Review



Mutual feedback between algal blooming and global warming*

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Global warming and algal blooms have been two of the most pressing problems faced by the Abstract world today. In recent decades, numerous studies indicated that global warming promoted the expansion of algal blooms. However, research on how algal blooms respond to global warming is scant. Global warming coupled with eutrophication promoted the rapid growth of phytoplankton, which resulted in an expansion of algal blooms. Algal blooms are affected by the combined effects of global warming, including increases in temperatures, CO₂ concentration, and nutrient input to aquatic systems by extreme weather events. Since the growth of phytoplankton requires CO₂, they appear to act as a carbon sink. Unfortunately, algal blooms will release CH_4 , CO_2 , and inorganic nitrogen when they die and decompose. As substrate nitrogen increases from decompose algal biomass, more N2O will be released by nitrification and denitrification. In comparison to CO₂, CH₄ has 28-fold and N₂O has 265-fold greenhouse effect. Moreover, algal blooms in the polar regions may contribute to melting glaciers and sea ice (will release greenhouse gas, which contribute to global warming) by reducing surface albedo, which consequently would accelerate global warming. Thus, algal blooms and global warming could form feedback loops which prevent human survival and development. Future researches shall examine the mechanism, trend, strength, and control strategies involved in this mutual feedback. Additionally, it will promote global projects of environmental protection combining governance greenhouse gas emissions and algal blooms, to form a geoengineering for regulating the cycles of carbon, nitrogen, and phosphorus.

Keyword: climate change; carbon neutrality; eutrophication; greenhouse gas; glaciers melting; geoengineering

1 INTRODUCTION

Algal bloom (or phytoplankton bloom) may be positively identified in eutrophic waters by the presence of a layer of blue-green scum or a stench froth in water surface. The majority of reports came from eutrophic inland waters and gave mean values for chlorophyll-*a* blooms ranging from 41 to 69 μ g/L, or 80 000 to 249 000 cells/mL, according to the analysis in several methodological approaches (field, field-experimental, and satellite data) and kinds of environments (coastal, marine, and continental ecosystems) (Frau, 2023). As a result of global climate change and eutrophication, algal blooms are spreading across the globe (Paerl and Huisman,

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2008; Huisman et al., 2018; Gray et al., 2020; Oziel et al., 2020; Hou et al., 2022). There have been algal blooms worldwide in aquatic severe ecosystems such as lakes, reservoirs, ponds, rivers, inland seas, and oceans (Smayda, 1997; Paerl and Huisman, 2008; Huisman et al., 2018). Algal blooms occurred even in the cold Antarctic and Arctic (Gray et al., 2020; Oziel et al., 2020) and on ice sheets (McCutcheon et al., 2021), as well as on snow in the polar regions (Segawa et al., 2018). Algal blooms cause hypoxia and disrupt food webs (Anderson, 1997; Conley, 2012), and produce toxins and undesirable taste and odor compounds (Cox et al., 2003; Rantala et al., 2003). As a result, algal blooms produce a hazard to drinking water supplies and have a negative impact on recreational and fishing activities in the affected areas. It poses a public health risk and has unfavorable ecological, economic, and water resource implications, as well as societal consequences (Brookes and Carey, 2011; Ho et al., 2019). Freshwater blooms have cost more than \$11.1 billion in annual losses in the United States and China alone, affecting drinking water supplies, aquatic production, recreation, and tourism (Bernard et al., 2014).

Algal blooms development is a highly complex process that depends on a number of variables, including meteorological parameters, hydrological parameters, water quality, algal growth, and migration. In addition to the recognized driver of eutrophication, climate warming is considered as one of the important reasons. Global warming is promoted by greenhouse gases, including CO₂, CH₄, N₂O, etc. (Kiehl and Trenberth, 1997). The more greenhouse gases are emitted, the more significant of temperature increase (Lashof and Ahuja, 1990; Tian et al., 2016). Global warming may lead to changes in precipitation patterns, increasing in extreme storms and soil warming, which may change the nutrients input and retention time in lakes and other aquatic systems (Rustad et al., 2001; Jack et al, 2011; Jeppesen et al., 2011). The increasing of global average temperature and CO_2 concentration ($CO_2(aq)$) may exacerbate algal blooms (Moss, 2011; Huisman et al., 2018). Hence, the impact of global warming on algal blooms has become a hot research topic in the past decades.

Given their apparent synergy, Moss et al. (2011) suggested that eutrophication and climate change (especially global warming) required coordinated

solutions. Li et al. (2021) examined the direct and indirect components that influenced greenhouse gas (GHG) emissions from eutrophic waters, such as dissolved oxygen, organic carbon, and nutrients, as well as dominant primary producers and algal blooms. They indicated that the existence and significance of feedback loops between freshwater eutrophication and GHG emissions were particularly underlined in light of the difficulties in regulating freshwater ecosystems and the Earth's climate (Li et al., 2021). Meerhoff et al. (2022) summarized advances on this issue and analyzed how eutrophication was being enhanced by climate change while also experiencing adverse feedback, especially in shallow lakes. However, the effects of algal blooms on global warming only received a little attention.

A carbon sink will be created as the growth of phytoplankton absorbs CO_2 . However, when phytoplankton dies or decomposes under anaerobic or hypoxic conditions, it releases CO_2 , CH_4 and inorganic nitrogen. In addition, the release of N_2O is enhanced by the increase in nitrogen content and the circulation rate (nitrification and denitrification) in aquatic systems. The details of above chemical processes/pathways are in complementary materials (Supplementary Figs.S1–S2).

Because the greenhouse effects of CH_4 and N_2O are 28 times and 265 times that of CO_2 , respectively (IPCC, 2014), the algal blooms will increase global warming potential. In addition, studies indicated that algal blooms in the poles and snow algae in glaciers may also contribute to the melting of snow and ice by reducing surface albedo (Arrigo et al., 2012; Boetius et al., 2013; Ganey et al., 2017). Based on this, we hypothesize that global warming and algal blooms would promote each other and strongly threaten the survival and development of human beings.

In order to promote researches in this field, we reviewed the progress in the interaction between algal blooms and global warming. Compared with the existing studies (Moss et al., 2011; Li et al., 2021; Meerhoff et al., 2022), this review focuses on the mutual feedback between algal blooms and global warming. We emphasize on the potential of global warming promoted by greenhouse gas during the whole life cycle of algal blooms as well as algal blooms might cause glaciers and sea ice to melt (will release greenhouse gas contribute to global warming) by decreased surface albedo.

2 IMPACT OF GLOBAL WARMING ON ALGAL BLOOMING

There are many ways of direct or indirect impacts of climate warming on algal bloom expansion (Fig.1; Table 1), which will be explained one by one below.

2.1 The effect of increasing temperature on algal blooming

Phytoplankton is the primary producer on the

earth (Behrenfeld et al., 2001, 2010; Behrenfeld, 2014) and temperature is one of the key factors restricting the growth of phytoplankton (Paerl and Huisman, 2008). According to the record of the occurrence and duration of algal blooms along the China's coast (from 1970 to 2015), Xiao et al. (2019b) found that frequency of algal blooms has increased at a rate of 40 ± 4 days per decade, but it was 5.50 ± 1.78 days per decade during earlier timing.

Global warming changed the community structure of phytoplankton. In Taihu Lake, the dominant

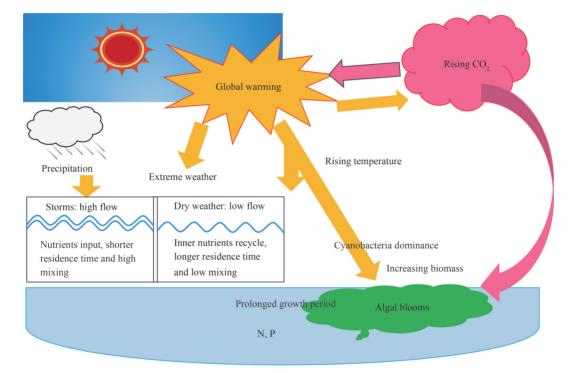


Fig.1 Interactions among environmental factors and complexity of the global warming impact on algal blooms

Table 1 Representative studies of the impact of global warming on algal blooming		
Sub-type	Торіс	Referen

Туре	Sub-type	Topic	Reference
	Alter the community structure of phytoplankton	Cyanobacteria will become dominant populations	Liu et al., 2011; Carey et al., 2012
Increasing temperature	Increase the biomass of phytoplankton	The biomass of phytoplankton will increase as temperature rises	Paerl and Huisman, 2008; Davidson et al., 2015
	Cause advanced phenology and prolonged growth period	The time of the beginning and/or the end of phytoplankton blooms are advanced and delayed	Weyhenmeyer, 2001; Ma et al., 2016; Zhang et al., 2018b
Rising CO ₂ concentration	Increase the biomass of phytoplankton	The growth and reproduction of phytoplankton biomass will be greatly affected	Verspagen et al., 2014; Visser et al., 2016
Other global	Reduce vertical mixing	Increased stratification could reduce vertical mixing and favor the retention of phytoplankton in upper water column	Doney, 2006; Huisman and Paerl, 2008; O'Neil et al., 2012
warming-related factors	Affect precipitation and drought patterns	High intensity rainfall events and droughts would increase bloom occurrences	Reichwaldt and Ghadouani, 2012; Ho and Michalak, 2020
	Other uncertain events	For example, wildfires led to a rapid increase in iron and other biogenic elements to induce algal blooming	Tang et al., 2021; Liu et al., 2022a

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populations of phytoplankton usually change with variation of temperature, and cyanobacteria will become dominant populations when temperature is above about 20 °C (Liu et al., 2011). It was reported that rising temperature promoted inhibiting effect of cyanobacteria growth on other species of phytoplankton (Carey et al., 2012). Moreover, the biomass of phytoplankton will increase as temperature rises under suitable condition (Davidson et al., 2015). It was found that phenology of phytoplankton was advanced and prolonged under temperature rise, and the temperature rise has shortened the winter. For example, the growth period of phytoplankton is at least one month earlier in the three major lakes in Sweden from summer to spring (Weyhenmeyer, 2001). Besides, the time of the beginning and end of cyanobacterial blooms were advanced and delayed by global warming in Taihu Lake, respectively (Zhang et al., 2018b). In Taihu Lake, cyanobacterial blooms had also been found in winter (Ma et al., 2016).

Taihu Lake has undergone considerable nutrients input reductions to prevent cyanobacterial blooms since 2007. However, significant cyanobacterial blooms continued throughout 2017 (Qin et al., 2021). It was synergetically sparked by substantial external loading from flooding in the Taihu basin in 2016 and a noticeably warmer winter in 2016-2017 (Qin et al., 2021, 2022). High rainfall and a warm winter were produced in 2016 by the super-strong El Niño event of 2015-2016 in conjunction with warm phase backdrops, such as the Atlantic Multidecadal Oscillation (AMO) and Pacific Decade Oscillation (PDO) (Qin et al., 2021). By accelerating internal nutrients cycling and escalating cyanobacterial blooms, regional climate anomalies enhanced eutrophication via a positive feedback mechanism (Qin et al., 2021, 2022).

Combined with the current situation of advanced phenology and prolonged growth period, it is feasible to expect that the algal blooms caused by rising temperature will be accompanied with widespread and long-lasting. In addition, changes in the vertical stratification of water bodies and meteorological changes brought by global warming, such as variations in winds, precipitation, etc., will also have an impact on the formation of algal blooms.

2.2 The impact of rising CO₂ concentration impact on algal blooming

Rising carbon dioxide, is responsible for more

than half of the impacts of global warming. which also affects the development of algal blooms. Since the Industrial Revolution, various greenhouse gases in the atmosphere have been increased significantly. Concentration of CO₂(aq) increased from 278×10⁻⁶ in 1750 to 390.5×10⁻⁶ in 2011 (IPCC, 2014). In addition, concentration of $CO_2(aq)$ is more than the highest value of 280×10⁻⁶ recorded in Antarctic ice cores for hundreds of thousands of years (Lenton et al., 2008). Concentration level of CO₂(aq) is several orders of magnitude higher than other greenhouse gases, and its greenhouse effect contribution rate exceeds 60% (Ma'mum et al., 2005). However, global warming may also increase CO₂ emissions by promoting the degradation of global organic carbon (Jenkinson et al., 1991; Cox et al., 2000; Koven et al., 2011; Crowther et al., 2016). Hence, $CO_2(aq)$ and rising temperatures may be mutually causal, and there has been a long-standing debate about the cause and effect.

As a huge carbon reservoir, the hydrosphere, especially the ocean, occupies more than 70% of the earth's area. Studies have shown that humans emit 5.5 billion tons of CO_2 into the atmosphere each year, and about 2 billion tons of CO₂ are absorbed by the ocean, accounting for 35% of the total emissions, while the land absorbs only 700 million tons (Riebesell et al., 2007; Rattan, 2008). The primary productivity of phytoplankton accounts for more than 50% of the total primary productivity of the earth (Field et al., 1998; Behrenfeld et al., 2001). The increasing $CO_2(aq)$ will increase the photosynthesis of phytoplankton and significantly increase the primary production capacity of phytoplankton (Hein and Sand-Jensen, 1997). An extensive number of studies have confirmed that when CO₂(aq) is double, the primary productivity in the water body can increase by about 10%-50% (Bowes, 1993; Morel et al., 1994; Ibelings and Maberly, 1998; Raven and Falkowski, 1999; Schippers et al., 2004; Meseck et al., 2007).

 CO_2 becomes more crucial when nutrients are not limiting (van Dam et al., 2018). The growth and reproduction of phytoplankton will be greatlyaffected by rising $CO_2(aq)$ in eutrophic waters, whereas this effect is much less pronounced in oligotrophic waters (Verspagen et al., 2014). According to Visser et al. (2016), a steeper gradient of increased atmospheric $CO_2(aq)$ will result in more CO_2 input. Algal blooms on the surface can absorb CO_2 , enhancing algal blooms in eutrophic waters. Phytoplankton with high-flux carbon absorption systems contribute to an increase in inorganic carbon availability while also displaying surprising diversity (Visser et al., 2016). This is due to that various phytoplankton strains combine their CO_2 and bicarbonate absorption systems in different ways. As a result, the genetic makeup of algal blooms may change (Collins and Bell, 2004).

The increase in $CO_2(aq)$ may change the previous control strategy that mainly controlled the input of nutrients. Under the context of global climate change, the influential factors of algal blooms include the input of external nitrogen and phosphorus, internal circulation, and a complex process are combined with global warming. In eutrophic waters, we can simultaneously regulate eutrophication and global warming by controlling algal blooms (particularly the salvage and harvest algal biomass to recycle carbon, nitrogen, and phosphorus). Due to nutrients limitation in oligotrophic waters, nutrients input should be allowed to increase phytoplankton biomass, which can result in significant carbon absorption. It can be treated as in eutrophic waters once the biomass of phytoplankton is enough to form algal blooms in oligotrophic area. It is worth noting that this is only a relatively ideal conceive. It also takes careful analysis on all the pros and cons. In brief, combining the control of algal blooms and greenhouse gas emissions may become a huge project for the environment protection of the earth in the future.

2.3 Other global warming-related factors and uncertain events effect on algal blooming

Aside from rising temperatures and CO₂, global warming promotes the expansion of algal blooms in many ways, such as to reduce vertical mixing and length the optimal growth period, to change precipitation and drought patterns, and to benefit bloom formation through captured nutrient loads (Paerl and Huisman, 2008). Global warming may lead to extreme climates, e.g., extreme precipitation and drought, extreme storms increasing, glaciers melting, and soil warming. These may increase the input of nutrients in the basin to lakes and other water bodies (Rustad et al., 2001; Brookshire et al., 2011; Jeppesen et al., 2011), which will increase the eutrophication of aquatic systems. Moreover, global warming will promote the growth of algae and exacerbate eutrophication problems (e.g., algal blooms) and anaerobic water bodies (Moss et al., 2011; Meerhoff et al., 2022). In particular, the observed trends in marine harmful algal blooms can be attributed to the ocean warming, heat waves, oxygen loss, eutrophication, and pollution (Gobler, 2020). These factors are also direct or indirect related to the global warming.

Global warming will bring about many other uncertain events, which may create an environment benefiting the formation of algal blooms, including increase in nutrient supply, temperature rise, carbon dioxide increase, and the formation of a stable hydrological environment. Therefore, the expansion of algal blooms impacted by uncertain events. For example, the wildfires in Australia have led to a rapid increase in carbon dioxide and algal blooms (Tang et al., 2021).

3 THE IMPACT OF ALGAL BLOOMS ON GLOBAL WARMING IN TURN

The direct and indirect contribution of algal blooms to climate warming is mainly the release of greenhouse gases when phytoplankton dies, as well as accelerating melting of sea ice and glaciers (Fig.1; Table 1).

3.1 The impact of algal blooms on carbon dioxide emission

The photosynthesis of phytoplankton gradually transports organic carbon to the top of food chain and produces particulate organic carbon (POC) that sedimentation (Jiao et al., 2010; Zhang et al., 2018a). Phytoplankton absorb carbon around 100 million tons from the atmosphere in the photic zone of the ocean every day (Behrenfeld et al., 2010). Although a large amount of the rising carbon dioxide in the atmosphere can effectively be absorbed, the "biological carbon sequestration" does not mean "carbon storage". The POC actual sinks to the bottom of the sea and the percentage eventually buried is only 0.1% of the primary productivity (IPCC, 2001). This means that although phytoplankton absorbs and transforms a large amount of carbon dioxide, the real long-term amount of departure from the global carbon cycle is very low. More carbon is transferred through the food chain, the effects of animal and plant excrement, microbial degradation, and respiration, which will be added to the global carbon cycle. Moreover, this process is short-lived, so the impact on such a long-term global climate change is fragile (Jiao et al., 2010; Zhang et al., 2018a). The decay of biomass of algal blooms significantly increased CO₂ emissions (Hansen et al., 1998; Li et al., 2021, 2023). The carbon in the dead organic matter will be decomposed by microorganisms and finally be released into the water body and the atmosphere in CO_2 . Therefore, algal blooms as sinks of carbon in the growth phase, but it is source in the stage of death and decomposition. Whether algal blooms can ultimately reduce $CO_2(aq)$ and slow down climate warming needs further researches, particularly if human intervene the carbon cycle by capturing CO_2 in a way that does not exacerbate global warming.

3.2 The impact of algal blooms on methane production

The concentration of methane in the atmosphere was about 1 774×10⁻⁹ in 2005, which was more than twice the concentration before industrialization (IPCC, 2007). The contribution rate of methane to global warming reached 16%, which was only lower than that of carbon dioxide. Although the concentration of methane was much lower than that of carbon dioxide, the efficiency of capturing heat was 28 times that of CO_2 , and it was increasing at a faster rate every year (IPCC, 2014). As an essential release source of global methane, methane source of water accounts for about 40%-50% of the global methane source (Whiting and Chanton, 1993). When algal biomass dies and decomposes, it will consume a large amount of dissolved oxygen in the water body, causing the water body to be in an anoxic and anaerobic state in the water area. The anaerobic environment of the water body is conducive to the production of methane (Knittel and Boetius, 2009), and related studies have shown that the amount of methane released increases with the increase of eutrophication status of the water body (Yang et al., 2011). The "biological pump" formed by the growth of phytoplankton will increase the organic matter content in the water body to a certain extent, and eventually lead to an increase in the organic matter in the sediment, which will lead to an increase in oxygen consumption and methane flux in the water (Bastviken et al., 2004). Contrary to what had been believed, aerobic methane production in water bodies may be the main method of methane production and release, and its flux is highly correlated with algal biomass (Bogard et al., 2014). Bižić et al. (2020) showed that cyanobacteria living in marine, freshwater, and terrestrial environments produced significant amounts of methane under light, dark, oxic, and anoxic conditions, establishing a link between methane production and light-driven primary productivity in a globally important and

ancient group of photoautotrophs. They discovered that during oxygenic photosynthesis, methane production increased. They hypothesized that cyanobacteria-produced methane leads to methane accumulation in oxygen-depleted marine and limnic surface waters. Because of global warming, frequent cyanobacterial blooms are expected to become more common, perhaps having a direct and positive feedback on climate change (Bižić et al., 2020).

Davidson et al. (2018) conducted an experiment to see how the effects of warming and eutrophication on CH_4 ebullition. Eutrophication alone raised the percentage contribution of ebullition from 51% to 75%, according to the researchers. On the other hand, warming treatments (increased 2–3 °C and 4–5 °C) and nutrient enrichment at showed synergistic impact, increasing mean annual ebullition by at least 1 900 mg CH_4 -C m²/a. Diffusive flux rose only marginally at higher temperatures (average 63 mg CH_4 -C m²/a) and exhibited no response to eutrophication.

In recent years, many studies showed that algal blooms increased the release of methane (Yan et al., 2019; Xu et al., 2020), which exacerbated global warming. The CH4 emission of lake could be increased due to eutrophication. As a result, the ratio of CH₄/CO₂ emission would be around 2 (Sun et al., 2021). Stronger stratification and surface warming boosted CH₄ emission, resulting in greater cyanobacterial biomass deposition and bottom water anoxia (Bartosiewicz et al., 2021). As eutrophication progresses, the effect of algal blooms on methane production would rapidly rise. Downing et al. (2021) reported that during 2015-2050, the total socio-economic losses due to CH4 emissions from eutrophication (usually algal blooms) in lakes and reservoirs were estimated to be US \$7.5-81 trillion. The potential savings of \$0.66-24 trillion would accrue from keeping methane emissions at present levels instead of the projected 20%-100% increase by 2050.

3.3 The impact of algal blooms on N₂O production

Nitrous oxide (N_2O) is a trace gas affecting climate and atmospheric chemistry. It is a long-lived greenhouse gas alongside carbon dioxide and methane. Although N_2O concentration in the atmosphere is much lower than that of CO_2 , singlemolecule of N_2O has a radiation absorption capacity of 296–340 times that of CO_2 , and contributes 5%–6% of the greenhouse effect (Houghton et al., 1996). The concentration of N_2O in the atmosphere was 325×10^{-9} in 2013, which was 20% higher than that before industrialization (IPCC, 2014). The sources of atmospheric N₂O mainly include oceans, rivers, soils, sediments, and human industrial and agricultural production (Khalil and Rasmussen, 1992). The ocean is an important natural source of atmospheric N₂O, and the N₂O transported from the ocean to the atmosphere accounts for 25%-33% of the total transport (Nevison et al., 1995; Seitzinger et al., 2000). Among them, high-productivity coastal waters include estuaries and upwelling areas with high contribution of 60% (Naqvi et al., 2000). Dissolved oxygen (DO) is the main controlling factor for the production or consumption of N₂O (Capone et al., 2008). Changes in DO concentration in water affect the production efficiency of N₂O in the ocean, and may eventually become a factor on the source/sink of N₂O in the ocean/atmosphere (Suntharalingam et al., 2000). Codispoti (2010) pointed out that the intensification of human activities will lead to the expansion of hypoxic or hypoxic water bodies in the world in future, change the production or consumption of N₂O, and then affect the global N₂O source and sink patterns.

The nitrate-nitrogen content affects N₂O flux in water bodies (Stow et al., 2005). As substrate nitrogen increase from decompose algal biomass, more N₂O will be released by nitrification and denitrification (Gruber and Galloway, 2008). The increasingly severe problem of eutrophication is bound to intensify the release of N₂O in water bodies. Microalgae in aquatic systems are considered an important source that significantly contributes by directly creating N₂O (Weathers, 1984; Wang et al., 2006; Plouviez et al., 2019; Burlacot et al., 2020; Hutchins and Capone, 2022). It was reported that algal blooms produced high mean N2O flux in eutrophic lakes (Khoiyangbam and Chingangbam, 2022; Liu et al., 2022b), particularly in lakes with annually algal blooming, e.g., Taihu Lake (Xiao et al., 2019a) and Lake Erie (Fernandez et al., 2020). Zhou et al. (2021) proposed a non-linear exponential model to explain the change in N₂O emission flux by the degree of eutrophication, and showed that in shallow lakes, Chl a and TN predicted 86% of the N₂O emission flux, demonstrating that nutrient-rich condition and algal buildup determine N₂O emission flux; and furthermore they pointed out that temperature and phytoplankton accumulationdecomposition influenced N₂O emission flow in a complex fashion.

3.4 Algal bloom accelerates glacier and sea ice melting

Although the Antarctic and Greenland ice sheets, along with smaller ice caps and glaciers, account for merely 10% of the global land surface, despite their limited extent, those ice masses contain a vast volume of water equivalent to a 77-m rise in global sea levels (Barry, 1981). Ice sheets were previously considered inert parts of the carbon cycle and were generally ignored in global modeling, which has been changed by researchers in the past over 10 years, as they found that there were specialized microbial communities, high rates of biogeochemical/physical weathering in ice sheets, and storage and cycling of organic carbon (>10⁴ PgC) and nutrients (Wadham et al., 2019). Bender et al. (1997) studied the fluctuation in atmospheric gas concentration on time scales from anthropogenic (past 200 years) to the glacial/interglacial (hundreds of thousands of years) periods and found that the fluctuation is due to air trapping in glacial ice.

It is a consensus that global warming accelerates the melting of glaciers, and melted glaciers have direct or indirect effect on global warming. The possible direct or indirect consequences of ice sheets include: (1) the sequestration or release of CO₂/CH₄ through microbial activity within the ice sheets; (2) the burial of terrestrial organic matter carried by rivers from ice sheets; (3) the release of CO₂ through respiration or absorption by primary production in the oceans; and (4) the production of export material-organic matter generated by primary production that is not recycled before sinking to the ocean floor (Wadham et al., 2019; Du et al., 2022). The presence of meltwater has the potential to stabilize the ocean column, leading to amplifying feedback mechanisms that enhance subsurface ocean warming and ice shelf melting (Hansen et al., 2016). The melting of glaciers contributes to the rise in sea levels, consequently exacerbating coastal erosion and intensifying storm surge, which is further combined by the effects of warming air and ocean temperatures, and resulted in more frequent and severe coastal storms (hurricanes and typhoons) (Hansen et al., 2016).

Many studies reported that the formation of algal blooms found in cold place with sea ice and on snow (Segawa et al., 2018; Engstrom et al., 2020; Gray et al., 2020; Onuma et al., 2022). Those algal blooms could undoubtedly accelerate the melting of glacier, sea ice and snow, and ultimately affect the global climate and environment (Healy and Khan, 2023). By reducing surface albedo, microbes can contribute to ice warming and contribute to glacier melt (Ganey et al., 2017). Their contribution to climate warming will grow with increased ice melt and nutrient input (Ganey et al., 2017).

Algal blooms in ocean in the polar regions may also melt sea-ice. The current thinning of sea ice and rising melt pond may result in increased under-ice productivity and ice-algae export from the surface to the deep sea (Boetius et al., 2013). Optical tests revealed that incident light in the ice beneath melt ponds (47%-59%) transmitted four times of that on neighboring snow-free ice (13%-18%) (Arrigo et al., 2012), suggesting that the melting rate was greatly increased. Algal blooms are becoming more prevalent in the Antarctic, the Arctic (Gray et al., 2020; Oziel et al., 2020), and on ice sheets (McCutcheon et al., 2021). By accelerating the melting of winter ice cap, algal blooms might contribute to global warming. Indeed, in recent years, there has been increasing evidence that algal blooms have accelerated the process of melting glaciers and sea ice, such as in the western Greenland Ice Sheet (Cook et al., 2020), southwestern Greenland Ice Sheet (Cook et al., 2020), the Greenland Ice Sheet (Williamson et al., 2020), Arctic (Lutz et al., 2016; Castagno et al., 2023), and Alaskan Icefield (Ganey et al., 2017). Except for the glaciers and sea ice, algal blooms may have the capacity to melt ice in winter ice-cover freshwater aquatic systems. In winter, algal blooms in freshwater have been observed (Ma et al., 2016), which consequently contributed to global warming.

4 DISCUSSION

4.1 Mutual feedback between global warming and algal blooming

Algal blooms release greenhouse gases directly

or indirectly via the melting of glaciers, which ultimately promote extreme weather and other outcomes on climate warming (Fig.2; Table 2). There are direct or indirect links between various processes and factors, reflecting the complexity of this issue. The quantitative research between multiprocess and multi-factor is thus highly demanded as research in this area remains scarce, calling for more data and evidence.

Climate warming promotes the expansion and occurrence of algal blooms directly by temperature rise or indirectly via increases in carbon dioxide concentration and extreme climate incidence (Fig.1; Table 1). Although many studies have been carried out on the issue, and evidence and data are relatively sufficient, the overall estimation is still lacking, especially the estimation at the global scale.

Algal blooms and climate warming have posed serious risks and losses to the advancement of human society and the economy in recent decades. A self-reinforcing cycle that may get more and more worsened due to the growth of algal blooms and the acceleration of climate change has been established (Fig.3). Regretfully, there is not much that we currently know about the closed loop of mutual promotion. Due to the complexity of this issue,

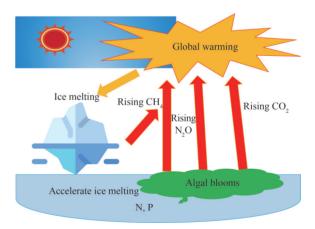


Fig.2 The impact of algal blooms on global warming in turn

Table 2 Representative studies of the imp	pact of algal blooms	on global w	arming in turn

Туре	Торіс	Reference
CO ₂ emission	The decay of algal blooms significantly increased CO_2 emissions	Hansen et al., 1998; Li et al., 2021, 2023
Methane production	Algal blooms increased the release of methane	Yan et al., 2019; Xu et al., 2020; Bartosiewicz et al., 2021; Sun et al., 2021
N_2O production	Algal blooms produced N_2O flux	Xiao et al., 2019a; Bižić et al., 2020; Fernandez et al., 2020; Zhou et al., 2021; Khoiyangbam and Chingangbam, 2022; Liu et al., 2022b
Melt glacier and sea ice	By reducing surface albedo, algal blooms can contribute to ice warming and glacier melt	Arrigo et al., 2012; Ganey et al., 2017; Healy and Khan, 2023

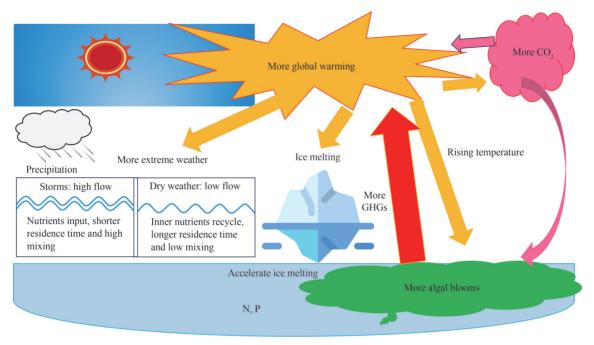


Fig.3 Mutual feedback between global warming and algal blooms

The relationship between algal blooms and global warming, directly or indirectly, is depicted in this schematic. Climate warming encourages the growth and sustaining of algae blooms by temperature rise directly, or indirectly by increases in CO_2 concentration and extreme climate appearance. In addition, algae blooms directly release greenhouse gases, promote glacier melting to release greenhouse gases, and indirectly promote extreme climate and other incidents of climate warming. Hence, a closed loop of mutual promotion between the escalation of climate warming and the growth of algal blooms could make our planet environment worse.

quantitative studies on each step of the process as well as quantitative estimation of the whole quantity are urgently needed. Quantitative research on the magnitude, pattern, and mechanism of their mutual feedback effects is very crucial.

Global warming promotes the expansion of algal blooms through mainly the increasing of temperature, $CO_2(aq)$, and nutrient input, and form more stable environment with long residence time. Undoubtedly, this is a process of capturing CO_2 to form a carbon sink. However, algal blooms enhance the release of CO₂ and CH₄ during the death and decomposition of phytoplankton. In addition, phytoplankton can also release CO_2 when they respire (i.e., at night). The increase of phytoplankton biomass, nitrogen content, and the acceleration of the cycle rate (nitrification and denitrification) promote the releasing of N₂O (Plouviez et al., 2019). As the greenhouse effect of CH₄ and N₂O are 28 times and 265 times that of CO₂ (IPCC, 2014), respectively, the algal blooms process will increase the global warming potential. Therefore, mutual backup by global warming and algal blooms will continue to deteriorate, and threaten the survival and development of human being. Although the impact of global warming on algal blooms has been a hot research topic in the past decades

(Glibert, 2020; Gobler, 2020), unfortunately, the effects of algal blooms on global warming received only little attention.

Medium-sized experiments in shallow lakes had proved that nutrient concentrations could control greenhouse gas fluxes more than temperature (Davidson et al., 2015). In addition, the treatment effects of temperature at low and high nutrient levels indicate that the positive effects of temperature are relatively weak. At low nutrient levels, even on the contrary, the amount of CO₂ released is decreased with increasing temperature and has no significant effect on the release of CH₄ and N₂O. The possible influence of temperature is indirect. For example, the annual total fluxes of both CH₄ and CO₂ and monthly observation data show that the abundance increase in aquatic plant at low nutrient levels is associated with a significant decrease in fluxes of CH_4 and CO_2 (Davidson et al., 2015). The abundance of aquatic plants is positively correlated with changes in temperature, which indicates that temperature indirectly affects plant abundance and thus the fluxes of CH₄ and CO₂. These results indicate that the fluxes of greenhouse gas in shallow lakes are controlled by factors indirectly related to temperature, such as the concentration of nutrients

and the abundance of primary producers (Davidson et al., 2015).

It is worth noting that one of the hazards of algal blooms is producing anaerobic water bodies, causing deaths of fish and shrimps, and even the formation of lifeless "dead zones". The production speed of CH_4 and N_2O is the fastest under anaerobic conditions. Therefore, how to form anaerobic in aquatic systems is the key for the mutual feedback between global warming and algal blooms. The anaerobic "dead zone" formed by algal blooms is increasing globally. Quantitative estimation on the CH_4 and N_2O produced by them will be the key issue of assessing the contribution of algal blooms to greenhouse gases.

In summary, algal blooms may increase the net warming potential of greenhouse gases and promote global warming. Existing studies have shown that global warming could also promote strongly algal blooms. Therefore, algal blooms and global warming promote each other (Fig.3). Future researches should focus on the strength and control strategy of mutual feedback between global warming and algal blooms. Researches on the issue will help deeply understand the process and mechanism of algal blooms and global warming, as well as develop control strategy and technology.

4.2 Outlook of countermeasure against algal blooms and global warming

Phytoplankton (or microalgae) is important in carbon cycle for its wide distribution and huge biomass in the world. The uptake of CO_2 by microalgae biomass from the atmosphere or other sources has been suggested as one of 10 pathways on CO_2 utilization and removal (Hepburn et al., 2019). Algal blooms also are contributed to carbon sequestration. Diatoms, for instance, precipitate carbon by their fucan polysaccharide during blooms (Vidal-Melgosa et al., 2021). Microbial production of recalcitrant dissolved organic matter by the "microbial carbon pump" (MCP) could be a long-term carbon storage in the oceans (Jiao et al., 2010).

It can be predicted that the interaction between global warming and algal blooms let us to consider the combination of algal bloom controlling and greenhouse gas emission mitigation in the future. The strategy of controlling algal blooms by reducing nitrogen and phosphorus will be developed into a global geoengineering for cycle regulation of carbon, nitrogen, and phosphorus.

The addition of iron into the ocean to increase

phytoplankton biomass for controlling carbon is one of typical example of research on mitigating global warming (Coale et al., 1996, 2004; Boyd et al., 2000, 2004, 2007; Watson et al., 2000; Blain et al., 2007). About one-third of the oceans in the world have a large excess of nitrogen and phosphorus nutrients, but the biomass of phytoplankton is very low. Such sea areas are called as the "high-nutrient and low-chlorophyll" (HNLC). Iron limits the productivity of phytoplankton in the HNLC sea area, which in turn affects the transport of carbon dioxide to the deep ocean. The addition of iron in the HNLC sea area can promote the growth of phytoplankton, accelerate the export of carbon from the surface of the ocean to the deep layer, and ultimately reduce the content of carbon dioxide in the atmosphere, thereby alleviating or changing the global climate change problem caused by the greenhouse effect. Some studies have proved the scientific rationality of ocean ironing (Buesseler and Boyd, 2003; Buesseler et al., 2004). However, many issues in further practice are still controversial (Schiermeier, 2009; Cao and Caldeira, 2010; Güssow et al., 2010).

Therefore, how to use phytoplankton resources is the key after fixing carbon. Because of the largescale use of algal biomass, it will expand the cycle of carbon and reduce its greenhouse effect time (exposure to CO_2 and CH_4 in the atmosphere). Moreover, the polluted nitrogen and phosphorus in the water body will become a resource commodity, which will reduce the pollution load of nitrogen and phosphorus in the water body and help reduce algal blooms, because it will lengthen the carbon cycle and lessen the warming effect (CO₂ and CH₄ exposure to the environment). This will simultaneously slow down the climate warming and benefit to the algal bloom control. Additionally, it may be a useful way to use a great amount of phytoplankton biomass for carbon sequestration. Many events are related to global warming, such as the Canadian wildfires that have continued for several months in 2023, can also be utilized for controlling the issues of algal blooms and climate change. Studies have shown that wildfires can increase the amount of iron and other biological elements, which ultimately lead to an increase in phytoplankton biomass and the outbreak of algal blooms (Tang et al., 2021; Liu et al., 2022a). It seems that better than the addition of iron into the ocean to increase phytoplankton biomass. However, it is difficult to predict where the material generated by wildfires will move, which is related to

No. 3

meteorological factors.

In conclusion, this paper summarizes the mutualfeedback effect between algal blooms and climate warming which will promote combination between algal blooms controlling and carbon neutralization; and built the theoretical basis for global protection geoengineering, by which carbon, nitrogen, and phosphorus cycles could be manipulated or controlled. This may be an important direction of environmental protection work in the next few decades.

5 DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

References

- Anderson D M. 1997. Turning back the harmful red tide. *Nature*, **388**(6642): 513-514, https://doi.org/10.1038/41415.
- Arrigo K R, Perovich D K, Pickart R S et al. 2012. Massive phytoplankton blooms under Arctic Sea ice. *Science*, **336**(6087): 1408, https://doi.org/10.1126/science.1215065.
- Barry R G. 1981. Trends in snow and ice research. *Eos*, *Transactions American Geophysical Union*, **62**(46): 1138-1144, https://doi.org/10.1029/EO062i046p01138-01.
- Bartosiewicz M, Maranger R, Przytulska A et al. 2021. Effects of phytoplankton blooms on fluxes and emissions of greenhouse gases in a eutrophic lake. *Water Research*, 196: 116985, https://doi.org/10.1016/j.watres.2021.116985.
- Bastviken D, Cole J, Pace M et al. 2004. Methane emissions from lakes: dependence of lake characteristics, two regional assessments, and a global estimate. *Global Biogeochemical Cycles*, **18**(4): GB4009, https://doi.org/ 10.1029/2004GB002238.
- Behrenfeld M J. 2014. Climate-mediated dance of the plankton. *Nature Climate Change*, **4**(10): 880-887, https://doi.org/10.1038/NCLIMATE2349.
- Behrenfeld M J, O'Malley R T, Siegel D A et al. 2010. Climate-driven trends in contemporary ocean productivity. *Nature*, 444(7120): 752-755, https://doi.org/10.1038/nature 05317.
- Behrenfeld M J, Randerson J T, McClain C R et al. 2001. Biospheric primary production during an ENSO transition. *Science*, **291**(5513): 2594-2597, https://doi.org/10.1126/ science.1055071.
- Bender M, Sowers T, Brook E. 1997. Gases in ice cores. Proceedings of the National Academy of Sciences of the United States of America, 94(16): 8343-8349, https://doi. org/10.1073/pnas.94.16.8343.
- Bernard S, Kudela R, Velo-Suarez L. 2014. Developing global capabilities for the observation and predication of harmful algal blooms. *In*: Djavidnia S, Cheung V, Ott M et al. eds. Oceans and Society: Blue Planet. Cambridge Scholars Publishing, Newcastle upon Tyne, UK.

- Bižić M, Klintzsch T, Ionescu D et al. 2020. Aquatic and terrestrial cyanobacteria produce methane. *Science Advances*, 6(3): eaax5343, https://doi.org/10.1126/sciadv.aax5343.
- Blain S, Quéguiner B, Armand L et al. 2007. Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. *Nature*, 446(7139): 1070-1074, https://doi.org/10. 1038/nature05700.
- Boetius A, Albrecht S, Bakker K et al. 2013. Export of algal biomass from the melting Arctic sea ice. *Science*, **339**(6126): 1430-1432, https://doi.org/10.1126/science.1231346.
- Bogard M J, del Giorgio P A, Boutet L et al. 2014. Oxic water column methanogenesis as a major component of aquatic CH₄ fluxes. *Nature Communications*, **5**: 5350, https://doi.org/10.1038/ncomms6350.
- Bowes G. 1993. Facing the inevitable: plants and increasing atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology*, **44**: 309-332, https://doi. org/10.1146/annurev.pp.44.060193.001521.
- Boyd P W, Jickells T, Law C S et al. 2007. Mesoscale iron enrichment experiments 1993-2005: synthesis and future directions. *Science*, **315**(5812): 612-617, https://doi.org/ 10.1126/science.1131669.
- Boyd P W, Law C S, Wong C S et al. 2004. The decline and fate of an iron-induced subarctic phytoplankton bloom. *Nature*, **428**(6982): 549-553, https://doi.org/10.1038/nature 02437.
- Boyd P W, Watson A J, Law C S et al. 2000. A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature*, **407**(6805): 695-702, https://doi.org/10.1038/35037500.
- Brookes J D, Carey C C. 2011. Resilience to blooms: Managing nitrogen and phosphorus pollution of fresh water may decrease the risk of cyanobacterial blooms, even in the face of warming temperatures. *Science*, **334**(6052): 46-47, https://doi.org/10.1126/science.1207349.
- Buesseler K O, Andrews J E, Pike S M et al. 2004. The effects of iron fertilization on carbon sequestration in the Southern Ocean. *Science*, **304**(5669): 414-417, https:// doi.org/10.1126/science.1086895.
- Buesseler K O, Boyd P W. 2003. Will ocean fertilization work? Science, 300(5616): 67-68, https://doi.org/10.1126/ science.1082959.
- Burlacot A, Richaud P, Gosset A et al. 2020. Algal photosynthesis converts nitric oxide into nitrous oxide. *Proceedings of the National Academy of Sciences of the United States of America*, **117**(5): 2704-2709, https://doi. org/10.1073/pnas.1915276117.
- Cao L, Caldeira K. 2010. Can ocean iron fertilization mitigate ocean acidification? A letter. *Climatic Change*, 99(1-2): 303-311, https://doi.org/10.1007/s10584-010-9799-4.
- Capone D G, Bronk D A, Mulholland M R et al. 2008. Nitrogen in the Marine Environment. Academic Press, New York.
- Carey C C, Ibelings B W, Hoffmann E P et al. 2012. Ecophysiological adaptations that favour freshwater cyanobacteria in a changing climate. *Water Research*, 46(5): 1394-1407, https://doi.org/10.1016/j.watres.2011. 12.016.

- Castagno A P, Wagner T J W, Cape M R et al. 2023. Increased sea ice melt as a driver of enhanced Arctic phytoplankton blooming. *Global Change Biology*, **29**(17): 5087-5098, https://doi.org/10.1111/gcb.16815.
- Coale K H, Johnson K S, Chavez F P et al. 2004. Southern Ocean iron enrichment experiment: carbon cycling in high- and low-Si waters. *Science*, **304**(5669): 408-414, https://doi.org/10.1126/science.1089778.
- Coale K H, Johnson K S, Fitzwater S E et al. 1996. A massive phytoplankton bloom induced by an ecosystemscale iron fertilization experiment in the equatorial Pacific Ocean. *Nature*, **383**(6600): 495-501, https://doi. org/10.1038/383495a0.
- Codispoti L A. 2010. Interesting times for marine N₂O: changes in ocean chemistry could exacerbate global warming by raising the atmospheric concentration of nitrous oxide, a potent greenhouse gas. *Science*, **327**(5971): 1339-1340, https://doi.org/10.1126/science.1184945.
- Collins S, Bell G. 2004. Phenotypic consequences of 1,000 generations of selection at elevated CO₂ in a green alga. *Nature*, **431**(7008): 566-569, https://doi.org/10.1038/nature 02945.
- Conley D J. 2012. Ecology: save the Baltic Sea. *Nature*, **486**(7404): 463-464, https://doi.org/10.1038/486463a.
- Cook J M, Tedstone A J, Williamson C et al. 2020. Glacier algae accelerate melt rates on the south-western Greenland Ice Sheet. *The Cryosphere*, 14(1): 309-330, https://doi. org/10.5194/tc-14-309-2020.
- Cox P A, Banack S A, Murch S J. 2003. Biomagnification of cyanobacterial neurotoxins and neurodegenerative disease among the Chamorro people of Guam. *Proceedings of* the National Academy of Sciences of the United States of America, 100(23): 13380-13383, https://doi.org/10.1073/ pnas.2235808100.
- Cox P M, Betts R A, Jones C D et al. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**(6809): 184-187, https://doi.org/10.1038/35047138.
- Crowther T W, Todd-Brown K E O, Rowe C W et al. 2016. Quantifying global soil carbon losses in response to warming. *Nature*, **540**(7631): 104-108, https://doi.org/10. 1038/nature20150.
- Davidson T A, Audet J, Jeppesen E et al. 2018. Synergy between nutrients and warming enhances methane ebullition from experimental lakes. *Nature Climate Change*, 8(2): 156-160, https://doi.org/10.1038/s41558-017-0063-z.
- Davidson T A, Audet J, Svenning J C et al. 2015. Eutrophication effects on greenhouse gas fluxes from shallow-lake mesocosms override those of climate warming. *Global Change Biology*, **21**(12): 4449-4463, https://doi.org/10.1111/gcb.13062.
- Doney S C. 2006. Plankton in a warmer world. *Nature*, 444(7120): 695-696, https://doi.org/10.1038/444695a.
- Downing J A, Polasky S, Olmstead S M et al. 2021. Protecting local water quality has global benefits. *Nature Communications*, **12**(1): 2709, https://doi.org/10.1038/ s41467-021-22836-3.
- Du Z H, Wang L, Wei Z Q et al. 2022. CH₄ and CO₂

observations from a melting high mountain glacier, Laohugou Glacier No. 12. *Advances in Climate Change Research*, **13**(1): 146-155, https://doi.org/10.1016/j.accre. 2021.11.007.

- Engstrom C B, Yakimovich K M, Quarmby L M. 2020. Variation in snow algae blooms in the Coast Range of British Columbia. *Frontiers in Microbiology*, **11**: 569, https://doi.org/10.3389/fmicb.2020.00569.
- Fernandez J M, Townsend-Small A, Zastepa A et al. 2020. Methane and nitrous oxide measured throughout Lake Erie over all seasons indicate highest emissions from the eutrophic Western Basin. *Journal of Great Lakes Research*, 46(6): 1604-1614.https://doi.org/10.1016/j.jglr.2020.09.011.
- Field C B, Behrenfeld M J, Randerson J T et al. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, **281**(5374): 237-240, https://doi.org/10.1126/science.281.5374.237.
- Frau D. 2023. Towards a quantitative definition of Cyanobacteria blooms. *Environmental Reviews*, **31**: 4, https://doi.org/ 10.1139/er-2022-0121.
- Ganey G Q, Loso M G, Burgess A B et al. 2017. The role of microbes in snowmelt and radiative forcing on an Alaskan icefield. *Nature Geoscience*, **10**(10): 754-759, https://doi.org/10.1038/ngeo3027.
- Glibert P M. 2020. Harmful algae at the complex nexus of eutrophication and climate change. *Harmful Algae*, **91**: 101583, https://doi.org/10.1016/j.hal.2019.03.001.
- Gobler C J. 2020. Climate change and harmful algal blooms: insights and perspective. *Harmful Algae*, **91**: 101731, https://doi.org/10.1016/j.hal.2019.101731.
- Gray A, Krolikowski M, Fretwell P et al. 2020. Remote sensing reveals Antarctic green snow algae as important terrestrial carbon sink. *Nature Communications*, 11(1): 2527, https://doi.org/10.1038/s41467-020-16018-w.
- Gruber N, Galloway J N. 2008. An Earth-system perspective of the global nitrogen cycle. *Nature*, **451**(7176): 293-296, https://doi.org/10.1038/nature06592.
- Güssow K, Proelss A, Oschlies A et al. 2010. Ocean iron fertilization: why further research is needed. *Marine Policy*, **34**(5): 911-918, https://doi.org/10.1016/j.marpol. 2010.01.015.
- Hansen J, Sato M, Hearty P et al. 2016. Ice melt, sea level rise and superstorms: evidence from paleoclimate data, climate modeling, and modern observations that 2 °C global warming could be dangerous. *Atmospheric Chemistry* and Physics, 16(6): 3761-3812, https://doi.org/10.5194/ acp-16-3761-2016.
- Hansen K, Mouridsen S, Kristensen E. 1998. The impact of Chironomus plumosus larvae on organic matter decay and nutrient (N, P) exchange in a shallow eutrophic lake sediment following a phytoplankton sedimentation. *Hydrobiologia*, **364**: 65-74, https://doi.org/10.1023/A: 1003155723143.
- Healy, S M, Khan A L. 2023. Albedo change from snow algae blooms can contribute substantially to snow melt in the North Cascades, USA. *Communications Earth & Environment*, 4: 142, https://doi.org/10.1038/s43247-023-00768-8.

- Hein M, Sand-Jensen K. 1997. CO₂ increases oceanic primary production. *Nature*, **388**(6642): 526-527, https:// doi.org/10.1038/41457.
- Hepburn C, Adlen E, Beddington J et al. 2019. The technological and economic prospects for CO₂ utilization and removal. *Nature*, 575(7781): 87-97, https://doi.org/ 10.1038/s41586-019-1681-6.
- Ho J C, Michalak A M. 2020. Exploring temperature and precipitation impacts on harmful algal blooms across continental U. S. lakes. *Limnology and Oceanography*, 65(5): 992-1009, https://doi.org/10.1002/lno.11365.
- Ho J C, Michalak A M, Pahlevan N. 2019. Widespread global increase in intense lake phytoplankton blooms since the 1980s. Nature, 574(7780): 667-670, https://doi.org/10. 1038/s41586-019-1648-7.
- Hou X J, Feng L, Dai Y H et al. 2022. Global mapping reveals increase in lacustrine algal blooms over the past decade. *Nature Geoscience*, **15**(2): 130-134, https://doi. org/10.1038/s41561-021-00887-x.
- Houghton J T, Meira Filho L G, Callander B A et al. 1996.
 Climate Change 1995: the Science of Climate Change.
 Contribution of Working Group I to the Second
 Assessment Report of the Intergovernmental Panel on
 Climate Change. Cambridge University Press, Cambridge.
- Huisman J, Codd G A, Paerl H W et al. 2018. Cyanobacterial blooms. *Nature Reviews Microbiology*, **16**(8): 471-483, https://doi.org/10.1038/s41579-018-0040-1.
- Hutchins D A, Capone D G. 2022. The marine nitrogen cycle: new developments and global change. *Nature Reviews Microbiology*, **20**(7): 401-414, https://doi.org/ 10.1038/s41579-022-00687-z.
- Ibelings B W, Maberly S C. 1998. Photoinhibition and the availability of inorganic carbon restrict photosynthesis by surface blooms of cyanobacteria. *Limnology and Oceanography*, 43(3): 408-419, https://doi.org/10.4319/ lo.1998.43.3.0408.
- IPCC. 2001. Climate Change 2001: the Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.
- IPCC. 2007. Climate Change 2007: The Physical Science Basis. Cambridge University Press, New York. 996p.
- IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva. 151p.
- Jack Brookshire E N, Gerber S, Webster J R et al. 2011. Direct effects of temperature on forest nitrogen cycling revealed through analysis of long-term watershed records. *Global Change Biology*, **17**(1): 297-308, https:// doi.org/10.1111/j.1365-2486.2010.02245.x.
- Jenkinson D S, Adams D E, Wild A. 1991. Model estimates of CO₂ emissions from soil in response to global warming. *Nature*, **351**(6324): 304-306, https://doi.org/10. 1038/351304a0.
- Jeppesen E, Kronvang B, Olesen J E et al. 2011. Climate change effects on nitrogen loading from cultivated catchments in Europe: implications for nitrogen retention,

ecological state of lakes and adaptation. *Hydrobiologia*, **663**(1): 1-21, https://doi.org/10.1038/351304a0.

- Jiao N Z, Herndl G J, Hansell D A et al. 2010. Microbial production of recalcitrant dissolved organic matter: longterm carbon storage in the global ocean. *Nature Reviews Microbiology*, 8(8): 593-599, https://doi.org/10.1038/nrmicro 2386.
- Khalil M A K, Rasmussen R A. 1992. The global sources of nitrous oxide. *Journal of Geophysical Research*, 97(D13): 14651-14660, https://doi.org/10.1029/92JD01222.
- Khoiyangbam R S, Chingangbam S S. 2022. Assessing seasonal variation of diffusive nitrous oxide emission from freshwater wetland in Keibul Lamjao National Park, Manipur Northeast India. *Atmospheric Environment: X*, 13: 100147, https://doi.org/10.1016/j.aeaoa.2022.100147.
- Kiehl J T, Trenberth K E. 1997. Earth's annual global mean energy budget. Bulletin of the American Meteorological Society, 78(2): 197-208, https://doi.org/10.1175/1520-0477.
- Knittel K, Boetius A. 2009. Anaerobic oxidation of methane: progress with an unknown process. *Annual review of Microbiology*, 63: 311-334, https://doi.org/10.1146/annurev. micro.61.080706.093130.
- Koven C D, Ringeval B, Friedlingstein P et al. 2011. Permafrost carbon-climate feedbacks accelerate global warming. Proceedings of the National Academy of Sciences of the United States of America, 108(36): 14769-14774, https://doi.org/10.1073/pnas.1103910108.
- Lashof D A, Ahuja D R. 1990. Relative contributions of greenhouse gas emissions to global warming. *Nature*, 344(6266): 529-531, https://doi.org/10.1038/344529a0.
- Lenton T M, Held H, Kriegler E et al. 2008. Tipping elements in the Earth's climate system. *Proceedings of the national Academy of Sciences of the United States of America*, **105**(6): 1786-1793, https://doi.org/10.1073/pnas. 0705414105.
- Li Y, Shang J H, Zhang C et al. 2021. The role of freshwater eutrophication in greenhouse gas emissions: a review. *Science of the Total Environment*, **768**: 144582, https:// doi.org/10.1016/j.scitotenv.2020.144582.
- Li Y X, Deng K K, Lin G J et al. 2023. Effects of physiologic activities of plankton on CO₂ flux in the Three Gorges Reservoir after rainfall during algal blooms. *Environmental Research*, **216**: 114649, https://doi.org/10.1016/j.envres. 2022.114649.
- Liu D Y, Zhou C R, Keesing J K et al. 2022a. Wildfires enhance phytoplankton production in tropical oceans. *Nature Communications*, **13**(1): 1348, https://doi.org/10. 1038/s41467-022-29013-0.
- Liu H Z, Jin Q, Luo J X et al. 2022b. Synergistic Effects of Aquatic Plants and Cyanobacterial Blooms on the Nitrous Oxide Emission from Wetlands. *Bulletin of Environmental Contamination and Toxicology*, **108**(3): 579-584, https://doi.org/10.1007/s00128-021-03332-2.
- Liu X, Lu X H, Chen Y W. 2011. The effects of temperature and nutrient ratios on *Microcystis* blooms in Lake Taihu, China: an 11-year investigation. *Harmful Algae*, 10(3): 337-343, https://doi.org/10.1016/j.hal.2010.12.002.
- Lutz S, Anesio A M, Raiswell R. 2016. The biogeography of

red snow microbiomes and their role in melting arctic glaciers. *Nature Communications*, 7: 11968, https://doi. org/10.1038/ncomms11968.

- Ma J R, Qin B Q, Paerl H W et al. 2016. The persistence of cyanobacterial (*Microcystis* spp.) blooms throughout winter in Lake Taihu, China. *Limnology and Oceanography*, 61(2): 711-722, https://doi.org/10.1002/lno.10246.
- Ma'mum S, Svendsen H F, Hoff K A et al. 2005. Selection of new absorbents for carbon dioxide capture. In Greenhouse Gas Control Technologies 7(p.45-53). Elsevier Science Ltd.
- McCutcheon J, Lutz S, Williamson C et al. 2021. Mineral phosphorus drives glacier algal blooms on the Greenland Ice Sheet. *Nature Communications*, **12**(1): 570, https:// doi.org/10.1038/s41467-020-20627-w.
- Meerhoff M, Audet J, Davidson T A et al. 2022. Feedback between climate change and eutrophication: revisiting the allied attack concept and how to strike back. *Inland Waters*, **12**(2): 187-204, https://doi.org/10.1080/20442041. 2022.2029317.
- Meseck S L, Smith B C, Wikfors G H et al. 2007. Nutrient interactions between phytoplankton and bacterioplankton under different carbon dioxide regimes. *Journal of Applied Phycology*, **19**(3): 229-237, https://doi.org/10.1007/s10811-006-9128-5.
- Morel F M M, Reinfelder J R, Roberts S B et al. 1994. Zinc and carbon co-limitation of marine phytoplankton. *Nature*, **369**(6483): 740-742, https://doi.org/10.1038/369740a0.
- Moss B, Kosten S, Meerhoff M et al. 2011. Allied attack: climate change and eutrophication. *Inland Waters*, 1(2): 101-105, https://doi.org/10.5268/IW-1.2.359.
- Naqvi S W A, Jayakumar D A, Narvekar P V et al. 2000. Increased marine production of N₂O due to intensifying anoxia on the Indian continental shelf. *Nature*, **408**(6810): 346-349, https://doi.org/10.1038/35042551.
- Nevison C D, Weiss R F, Erickson III D J. 1995. Global oceanic emissions of nitrous oxide. *Journal of Geophysical Research: Oceans*, **100**(C8): 15809-15820, https://doi.org/10.1029/95JC00684.
- O'Neil J M, Davis T W, Burford M A, et al. 2012. The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change. *Harmful Algae*, 14: 313-334, https://doi.org/10.1016/j.hal.2011.10.027.
- Onuma Y, Yoshimura K, Takeuchi N. 2022. Global simulation of snow algal blooming by coupling a land surface and newly developed snow algae models. *Journal* of Geophysical Research: Biogeosciences, **127**(2): e2021JG006339, https://doi.org/10.1029/2021JG006339.
- Oziel L, Baudena A, Ardyna M et al. 2020. Faster Atlantic currents drive poleward expansion of temperate phytoplankton in the Arctic Ocean. *Nature Communications*, **11**(1): 1705, https://doi.org/10.1038/ s41467-020-15485-5.
- Paerl H W, Huisman J. 2008. Blooms like it hot. *Science*, **320**(5872): 57-58, https://doi.org/10.1126/science.1155398.
- Plouviez M, Shilton A, Packer M A et al. 2019. Nitrous oxide emissions from microalgae: potential pathways and significance. *Journal of Applied Phycology*, **31**(1): 1-8, https://doi.org/10.1007/s10811-018-1531-1.

- Qin B Q, Deng J M, Shi K et al. 2021. Extreme climate anomalies enhancing cyanobacterial blooms in Eutrophic Lake Taihu, China. *Water Resources Research*, 57(7): e2020WR029371, https://doi.org/10.1029/2020WR029371.
- Qin B Q, Zhang Y L, Deng J M et al. 2022. Polluted lake restoration to promote sustainability in the Yangtze River Basin, China. *National Science Review*, 9(1): nwab207, https://doi.org/10.1093/nsr/nwab207.
- Rantala A, Fewer D P, Hisbergues M et al. 2003. Phylogenetic evidence for the early evolution of microcystin synthesis. *Proceedings of the National Academy of Sciences of the United States of America*, **101**(2): 568-573, https://doi. org/10.1073/pnas.0304489101.
- Rattan L. 2008. Carbon sequestration. Philosophical Transactions of the Royal Society B: Biological Sciences, 363(1492): 815-830, https://doi.org/10.1098/rstb.2007.2185.
- Raven J A, Falkowski P G. 1999. Oceanic sinks for atmospheric CO₂. *Plant, Cell & Environment*, **22**(6): 741-755, https://doi.org/10.1046/j.1365-3040.1999.00419.x.
- Reichwaldt E S, Ghadouani A. 2012. Effects of rainfall patterns on toxic cyanobacterial blooms in a changing climate: between simplistic scenarios and complex dynamics. *Water Research*, 46(5): 1372-1393, https://doi. org/10.1016/j.watres.2011.11.052.
- Riebesell U, Schulz K G, Bellerby R G J et al. 2007. Enhanced biological carbon consumption in a high CO₂ ocean. *Nature*, **450**(7169): 545-548, https://doi.org/10. 1038/nature06267.
- Rustad L, Campbell J, Marion G et al. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**(4): 543-562, https://doi.org/10.1007/s004420000544.
- Schiermeier Q. 2009. Ocean fertilization: dead in the water? Nature, 457(7229): 521, https://doi.org/10.1038/457520b.
- Schippers P, Lürling M, Scheffer M. 2004. Increase of atmospheric CO₂ promotes phytoplankton productivity. *Ecology Letters*, 7(6): 446-451, https://doi.org/10.1111/j. 1461-0248.2004.00597.x.
- Segawa T, Matsuzaki R, Takeuchi N et al. 2018. Bipolar dispersal of red-snow algae. *Nature Communications*, 9(1): 3094, https://doi.org/10.1038/s41467-018-05521-w.
- Seitzinger S P, Kroeze C, Styles R V. 2000. Global distribution of N₂O emissions from aquatic systems: natural emissions and anthropogenic effects. *Chemosphere-Global Change Science*, 2(3-4): 267-279, https://doi.org/ 10.1016/S1465-9972(00)00015-5.
- Smayda T J. 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography*, **42**(5part2): 1137-1153, https://doi.org/10.4319/lo.1997.42.5_part_2.1137.
- Stow C A, Walker J T, Cardoch L et al. 2005. N₂O emissions from streams in the Neuse River watershed, North Carolina. *Environmental Science & Technology*, **39**(18): 6999-7004, https://doi.org/10.1021/es0500355.
- Sun H Y, Lu X X, Yu R H et al. 2021. Eutrophication decreased CO₂ but increased CH₄ emissions from lake: a case study of a shallow Lake Ulansuhai. *Water Research*,

201: 117363, https://doi.org/10.1016/j.watres.2021.117363.

- Suntharalingam P, Sarmiento J L, Toggweiler J R. 2000. Global significance of nitrous-oxide production and transport from oceanic low-oxygen zones: a modeling study. *Global Biogeochemical Cycles*, 14(4): 1353-1370, https://doi.org/10.1029/1999GB900100.
- Tang W Y, Llort J, Weis J et al. 2021. Widespread phytoplankton blooms triggered by 2019-2020 Australian wildfires. *Nature*, **597**(7876): 370-375, https://doi.org/10. 1038/s41586-021-03805-8.
- Tian H Q, Lu C Q, Ciais P et al. 2016. The terrestrial biosphere as a net source of greenhouse gases to the atmosphere. *Nature*, 531(7593): 225-228, https://doi.org/ 10.1038/nature16946.
- van Dam B R, Tobias C, Holbach A et al. 2018. CO₂ limited conditions favor cyanobacteria in a hypereutrophic lake: an empirical and theoretical stable isotope study. *Limnology and Oceanography*, **63**(4): 1643-1659, https:// doi.org/10.1002/lno.10798.
- Verspagen J M H, Van de Waal D B, Finke J F et al. 2014. Contrasting effects of rising CO₂ on primary production and ecological stoichiometry at different nutrient levels. *Ecology Letters*, **17**(8): 951-960, https://doi.org/10.1111/ ele.12298.
- Vidal-Melgosa S, Sichert A, Francis T B et al. 2021. Diatom fucan polysaccharide precipitates carbon during algal blooms. *Nature Communications*, **12**(1): 1150, https:// doi.org/10.1038/s41467-021-21009-6.
- Visser P M, Verspagen J M H, Sandrini G et al. 2016. How rising CO₂ and global warming may stimulate harmful cyanobacterial blooms. *Harmful Algae*, 54: 145-159, https://doi.org/10.1016/j.hal.2015.12.006.
- Wadham J L, Hawkings J R, Tarasov L et al. 2019. Ice sheets matter for the global carbon cycle. *Nature Communications*, 10(1): 3567, https://doi.org/10.1038/s41467-019-11394-4.
- Wang H J, Wang W D, Yin C Q et al. 2006. Littoral zones as the "hotspots" of nitrous oxide (N₂O) emission in a hyper-eutrophic lake in China. *Atmospheric Environment*, 40(28): 5522-5527, https://doi.org/10.1016/j.atmosenv. 2006.05.032.
- Watson A J, Bakker D C E, Ridgwell A J et al. 2000. Effect of iron supply on Southern Ocean CO₂ uptake and implications for glacial atmospheric CO₂. *Nature*, 407(6805): 730-733, https://doi.org/10.1038/35037561.
- Weathers P J. 1984. N₂O evolution by green algae. *Applied* and Environmental Microbiology, **48**(6): 1251-1253, https://doi.org/10.1038/35037561.

Weyhenmeyer G A. 2001. Warmer winters: are planktonic

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algal populations in Sweden's largest lakes affected? *Ambio: A Journal of the Human Environment*, **30**(8): 565-571, https://doi.org/10.1579/0044-7447-30.8.565.

- Whiting G J, Chanton J P. 1993. Primary production control of methane emission from wetlands. *Nature*, **364**(6440): 794-795, https://doi.org/10.1038/364794a0.
- Williamson C J, Cook J, Tedstone A et al. 2020. Algal photophysiology drives darkening and melt of the Greenland Ice Sheet. Proceedings of the National Academy of Sciences of the United States of America, 117(11): 5694-5705, https://doi.org/10.1073/pnas.1918412117.
- Xiao Q T, Xu X F, Zhang M et al. 2019a. Coregulation of nitrous oxide emissions by nitrogen and temperature in China's third largest freshwater lake (Lake Taihu). *Limnology and Oceanography*, 64(3): 1070-1086, https:// doi.org/10.1002/lno.11098.
- Xiao X, Agustí S, Pan Y R et al. 2019b. Warming amplifies the frequency of harmful algal blooms with eutrophication in Chinese coastal waters. *Environmental Science & Technology*, **53**(22): 13031-13041, https://doi.org/10.1021/ acs.est.9b03726.
- Xu H L, Li H, Tang Z Z et al. 2020. Underestimated methane production triggered by phytoplankton succession in river-reservoir systems: evidence from a microcosm study. *Water Research*, **185**: 116233, https://doi.org/10. 1016/j.watres.2020.116233.
- Yan X C, Xu X G, Ji M et al. 2019. Cyanobacteria blooms: a neglected facilitator of CH₄ production in eutrophic lakes. *Science of the Total Environment*, **651**: 466-474, https://doi.org/10.1016/j.scitotenv.2018.09.197.
- Yang H, Xie P, Ni L Y et al. 2011. Underestimation of CH₄ emission from freshwater lakes in China. *Environmental Science & Technology*, **45**(10): 4203-4204, https://doi. org/10.1021/es2010336.
- Zhang C L, Dang H Y, Azam F et al. 2018a. Evolving paradigms in biological carbon cycling in the ocean. *National Science Review*, 5(4): 481-499, https://doi.org/ 10.1093/nsr/nwy074.
- Zhang Y L, Qin B Q, Zhu G W et al. 2018b. Profound changes in the physical environment of Lake Taihu from 25 years of long-term observations: implications for algal bloom outbreaks and aquatic macrophyte loss. *Water Resources Research*, 54(7): 4319-4331, https://doi. org/10.1029/2017WR022401.
- Zhou Y W, Xu X G, Song K et al. 2021. Nonlinear pattern and algal dual-impact in N₂O emission with increasing trophic levels in shallow lakes. *Water Research*, **203**: 117489, https://doi.org/10.1016/j.watres.2021.117489.

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