Lakes Research, 2012, 38(1): 18-30.
54. Anderson S P, Fernald K M H, Anderson R S, et al. Physical and chemical characterization of a spring flood event, Bench Glacier, Alaska, USA:evidence for water storage[J]. Journal of Glaciology, 1999, 45(150): 177-189.
55. Weyhenmeyer G A, Obertegger U, Rudebeck H, et al. Towards critical white ice conditions in lakes under global warming[J]. Nature communications, 2022, 13(1): 4974.
56. Wüest A, Pasche N, Ibelings B W, et al. Life under ice in Lake Onego(Russia)–an interdisciplinary winter limnology study[J]. Inland Waters, 2019, 9(2): 125-129.
57. Hébert M P, Beisner B E, Rautio M, et al. Warming winters in lakes: Later ice onset promotes consumer overwintering and shapes springtime planktonic food webs[J]. Proceedings of the National Academy of Sciences, 2021, 118(48): e2114840118.
58. Kirillin G, Leppäranta M, Terzhevik A, et al. Physics of seasonally ice-covered lakes: a review[J]. Aquatic sciences, 2012, 74: 659-682.
59. Peeters F, Straile D, Lorke A, et al. Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate[J]. Global Change Biology, 2007, 13(9): 1898-1909.
60. Huber V, Adrian R, Gerten D. Phytoplankton response to climate warming modified by trophic state[J]. Limnology and Oceanography, 2008, 53(1): 1-13.
61. O'Reilly C M, Sharma S, Gray D K, et al. Rapid and highly variable warming of lake surface waters around the globe[J]. Geophysical Research Letters, 2015, 42(24): 10,773-10,781.
62. Keller W. Implications of climate warming for Boreal Shield lakes: a review and synthesis[J]. Environmental Reviews, 2007, 15(NA): 99-112.
63. Kumar N, Grogan P, Chu H, et al. The effect of freeze-thaw conditionson arctic soil bacterial communities[J]. Biology, 2013, 2(1): 356-377.
64. Jawak S D, Kulkarni K, Luis A J. A review on extraction of lakes from remotely sensed optical satellite data with a special focus on cryospheric lakes[J]. Advances in Remote Sensing, 2015, 4(3): 196-213.
65. Siegert M J, Makinson K, Blake D, et al. An assessment of deep hot-water drilling as a means to undertake direct measurement and sampling ofAntarctic subglacial lakes: Experience and lessons learned from the Lake Ellsworth field season 2012/13[J]. Annals of Glaciology, 2014, 55(65): 59-73.
66. Patterson J C, Hamblin P F. Thermal simulation of a lake with winter ice cover 1[J]. Limnology and Oceanography, 1988, 33(3): 323-338.
67. Toporowska M, Pawlik-Skowronska B, Krupa D, et al. Winter versus summer blooming of phytoplankton in a shallow lake: effect of hypertrophic conditions[J]. Polish Journal of Ecology, 2010, 58(1): 3-12.
68. Richardson D C, Filazzola A, Woolway R I, et al. Nonlinear responses in interannual variability of lake ice to climate change[J]. Limnology and Oceanography, 2024, 69(4): 789-801.

69. Ozersky T, Bramburger A J, Elgin A K, et al. The changing face of winter: lessons and questions from the Laurentian Great Lakes[J]. 2021.
70. Yang F, Cen R, Feng W, et al. Dynamic simulation of nutrient distribution in lakes during ice cover growth and ablation[J]. Chemosphere, 2021, 281: 130781.
71. Walsby A E, Hayes P K, Boje R. The gas vesicles, buoyancy and vertical distribution of cyanobacteria in the Baltic Sea[J]. European Journal of Phycology, 1995, 30(2): 87-94.
72. Pozdnoukhov A, Foresti L, Kanevski M. Data-driven topo-climatic mapping with machine learning methods[J]. Natural hazards, 2009, 50: 497-518.
73. Giusti E, Marsili-Libelli S. Spatio-temporal dissolved oxygen dynamics in the Orbetello lagoon by fuzzy pattern recognition[J]. Ecological Modelling, 2009, 220(19): 2415-2426.
74. Ralston D K, Moore S K. Modeling harmful algal blooms in a changing climate[J]. Harmful Algae, 2020, 91: 101729.
75. Havens K E. Cyanobacteria blooms: effects on aquatic ecosystems[J]. Cyanobacterial harmful algal blooms: state of the science and research needs, 2008: 733-747.
76. Wilhelm S W, Farnsley S E, LeCleir G R, et al. The relationships between nutrients, cyanobacterial toxins and the microbial community in Taihu (Lake Tai), China[J]. Harmful Algae, 2011, 10(2): 207-215.
77. Wüest A, Lorke A. Small-scale hydrodynamics in lakes[J]. Annual Review of fluid mechanics, 2003, 35(1): 373-412.
78. Bouffard D, Wüest A. Convection in lakes[J]. Annual Review of Fluid Mechanics, 2019, 51(1): 189-215.
79. Bengtsson L, Malm J, Terzhevik A, et al. Field investigation of winter thermo-and hydrodynamics in a small Karelian lake[J]. Limnology and oceanography, 1996, 41(7): 1502-1513.
80. Hodges B R, Imberger J, Laval B, et al. Modeling the hydrodynamics of stratified lakes[C]//Hydroinformatics 2000 conference. Iowa Institute of Hydraulics Research, 2000, 4: 23-27.
81. Freeman E C, Creed I F, Jones B, et al. Global changes may be promoting a rise in select cyanobacteria in nutrient-poor northern lakes[J]. Global Change Biology, 2020, 26(9): 4966-4987.
82. Priscu J C, Adams E E, Paerl H W, et al. Perennial Antarctic lake ice: a refuge for cyanobacteria in an extreme environment[J]. Life in ancient ice, 2005: 22-49.
83. Rühland K, Paterson A M, Smol J P. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes[J]. Global Change Biology, 2008, 14(11): 2740-2754.
84. Anderson N J. Diatoms, temperature and climatic change[J]. European Journal of Phycology, 2000, 35(4): 307-314.
85. Elser J J, Wu C, González A L, et al. Key rules of life and the fading cryosphere: Impacts in alpine lakes and streams[J]. Global change biology, 2020, 26(12): 6644-6656.
86. MacCallum S N, Merchant C J. Surface water temperature observations of large lakes by optimal estimation[J]. Canadian Journal of Remote Sensing, 2012, 38(1): 25-45.
87. Pernica P, North R L, Baulch H M. In the cold light of day: The potential importance of under-ice convective mixed layers to primary producers[J]. Inland Waters, 2017, 7(2): 138-150.
88. Leppäranta M. Freezing of lakes and the evolution of their ice cover[M]. Berlin/Heidelberg, Germany: Springer, 2015.
89. Smetacek V. Diatoms and the ocean carbon cycle[J]. Protist, 1999, 150(1): 25-32.
90. Bopp L, Aumont O, Cadule P, et al. Response of diatoms distribution to global warming and potential implications: A global model study[J]. Geophysical Research Letters, 2005, 32(19).
91. Weyhenmeyer G A. Warmer winters: are planktonic algal populations in Sweden's largest lakes affected?[J]. AMBIO: A Journal of the Human Environment, 2001, 30(8): 565-571.
92. Katz S L, Izmest'eva L R, Hampton S E, et al. The "M elosira years" of Lake B aikal: Winter environmental conditions at ice onset predict under-ice algal blooms in spring[J]. Limnology and Oceanography, 2015, 60(6): 1950-1964.
93. Coffer M M, Schaeffer B A, Darling J A, et al. Quantifying national and regional cyanobacterial occurrence in US lakes using satellite remote sensing[J]. Ecological Indicators, 2020, 111: 105976.
94. Jungblut A D, Vincent W F. Cyanobacteria in polar and alpine ecosystems[J]. Psychrophiles: from biodiversity to biotechnology, 2017: 181-206.
95. Eckerstorfer M, Bühler Y, Frauenfelder R, et al. Remote sensing of snow avalanches: Recent advances, potential, and limitations[J]. Cold Regions Science and Technology, 2016, 121: 126-140.
96. Martynov A, Sushama L, Laprise R. Simulation of temperate freezing lakes by one-dimensional lake models: performance assessment for interactive coupling with regional climate models[J]. Boreal environment research, 2010, 15(2): 143.
97. Surdu C M, Duguay C R, Brown L C, et al. Response of ice cover on shallow lakes of the North Slope of Alaska to contemporary climate conditions (1950–2011): radar remote-sensing and numerical modeling data analysis[J]. The Cryosphere, 2014, 8(1): 167-180.
98. Jia X, Willard J, Karpatne A, et al. Physics-guided machine learning for scientific discovery: An application in simulating lake temperature profiles[J]. ACM/IMS Transactions on Data Science, 2021, 2(3): 1-26.

99. Guerrero J L, Pernica P, Wheater H, et al. Parameter sensitivity analysis of a 1-D cold region lake model for land-surface schemes[J]. Hydrology and Earth System Sciences, 2017, 21(12): 6345-6362.
100. Hampton S E, Moore M V, Ozersky T, et al. Heating up a cold subject: prospects for under-ice plankton research in lakes[J]. Journal of plankton research, 2015, 37(2): 277-284.
101. Woolway R I, Merchant C J. Amplified surface temperature response of cold, deep lakes to inter-annual air temperature variability[J]. Scientific Reports, 2017, 7(1): 4130.
102. Ozersky T, Bramburger A J, Elgin A K, et al. The changing face of winter: lessons and questions from the Laurentian Great Lakes[J]. 2021.
103. Malmaeus J M, Blenckner T, Markensten H, et al. Lake phosphorus dynamics and climate warming: A mechanistic model approach[J]. Ecological Modelling, 2006, 190(1-2): 1-14.
104. Yang B, Wells M G, Li J, et al. Mixing, stratification, and plankton under lake-ice during winter in a large lake: Implications for spring dissolved oxygen levels[J]. Limnology and Oceanography, 2020, 65(11): 2713-2729.
105. Arp C D, Jones B M, Whitman M, et al. Lake Temperature and Ice Cover Regimes in the Alaskan Subarctic and Arctic: Integrated Monitoring, Remote Sensing, and Modeling 1[J]. JAWRA Journal of the American Water Resources Association, 2010, 46(4): 777-791.
106. Ho J C, Michalak A M, Pahlevan N. Widespread global increase in intense lake phytoplankton blooms since the 1980s[J]. Nature, 2019, 574(7780): 667-670.