CURRENT EVIDENCE

Blooms also like it cold

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Scientific Significance Statement

Understanding drivers of cyanobacterial blooms in freshwater lakes has primarily focused on high temperatures, as laboratory experiments have demonstrated a high temperature optimum for growth. However, there is considerable evidence that cyanobacterial blooms also occur in cold water temperatures, including ice-covered conditions. This study documents wide-ranging cold-water cyanobacterial blooms and identifies abiotic and biotic drivers of blooms in cold water temperatures.

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Abstract

Cyanobacterial blooms have substantial direct and indirect negative impacts on freshwater ecosystems including releasing toxins, blocking light needed by other organisms, and depleting oxygen. There is growing concern over the potential for climate change to promote cyanobacterial blooms, as the positive effects of increasing lake surface temperature on cyanobacterial growth are well documented in the literature; however, there is increasing evidence that cyanobacterial blooms are also being initiated and persisting in relatively cold-water temperatures (< 15°C), including ice-covered conditions. In this work, we provide evidence of freshwater cold-water cyanobacterial blooms, review abiotic drivers and physiological adaptations leading to these blooms, offer a typology of these lesser-studied cold-water cyanobacterial blooms, and discuss their occurrence under changing climate conditions.

Globally, freshwater systems are experiencing an increased frequency of phytoplankton bloom events (Carey et al. 2012; Brooks et al. 2017; Ho et al. 2019). Phytoplankton blooms, and in particular cyanobacterial blooms, are of increasing concern due to their potential to produce toxins, nuisance taste and odor metabolites, and affect ecological and public health (Brooks et al. 2016; Chorus and Welker 2021). Although the individual effects of bloom drivers and the importance of individual algal or cyanobacterial traits (sensu Mantzouki et al. 2016) are reasonably well understood, a complete picture of the dynamic interactions among drivers, phytoplankton traits, and the microbial phycosphere is still lacking (Thomas et al. 2017; Cook 2020), which makes appropriate bloom risk assessment and management challenging (Ibelings et al. 2014).

Relatively high surface water temperatures in lakes (20°C and above) have been linked to increased phytoplankton biomass at all spatial scales, including the continental scale (Beaulieu et al. 2013; Ho and Michalak 2020). Thus, the alarm has been raised over the potential proliferation of nuisance and harmful blooms with a warming climate (Paerl and Huisman 2008; Huisman et al. 2018; Woolway et al. 2022). Increasing water temperatures resulting from climate change have received attention because many species of bloom-forming phytoplankton, primarily cyanobacteria, have been experimentally shown to have relatively high temperature optima for growth (> 25°C, Robarts and Zohary 1987; Paerl and Huisman 2008; Lürling et al. 2013). Although "blooms like it hot" (sensu Paerl and Huisman 2008), cyanobacterial blooms can also occur at temperatures substantially lower than current paradigms predict, which we further examine in this study.

There are a growing number of peer-reviewed publications and anecdotal evidence demonstrating that cyanobacterial blooms occur in cold waters. We posit that some blooms might also like it cold (Babanazarova et al. 2013; Bižić-Ionescu et al. 2014) through examination of documented cyanobacterial blooms, physiological traits, and potential abiotic mechanisms leading to cold-water cyanobacterial blooms. We adopt the definition of a freshwater bloom as an accumulation of phytoplankton biomass in the water column or littoral regions, which may lead to strong discoloration of the water, the occurrence of aggregations (scums) on the surface or edge of the lake, or chlorophyll maxima in the metalimnion (Giling et al. 2017; Leach et al. 2018; Reinl et al. 2020; Reinl et al. 2021). We specifically focus on cyanobacteria because of their ability to form harmful algal blooms (HABs) and the current cyanobacteria-temperature paradigm that dictates that cyanobacterial blooms are only observed in warm water temperatures. Furthermore, we define a "cold-water cyanobacterial bloom" as a cyanobacterial bloom that is observed when the water temperature is < 15°C, well below typical growth optima for cyanobacteria (> 25°C, Paerl and Huisman 2008; Lürling et al. 2013). Here, we summarize observations of cyanobacterial blooms occurring at cooler temperatures (< 15°C) in freshwater lakes, review underlying physiological and ecological mechanisms, offer a typology of these lesser-studied cold-water cyanobacterial blooms, and discuss their future under changing climate conditions.

Observations of cold-water cyanobacterial blooms

We identified 37 cold-water cyanobacterial blooms from various sources (Fig. 1; Table 1). Of these, 23 were documented in peer-reviewed publications, and the remaining observations were reported in news outlets, reports, unpublished data, or from personal observations. The surface water conditions at the time of observation ranged from ice-covered to 15°C, with 19 blooms occurring during ice-covered conditions. The observations were widespread but concentrated in Europe and the United States, which is likely an artifact of sampling/reporting bias rather than an important geographical factor. Cyanobacterial blooms presented here occur in lakes spanning the full spectrum of trophic states (based on Carlson TSI; Carlson 1977), with the majority being eutrophic (13), followed by mesotrophic (9), oligotrophic (7), and hypereutrophic (5).

Documented cold-water cyanobacterial blooms encompassed many of the common taxonomic groups described in blooms associated with warmer temperatures. Members of Nostocales were the most common taxa, followed by Chroococcales, Oscillatoriales, and a single occurrence each of Synechococcales and Pseudanabaenales (Izaguirre et al. 2001; Babanazarova et al. 2013; Ma et al. 2016; Wejnerowski et al. 2018; Fuentes et al. 2021). Specifically, *Dolichospermum* (formerly *Anabaena*)
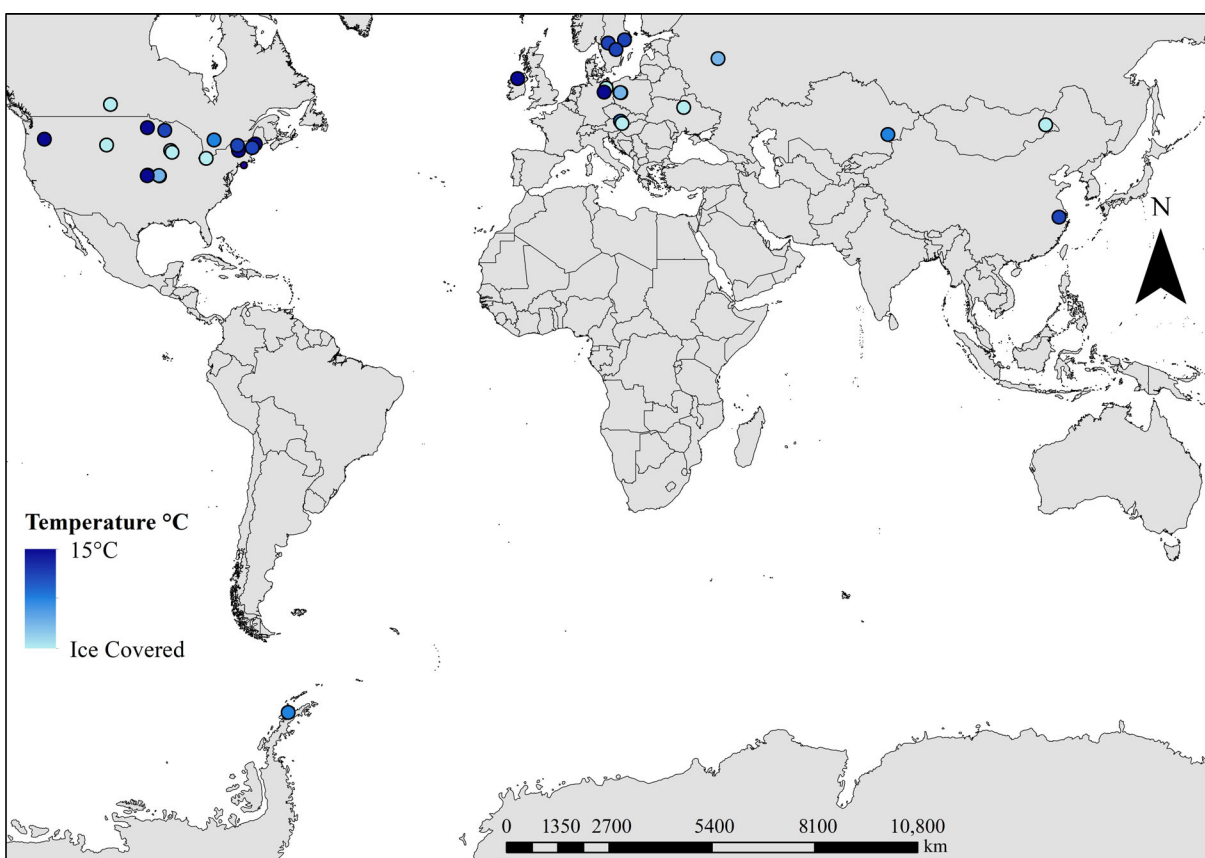
Fig. 1. Locations of cyanobacterial blooms occurring in water temperatures < 15°C (range: 0–15°C). Cold-water cyanobacterial blooms were observed beneath ice cover in 19 of 37 observations.

and *Aphanizomenon*, both in Nostocales, were the most commonly documented taxa, demonstrating that taxa that often bloom in warm waters can also bloom in cold-water conditions. Other notable bloom-forming cyanobacterial taxa—such as *Microcystis*, *Planktothrix*, and *Limnothrix*—were likewise observed in cold waters (Mankiewicz-Boczek et al. 2011; Babanazarova et al. 2013; Bižić-Ionescu et al. 2014; Persaud et al. 2015).

We also found ample anecdotal evidence through citizen science programs in the United States such as the Bloomwatch App (2016) and the Cyanoscope programs (2016) for reporting cold-water cyanobacterial blooms. The Bloomwatch App was developed by the U.S. Environmental Protection Agency (EPA) and allows users to report cyanobacterial blooms including the location, extent, and weather conditions. We searched reports in the Bloomwatch App for blooms reported from the months of November through April in states above the 40°N latitude line, as the average air temperature during this period is typically below 15°C, and found three blooms had been reported. The Cyanoscope program is also directed by the U.S. EPA and utilizes crowdsourcing and microscope kits to track cyanobacterial blooms. Using the same criteria as

above, we found an additional 50 observations of verified cyanobacterial blooms during those months.

Although this picture of cold-water cyanobacterial blooms is necessarily incomplete, it illustrates that cyanobacterial blooms do indeed occur in cold-water conditions. Furthermore, these blooms can occur in a wide range of lake types and be dominated by a variety of species. The observations are likely a small sample of the true number of cold-water cyanobacterial bloom occurrences but provide compelling evidence that there is a gap in our knowledge regarding cyanobacterial bloom ecology.

Adaptations favoring cold-water cyanobacterial blooms

Psychrotolerant vs. psychrophilic

Although cyanobacterial blooms are typically associated with warm waters, many species of cyanobacteria fall within the various definitions of psychrotolerant and psychrophilic, with most cyanobacteria being at least psychrotolerant. Psychrophilic organisms tend to prefer cold water and have lower temperature optima, whereas psychrotolerant organisms have higher temperature optima, but can tolerate cold temperatures

Table 1. Documentation of cold-water cyanobacterial blooms described in this study. Lake information included Latitude (Lat) and Longitude (Lon) as decimal degrees, lake depth (mean, max, no data indicated by a dash), trophic state (determined by Carlson's Trophic State Index; Carlson, 1977), whether ice was present at the time of bloom observation, temperature when bloom was observed, the depth of the bloom, and a reference for the event. DCL is deep chlorophyll layer.

Lake name	Lat, Lon	Lake depth m (mean, max)	Trophic state	Ice (Y/N)	Temp (°C)	Species	Bloom depth	References
Alte Donau	48.24, 16.43	2.3, 6.8	Mesotrophic to Eutrophic	N	< 5	*Raphidiopsis raciborskii*	Surface	Dokulil et al. (2014)
Bethel Lake	38.9, −92.34	1.8, 4.2	Eutrophic	N	11.6	*Dolichospermum affinis*	Shoreline sample	Kinzinger (2021)
Brandy Lake	46.11, 79.52	3.5, 7.5	Eutrophic	Y	<15 C	*Aphanizomenon* spp. and *Dolichospermum* spp.	Surface	Persaud et al. (2015)
Cross Reservoir	39.05, −95.18	4.5, 12.35	Mesotrophic	N	Did not measure, but < 15 (snowed days leading up to turnover)	*Aphanizomenon* sp.	DCL to surface at turnover	T. Harris pers. observ. of fall overturn bloom
Dairy Farm Lake	38.99, −92.49	2.2, 4.6	Hypereutrophic	N	1.6	Unknown	Isothermal-phycocyanin peak from YSI at bottom of water column	Cianci-Gaskill (2021)
Devil's Lake	43.42, −89.73	9.3, 14.3	Oligotrophic to mesotrophic	Y	<5, ice present near shores	*Dolichospermum circinalis* and *Aphanizomenon flos-aquae*	Surface	https://blog.limnology.wisc.edu/2020/12/16/algae-blooms-arent-just-for-summer/; Fig. 2D
Fernan Lake	47.67, 116.75	4, 8	Eutrophic	Y	Under ice	*Microcystis* spp., *Dolichospermum* spp., *Gloeotrichia* spp.	Ice layer	Unpublished data from Sarah Burnet/Frank Wilhelm/IDEQ
Former Ukraine peat quarry	50.35, 31.34	7, 13.5	Hyper-eutrophic	Y	Under Ice	*Aphanizomenon gracile*	Surface	Shcherbak et al. (2019)
Keyhole Reservoir	44.36, −104.85	−, 21.3	Eutrophic	Y	Under ice	Cyanobacteria	Surface	http://www.buffalobulletin.com/news/article_85fd34c8-8c15-11eb-a486-fb4fe5f313c4.html
Lake Bytynskie	52.51, 16.51	3.5, 7.0	Eutrophic	Y	3	*Planktothrix agardhii*	Surface	Mankiewicz-Boczek et al. (2011)
Lake Erie	42.07, −81.34	18.89, 64	Eutrophic	Y	Under/within ice	*Synechococcus* sp.	Surface	Twiss et al. (2012)

(Continues)

Table 1. Continued

Lake name	Lat, Lon	Lake depth m (mean, max)	Trophic state	Ice (Y/N)	Temp (°C)	Species	Bloom depth	References
Lake George	43.43, −73.71	19.2, 57	Oligotrophic	N	12–18, fluctuated due to turnover in progress	*Dolichospermum fuscum*	Surface	https://www.timesunion.com/news/article/Lake-George-tainted-by-harmful-algal-blooms-15767240.php https://www.lakegeorgemirror.com/lake-georges-harmful-algal-blooms-non-toxic-but-alarming-nonetheless/
Lake Itasca	47.22, −95.2	5.27, 12.2	Mesotrophic	N	12.7	*Dolichospermum* spp.	Surface	L. Knoll pers. observ.
Lake Lubosińskie	52.53, 16.38	2.2, −	Eutrophic	Y	3	*Planktothrix agardhii*, *Limnothrix redekei*, and *Aphanizomenon gracile*	Surface	Wejnerowski et al. (2018), Ptak et al. (2021)
Lake Lubosińskie	52.53, 16.38	2.6, 3.7	Eutrophic	Y	3	*Planktothrix agardhii*	Surface	Mankiewicz-Boczek et al. (2011)
Lake Mendota	43.11, −89.42	13, 25	Eutrophic	Y	Under Ice	*Aphanizomenon* sp.	Surface	R. Lathrop pers. observ. of bloom that lasted from Fall 1989 to Spring 1990
Lake Nero	57.16, 39.44	1.6, 4.7	Hyper-eutrophic	Y	1.7	*Limnothrix*, *Pseudanabaena*, and *Planktothrix*	Surface/bottom	Babanazarova and Lyashenko (2007) and Babanazarova et al. (2013)
Lake Rupanco	40.83, −72.43	−, 274	Oligotrophic	N	5–8	*Microcystis aeruginosa*	30 m	Fuentes et al. (2021)
Lake Stechlin	53.17, 13.03	23, 70	Oligotrophic	N	< 15	*Dolichospermum* (primary), *Aphanizomenon*, and *Planktothrix*	Surface	Kasprzak et al. (2017)
Lake Stechlin	53.17, 13.03	23, 70	Mesotrophic	Y	−5 to 5	*Planktothrix rubescens*	Surface, mixed water layer	FRED and internal database, personal observation photos; Berger et al. (2021)
Lake Stechlin	53.17, 13.03	23, 70	Oligotrophic	Y	0–10	*Ap. flos-aquae*	DCL brought to surface	Üveges et al. (2012), Bižić-Ionescu et al. (2014)

(Continues)

Table 1. Continued

Lake name	Lat, Lon	Lake depth m (mean, max)	Trophic state	Ice (Y/N)	Temp (°C)	Species	Bloom depth	References
Lake Taihu	30.93, 119.88	1.9, 2.6	Eutrophic	Y	<10	Microcystis spp.	Surface	Ma et al. (2016)
Lake Tiefer See	52.59, 12.53	–, 62	Oligotrophic to mesotrophic	N	<15	Cyanobacteria	DCL	Nwosu et al. (2021)
Lough Neagh	54.49, −7.85	8.9, 34	Hypereutrophic	N	<15	Planktothrix agardhii and Pseudanabaena spp.	Surface, mixed water layer	Elliott et al. (2016)
Mälaren	59.47, 17.37	13, 63	Eutrophic	N	<10	Aphanizomenon sp.	Surface	Weyhenmeyer (2001)
Mirror Lake	44.29, −73.98	4.2, 18	Oligotrophic	Y	8.5	Cyanobacteria	Surface	https://www.adkwatershed.org/press-releases/hab-mirror-lake-2020
Neusiedler see	47.87, 16.77	1.2, 1.8	Eutrophic	Y	Under ice	Aphanocapsa incerta, Oscillatoria, and Dolichospermum	Surface	Dokulil et al. (2014)
Otero lake	−64.15, −61.97	–, 3.2	Eutrophic	Y	1.1–6.7	Synechococcus sp.	Surface	Izaguirre et al. (2001)
Pasqua Lake	50.79, −103.96	–, 16	Hypereutrophic	Y	Under ice	Aphanizomenon sp.	Ice layer	Haig et al. (2022)
Salmon Lake	44.53, −69.77	7, 17	Mesotrophic	N	<15	Aphanizomenon sp.	Surface	D. Wain pers. observ. in Nov 2020; Fig. 2E
Siskiwit Lake	46.8, −91.13	1, 4	Mesotrophic	N	During bloom, air temp. was 5.5°C. Water temp. was not measured, but field notes indicate it was estimated at 10–12°C	Dolichospermum spp.	Surface	https://dnr.wi.gov/lakes/clmn/reports/tsigraph.aspx?stationid=043089
Thomas Pond	43.92, −70.5	6.7, 19.5	Mesotrophic	N	<10	Dolichospermum sp. (lemmermannii?)	Surface	B. Peierls pers. observ.
Three Mile Lake	45.19, −79.47	3.4, 12	Mesotrophic	Y	<15 C	Aphanizomenon spp. and Dolichospermum spp.	Surface	Persaud et al. (2015)
Vättern	58.30, 15.38	40, 128	Oligotrophic	N	<10	Aphanizomenon sp.	Surface	Weyhenmeyer (2001)
Vänern	59.09, 13.5	27, 106	Oligotrophic to mesotrophic	N	<10	Aphanizomenon sp.	Surface	Weyhenmeyer (2001)

(Continues)

Table 1. Continued

Lake name	Lat, Lon	Lake depth m (mean, max)	Trophic state	Ice (Y/N)	Temp (°C)	Species	Bloom depth	References
West Campus Pond	38.94, −95.26	−, 4	Mesotrophic	N	<15	*Dolichospermum* sp. and *Microcystis* sp.	Surface	T. Harris pers. observ. in Nov 2018; Fig. 2C
Willow Creek Reservoir	45.34, −119.54	12, 26	Eutrophic	N	<15	*Microcystis* spp., *Aphanizomenon* spp., and *Dolichospermum* spp.	< 6 m	Unpublished data from Sarah Burnet/Frank Wilhelm/USACE

(Quesada and Vincent 2012). Psychrophilic bacteria have temperature optima of < 15°C and can grow in temperatures up to 20°C. Psychrotolerant bacteria have a temperature optima of > 15°C with maximum growth temperatures of up to 40°C (Baross and Morita 1978; Nadeau and Castenholz 2000), as has been documented in many experimental studies of cyanobacteria (Robarts and Zohary 1987; Paerl and Huisman 2008). An important nuance, however, is that the optimal growth temperature for cyanobacteria is typically cited as a single value and few studies include temperature treatments < 15°C, run experiments long enough to allow significant growth under these conditions, or examine in situ growth responses at < 15°C. Even for taxa with an optimal temperature > 15°C, rapid growth leading to bloom formation can still occur at temperatures below that optimum due to the exponential relationship between growth rate and temperature. For example, cyanobacterial growth rate is reduced at lower temperatures, but the exponential change in growth response as a function of temperature means that even a small increase in temperature, well below the experimental optima, can result in substantial gains in growth. These are important distinctions for interpreting experimentally-derived temperature optima for growth, and for differentiating between an organism's fundamental and realized niches.

Taxa commonly used in laboratory experiments were also often isolated from strains that were collected during the spring or summer (Lürling et al. 2013), and these strains are likely adapted to warmer temperatures as opposed to strains present in fall, winter, and early spring, when temperatures are cooler. Zapomělová et al. (2010) evaluated the response of growth and morphology of different strains of *Anabaena* species to changes in temperatures and found considerable differences in temperature optima for two strains of *Anabaena lemmermannii*, ranging between 18.5°C and 25.5°C for one strain, and 13.5°C and 18.5°C for the other. Similarly, ranges of 19.5–25.5°C and 25.0–29.0°C were observed for two strains of *Anabaena flos-aquae*, 16.0–21.0°C and 18.5–23.5°C for two strains of *Anabaena mendotae*, and 17.5–22.5°C and 22.0–28.0°C for *Anabaena cirinalis*. Thus, some species that would be classified as being psychrotolerant may even include strains that are psychrophilic.

Adaptations of cyanobacteria supporting cold-water blooms

Low water temperatures can lead to stiffening of membranes, slowing of physiological processes, and at very cold temperatures, ice crystal formation. Cyanobacteria adaptations to cold conditions include the development of more fluid biological membranes through the accumulation of polyunsaturated fatty acids acyl chains, evolution of cold shock and antifreeze proteins, and modulation of the kinetics of key enzymes (Chintalapati et al. 2004; Morgan-Kiss et al. 2006). Other freshwater cyanobacteria are also able to produce unsaturated fatty acids via acyl-lipid desaturases in response to cold
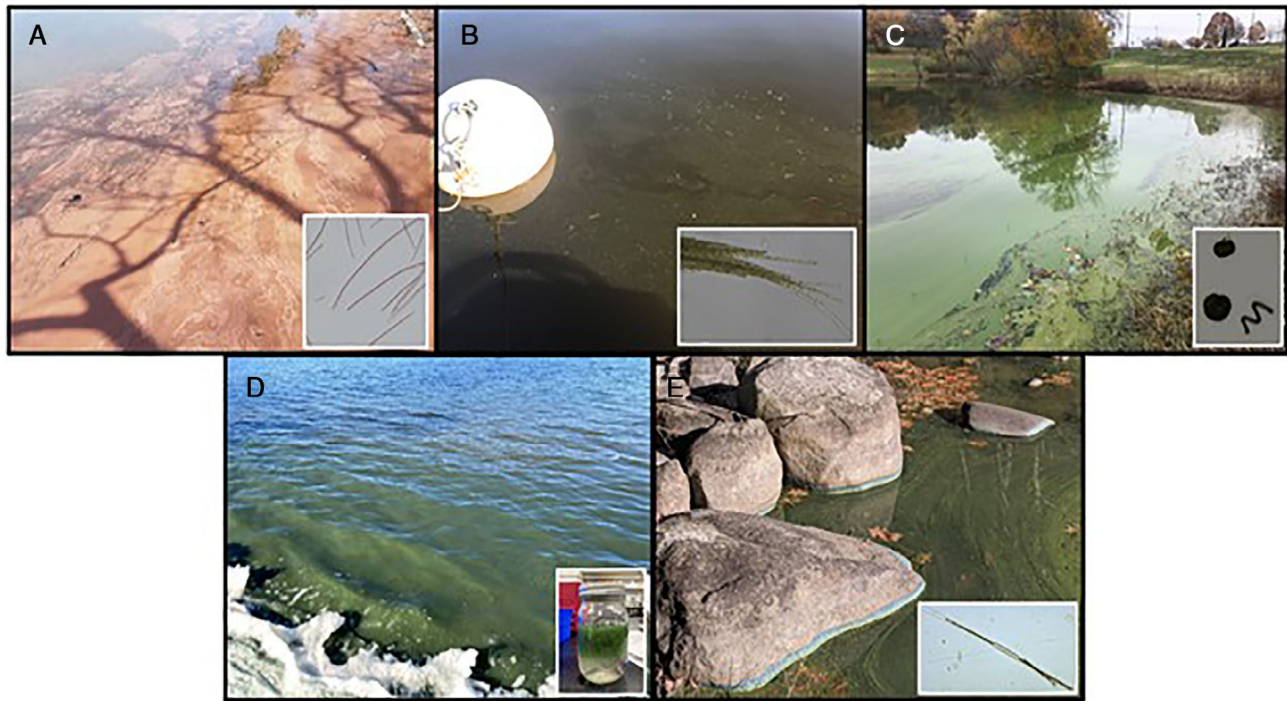
Fig. 2. Photos of cold-water cyanobacterial surface scums including: (**A**) *Planktothrix rubescens* on the 11th of April 2020 in Lake Stechlin (Photo Credit: HPG, Doris Ilicic); (**B**) *Aphanizomenon* sp. on the 31st of October 2018 in Cross Reservoir, Kansas, USA (Photo Credit: TDH); (**C**) *Dolichospermum* sp. and *Microcystis* sp. on the1st of November 2018 in West Campus Lake, Kansas, USA (Photo Credit: TDH); (**D**) *Dolichospermum circinalis* and *Aphanizomenon flos-aquae* on the 1st of December 2020 in Devil's Lake, Wisconsin (Photo Credit: Richard Lathrop); and (**E**) *Aphanizomenon* sp. On the 9th of November 2020 in Salmon Lake, Maine (Photo Credit: DJW).

temperatures (Murata and Wada 1995). In addition to these survival mechanisms under cold water temperature conditions, some taxa of cyanobacteria harbor strains with a wide range of optimal temperatures, allowing for rapid reproduction at relatively low temperatures. In one study, high plasticity in photosynthetic rate as a function of temperature was been observed for *Aphanizomenon flos-aquae* depending on light conditions (Üveges et al. 2012). The maximum photosynthetic rate of a winter population of *Ap. flos-aquae* was positively related to temperatures between 2°C and 30°C, but at the lowest experimental irradiance levels, 7.5 and 30 μmol m^{-2} s^{-1} PAR, the photosynthetic rate was lower at high temperatures (≥ 20°C) compared to low temperatures (≤ 10°C), demonstrating that at low irradiance, photosynthetic activity can be inversely correlated with temperature. Thus, cold water temperatures can be more favorable under low-light conditions, which often occur during winter. Other cyanobacteria such as *Limnothrix redekei* and *Pseudanabaena limnetica* may also actively grow at relatively low temperatures when light or nutrient conditions are favorable (Babanazarova et al. 2013). In Chaohu Lake, located in eastern China, *Dolichospermum flos-aquae* blooms have been observed in 2.5–3.9°C surface water temperatures in January; however, up to 25% of the cells were akinetes, indicating the bloom was senescing at this time (Xiao et al. 2015). This plasticity has also been observed

for *Raphidiopsis raciborskii* (formerly *Cylindrospermopsis* sp., Chonudomkul et al. 2004; Dokulil 2016). Dokulil and Teubner (2000) also showed that many cyanobacteria have a wide range of temperature optima from near 0°C to approximately 25°C, and that *Planktothrix rubescens* and *Planktothrix agardhii*, in particular, prefer cold water temperatures. Indeed, Anneville et al. (2015) indicated that heat waves during summer time inhibit rather than promote blooms of this species. As noted in the section above, cyanobacteria can also grow at suboptimal temperatures and in cases where temperatures are low (< 15°C), relatively slow growth can lead to an accumulation and aggregation of biomass over time, resulting in cold-water cyanobacterial blooms.

The onset of cold-water cyanobacterial blooms can also be triggered by benthic recruitment from resting stages (i.e., low metabolic vegetative cells or life stages such as akinetes) that settle on the sediment surface (Hansson 1996; Carey et al. 2014; Urrutia-Cordero et al. 2020). The recruitment of dormant cyanobacterial cells from sediment is often positively correlated with temperature for many cyanobacterial taxa (Cottingham et al. 2021); however, during a laboratory study, akinete germination was most active at 5°C and 10°C (Kim et al. 2005). Once germination occurs, slow growth can continue through spring while temperatures are cool, allowing for the accumulation and aggregation of biomass, and potentially

resulting in late spring or early summer blooms that may persist as temperatures rise into summer. Although the lowest possible temperatures under which cyanobacteria are recruited from sediment remains uncertain, it likely varies with differences in genetic plasticity among strains and lake-specific characteristics, such as morphometry, water chemistry, and biological communities. For instance, certain strains of benthic bacteria facilitate the recruitment of *Microcystis aeruginosa* cells at temperatures lower than their normal threshold by altering physiochemical conditions at the sediment–water interface (Zou et al. 2018; Cai et al. 2021). Recruitment from resting stages may play an important role in initiating cold-water cyanobacterial blooms, but a holistic understanding of their role in bloom initiation is yet to be elucidated.

Light is often a limiting factor for phytoplankton growth during winter months when the photoperiod is shorter. The absence or presence of ice cover can strongly affect the light quantity and quality, depending on ice characteristics (Lundberg et al. 2007; Cavaliere et al. 2021; Weyhenmeyer et al. 2022). There are many taxon-specific traits that enable survival/growth during low-light conditions including shifts from a photochemically active state to a heterotrophic state adapted to low light (i.e., mixotrophy, e.g., *Spirulina*; Vonshak et al. 2000), optimizing light absorption efficiency and photosynthetic capacity via pigment packing and increased chlorophyll *a* (Chl *a*) content (Hawes and Schwarz 2001; Palmer et al. 2013; Lewis et al. 2019), and shifting light absorption toward the blue-green spectrum under ice (Rochet et al. 1986). Several occurrences of non-nitrogen-fixing cyanobacteria including *Pseudanabaena limnetica*, *Planktolyngbya limnetica*, *Limnothrix* spp., *L. redekei*, *Planktothrix agardhii*, and N_2-fixing species including *Aphanizomenon gracile* and *Cuspidothrix issatschenkoi* were observed in Lake Warnolty in Poland throughout the period March 2016–February 2017 (Napiórkowska-Krzebietke et al. 2021). These filamentous, shade-adapted cyanobacteria were highly abundant even during ice-covered periods, due to their ability to adapt to low-light conditions and low temperatures (Reynolds et al. 2002; Padisák et al. 2009). By surviving extended periods of reduced light, these taxa have a competitive advantage when light returns. Although ice cover can often lead to substantial light limitation, in some cases it can result in inverse stratification, creating a surface layer where irradiance is higher compared to average values in a fully mixed layer (Cavaliere et al. 2021).

Ice cover can also offer water column stability which favors phytoplankton taxa that can maintain buoyancy, allowing them to adjust their vertical and horizontal position throughout the water column according to their needs (e.g., more light directly below the ice, but more nutrients and inorganic carbon further down). For example, *Ap. flos-aquae* (Bižić-Ionescu et al. 2014) or *Planktothrix rubescens* (Berger et al. 2021; Knapp et al. 2021) can actively grow during winter periods when lake mixing is reduced. However, under high-light conditions and lower temperatures buoyancy can be reduced (Kromkamp 1987). In some cases, heat fluxes from the sediments or increased solar radiation in spring can also promote convective mixing under ice (Bouffard et al. 2019), resulting in conditions that favor cyanobacteria due to the redistribution of nutrients in the water column but also constrain cyanobacteria due to reduced water column stability (Posch et al. 2012). Other adaptations to limited lake mixing include attachment to ice sheets and surface slush and association with ice air pockets. For example, in Lake Erie, dense concentrations of viable cyanobacteria (similar to summer levels) were found within the ice sheet (Twiss et al. 2012). Thus, the presence of ice can provide an array of support for cyanobacterial blooms in cold-water conditions, but these benefits are potentially limited by cyanobacterial physiology and under-ice mixing.

Types of cold-water cyanobacterial blooms: modes of development

Based on our collected observations and current knowledge of bloom-forming processes and winter limnology, we propose three bloom types based on how cold-water cyanobacterial blooms are formed: (1) surface blooms that were initiated and persisted in cold-water temperature conditions; (2) metalimnetic cyanobacterial blooms (i.e., deep chlorophyll layers [DCLs]), which in some cases, are brought up to the surface through physical processes such as mixing caused by internal seiches, lake overturn, and upwelling; and (3) blooms that were initiated in warm water conditions and persisted in cold water temperatures (Fig. 3). These three types of blooms can occur in isolation, sequentially, or simultaneously, and can persist for extensive periods of time.

Surface cyanobacterial blooms initiated in cold water temperatures

Cold-water cyanobacterial blooms occur in a wide range of light, temperature, and nutrient conditions. These blooms are formed through a number of physiological adaptations including adaptations to low temperature, and in some cases, to low light, nutrients, and/or limited mixing conditions, particularly when lakes are covered by ice. Cold-water cyanobacterial blooms are also developed through the slow accumulation of biomass under suboptimal growth conditions. Physical drivers, like upwelling and mixing events, may also promote blooms that are initiated when water temperatures are cold by providing hypolimnetic nutrients. Several taxa, such as *Planktothrix*, *Dolichospermum*, and even *Microcystis*, respond to lake mixing events that supply nutrients from the hypolimnion across the water column (Head et al. 1999; Bormans et al. 2016). These hypolimnion-derived nutrients may then support late fall/early winter cyanobacterial blooms. For example, late fall blooms of *Microcystis* sp. were observed after fall turnover in November 2021 in Lake Champlain and Lake Carmi, Vermont and also in West Campus Pond, Kansas, USA (A.A. Morales-Williams and T.D. Harris, unpubl. Fig. 2C). In Lake Zurich, *Planktothrix*
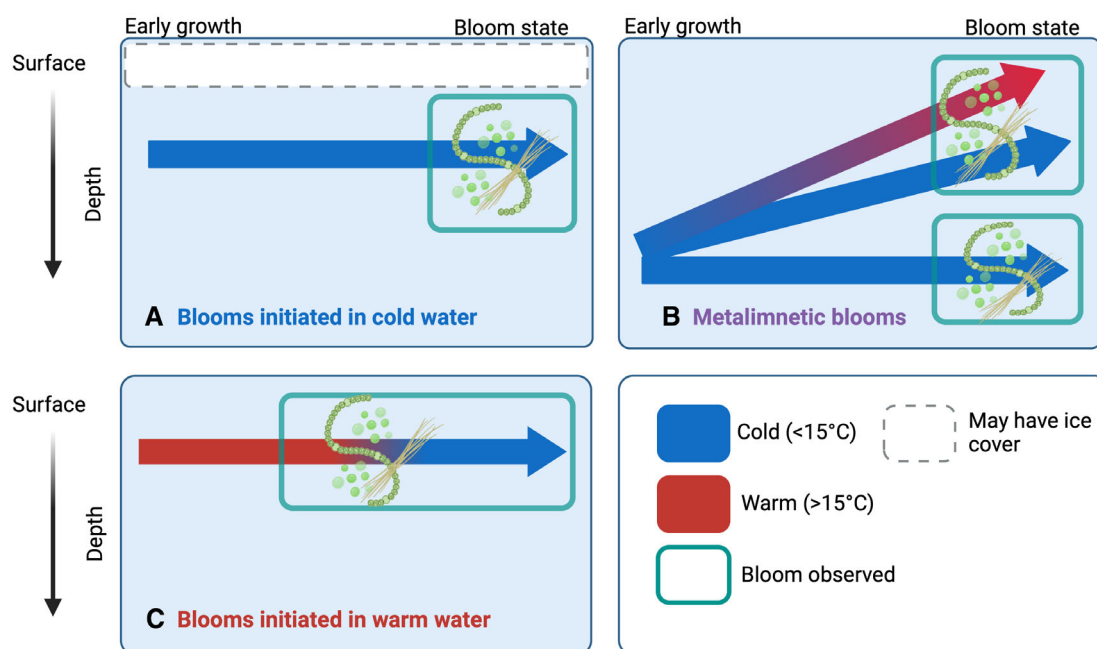
Fig. 3. Concept diagram showing the three bloom types: (**A**) blooms initiated in cold water, (**B**) metalimnetic blooms, and (**C**) blooms initiated in warmer temperatures that persist in cold temperatures. Figure made with Biorender.com.

Box 1. Surface cyanobacterial blooms initiated in cold water temperatures case study.

A case study for an intensive under-ice bloom is well described for Lake Stechlin (Bižić-Ionescu et al. 2014). An extremely dense bloom of *Aphanizomenon flos-aquae* occurred in winter 2009–2010 after ice formation in December. The bloom was initiated by increased nutrient availability from overturn in late fall. Initial ice formation was clear through the following February and approximately 30 cm thick. Inverse stratification was observed during the bloom as well. The bloom developed under the ice until it became light limited due to snow coverage, exerting a pronounced physiological stress on the cyanobacterial bloom. The breakdown of this bloom fueled a fivefold increase in bacterial production compared with spring peak production the year prior. Evaluation of the bloom morphometry showed the presence of polyphosphate granules and a lack of heterocysts. The authors of the study note that heterocysts are typical of this species in summer blooms.

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rubescens blooms can persist throughout the year when lake conditions such as lake mixing permit (Knapp et al. 2021). This phenomenon has also been observed in other temperate, usually ice-covered lakes such as Lake Stechlin during warm winters (Berger et al. 2021). In the subsequent spring mixing period, cyanobacterial cells are mixed throughout the entire water column and following full mixing events, buoyant cells can rise to the surface and be transported downwind, causing surface accumulations at the shoreline (Fig. 2A, Lake Stechlin; Box 1).

Cold-water cyanobacterial blooms originating from the metalimnion

Cyanobacterial blooms can exist as metalimnetic blooms or DCLs, which in some cases can directly emerge from deep, relatively cool waters into the lake surface due to strong physical dynamics (e.g., turnover, mixing, upwelling, seiche). This emergence typically occurs during the late fall and early spring seasons when mixing events are more common, or during intense storm events (Fig. 2A). For example, Micheletti et al. (1998) showed that a DCL comprised of *Pl. rubescens* was mixed throughout the water column of Lake Zurich during lake overturn; however, the highest biomass of *Pl. rubescens* after overturn was at the surface. Others have also observed cyanobacterial DCLs surfacing after lake overturn (Dokulil and Teubner 2012), even in relatively small glacial lakes and reservoirs (Pannard et al. 2020; Fig. 2B). Cyanobacteria-dominated DCLs can surface in summer due to windy, relatively cold weather, which can cause lake surface mixed layers to cool and deepen, and in turn translocate DCLs just below the thermocline into surface waters (Kasprzak et al. 2017). Metalimnetic blooms are often overlooked in cyanobacterial bloom reporting, likely because people do not

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Box 2. Cold-water cyanobacterial blooms originating from the metalimnion case study.

Kasprzak et al. (2017) documented a bloom during an exceptional storm passing over northern Germany where air temperatures were reduced from 19°C to 14°C in July 2011, cooling down the lake surface mixed layer by > 2°C and deepening it by approximately 2 m. Thermocline deepening by the storm translocated a cold-adapted cyanobacteria-dominated DCL, located below the thermocline in temperatures ranging from 12°C to 14°C. The bloom was dominated by *Dolichospermum* spp., with *Aphanizomenon flos-aquae* and *Planktothrix agardhii* in lower abundances. The bloom spanned from approximately 9 m depth into the surface mixed layer, thereby physically mixing the DCL into the surface mixed layer, and in turn inducing an unprecedented state change from clearwater to turbid conditions that lasted for several weeks.

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come in direct contact with them, but their position in the water columns does not diminish their relevance for ecological and/or public health. For example, drinking water intakes are often positioned well below the surface of lakes, and could be susceptible to withdrawing drinking water containing potentially toxic cyanobacteria (Albay et al. 2003). Furthermore, as noted above, in some instances these metalimnetic blooms can be brought to the surface, increasing the likelihood that humans and wildlife will come into contact with these blooms (Box 2).

Blooms that were initiated in warmer water temperatures

In some cases, blooms observed during cooler water temperatures (< 15°C) begin when water temperatures are warmer and can be considered a consequence of remnant or carryover effects. These blooms may be dependent on a variety of biological or physicochemical conditions (e.g., high phytoplankton standing biomass, fall turnover and internal nutrient loading, transient warm water temperatures, wind-driven mixing, light availability, or reduced grazing pressure on phytoplankton communities) that set the stage for elevated phytoplankton biomass when water temperatures fall at or below 15°C. For example, late summer blooms may persist into the fall and/or winter or as temperatures increase into spring. In Lake Taihu (China), winter blooms of a cold-tolerant strain of *Microcystis* were largely attributed to remnant fall blooms that formed when temperatures were warmer rather than arising after temperatures became cold (Ma et al. 2016). Observations of blue-stained water and blue-stained littoral ice in a eutrophic prairie lake in Canada were the result of a late fall surface bloom of *A. flos-aquae* that was trapped in the ice (Haig

et al. 2022). Although these blooms were not initiated in cold temperatures, their endurance in cold water temperatures is important in understanding how blooms form, persist, senesce, and their role in winter limnology. Furthermore, these types of blooms present a unique management challenge, as it was previously assumed that these blooms die-off and dissipate when temperatures become cold (Box 3).

Other factors contributing to cold-water cyanobacterial blooms

Loss process that support cold-water cyanobacterial blooms

Cyanobacterial blooms form when reproductive rates of bloom-forming species override their mortality rates caused by different loss processes (Oliver et al. 2012). Experimental evidence suggests that many bloom-forming cyanobacteria species may be psychrotolerant, thus bloom formation and/or persistence may still occur if loss processes are lower than reproductive rates at cold temperatures. Several important loss processes show strong temperature dependencies and should thereby be further explored as potential drivers of cold-water cyanobacterial blooms. For example, fundamental metabolic processes such as photosynthesis and respiration increase at different rates with temperature, with respiration showing much greater sensitivity than photosynthesis (Brown et al. 2004). This stronger sensitivity of respiration means that while lower water temperatures lead to lower photosynthesis and respiration, the balance between photosynthesis and respiration results in overall positive, albeit relatively slow, net growth.

Box 3. Blooms that were initiated in warmer water temperatures case study.

Haig et al. (2022) serve as a case study for blooms initiated in warm water that persist into cold temperatures. Shoreline blooms of *Aphanizomenon flos-aquae* were observed in October 2020 in Pasqua Lake, Canada and were subsequently frozen within littoral ice during late fall-early winter. In March 2021, local residents reported intensive blue staining of the ice, sourced from the cyanobacterial pigment phycocyanin, indicating that the *Ap. flos-aquae* bloom from fall 2020 was still within the ice. The blue stain in the ice lasted 4 weeks. Although the microcystin concentrations were relatively low ($\sim 0.2 \ \mu g \ L^{-1}$), the blue ice staining served as an ecological surprise to local residents and researchers alike, and clearly shows that blooms that form in relatively warm waters, and their metabolites, can become trapped within or under-ice and persist for months.

Cyanobacteria have been shown to be successful at minimizing losses from zooplankton grazing compared to other eukaryotic taxa (Ger et al. 2016), and zooplankton grazing rates are positively correlated with temperature, meaning that as temperatures decrease, so does zooplankton grazing (Peters and Downing 1984; Pulsifer and Laws 2021). Furthermore, zooplankton communities at low temperatures are often dominated by selective-feeding copepods (Ekvall et al. 2015; Hrycik and Stockwell 2021), partly because of their ability to withstand temporary shortages in food availability with lipid stores (Grosbois and Rautio 2018). Hence, the dominance of selective vs. generalist feeding modes among cold-adapted zooplankton populations could be an additional factor further reducing grazing pressure on cold-water cyanobacterial blooms due to greater zooplankton preference for more accessible and quality food (Ger et al. 2016). It is important to note that although selective feeders can also graze on cyanobacteria, especially when other food sources become scarce, the grazing selection of cyanobacteria will be influenced by cyanobacterial traits expressed at the population and even subpopulation level (Ger et al. 2016). For example, selective feeding copepods generally select non-toxic over toxic cyanobacterial stains, and this selection interacts with other cyanobacterial traits such as their size range (Rangel et al. 2020). Cyanobacteria can also display considerable variability in C : N : P ratios depending on fluctuations in light and nutrient availability (Geider and La Roche 2002; Bertilsson et al. 2003). This variability in biochemical composition of cyanobacteria can have strong effects on zooplankton consumers, and consequently on their grazing losses, though it is an aspect which remains relatively unexplored (Ger et al. 2016).

Loss of biomass due to infections is also reduced at low temperatures. Recent studies have shown that chytrid parasites can exert strong top-down control on specific bloom-forming cyanobacteria populations (Frenken et al. 2017), and that abiotic factors, such as temperature, can be strong modulators of chytrid disease outcomes (Gsell et al. 2013; Rohrlack et al. 2015). For example, Agha et al. (2018) showed in a cyanobacteria-chytrid experimental system that chytrid parasites do not cause infections at 8°C, and that cyanobacteria can thereby find refuge from infection at low temperatures. These findings are supported by observations from a Norwegian lake where *Planktothrix* populations could develop free of chytrid infections within similar cold refuges, which in turn resulted in sporadic blooms even under ice (Rohrlack et al. 2015). In contrast, Gsell et al. (2022) recently analyzed 12 years of lake monitoring data and found that chytrid infections on phytoplankton taxa can occur all year around, but cyanobacteria were one of the least affected phytoplankton groups. These results indicate that cyanobacterial loss processes from certain parasitic infections may be relieved by low temperatures, thus supporting growth in cold-water conditions.

There is also evidence that cold temperatures can limit mortality rates caused by viral infections, suggesting that cold-water blooms may suffer low mortality losses caused by viral infections. In a recent review on cyanophage–host relationships, Grasso et al. (2022) comprehensively summarized main mechanisms by which increasing temperature may modulate such infections, including increased cyanophage–host contact rate due to decreased water viscosity (Murry and Jackson 1992; Cheng et al. 2017), as well as increased phage reproductive output from infected hosts (Chu et al. 2011). Hence, there seems to be an emerging relationship between elevated water temperature and cyanophage infectivity based on both experimental and field observations (Grasso et al. 2022). More work is needed to determine whether mismatches exist between the breadth of temperature tolerance for cyanophages and their cyanobacterial hosts, and whether this may facilitate cold-water bloom formation.

Competition with other taxa

Eukaryotic algae frequently outcompete cyanobacteria in winter, but cyanobacterial dominance or co-occurrence with other taxa does occur under certain conditions. This appears to be most common in eutrophic and hypereutrophic lakes but has also been observed in mesotrophic systems. In hypereutrophic Lake Taihu, *Microcystis* sp. persists through the winter at lowered metabolic rates. This decreases loss rates and sustains blooms, seeding the population for rapid growth during warm seasons (Ma et al. 2016). Similar trends have been observed in hypereutrophic lakes in Poland, where blooms of filamentous *Planktothrix agardhii* and *L. redekei* co-occur with *Stephanodiscus minutulus* at 2°C (Toporowska et al. 2010). This co-occurrence may be explained by initial rapid growth of large diatoms in response to mixing-induced nutrient pulses followed by cyanobacteria proliferation as the nutrient pulse is depleted (Salmaso and Cerasino 2012). In mesotrophic Lake Annecy, carryover of cyanobacteria from warm fall conditions into winter facilitated cold-water blooms of coccoid cyanobacteria, including *Aphanocapsa* sp., *Aphanothece* sp., and *Chroococcus* sp. In this case, it is possible that blooms were sustained by mixotrophy, as some species of *Aphanocapsa* are able to assimilate organic matter (Anneville et al. 2015). This metabolic strategy allows them to persist below the photic zone in nutrient-rich, light-limited conditions, outcompeting obligate photoautotrophs. Although bloom-forming cyanobacteria are often viewed as *r*-selected opportunists that outcompete chlorophytes, diatoms, and other eukaryotes only at high temperatures in summer and early fall, the literature reviewed here revealed that these cyanobacteria, at least as a group, have a wide range of fundamental niches, while individual taxa can thrive and form blooms as winners of *K*-selection, supported by the benefits of small cells (Raven 1998) and the ability to exist as unicells or form colonies of various sizes according to the environmental conditions (Yokota and Sterner 2010). In some cases, observations of cyanobacterial increases above certain thermal thresholds may be a mere reflection of the typical surface temperature at which a given lake starts to stratify (Reynolds and Walsby 1975), when the loss rates

of larger-celled diatoms and chlorophytes to sinking and grazing increase, and the establishment of a stable thermocline starts to compartmentalize biogeochemical exchange between the epilimnion and the hypolimnion.

Cold-water cyanobacterial blooms under future conditions

Effects of climate change on cold-water cyanobacterial blooms in the future will be dictated by changes in factors such as light, thermal structure, and nutrient availability. Light penetration may be altered through changes in ice quality and quantity as outlined in the Lake Ice Continuum concept (Cavaliere et al. 2021). With more lakes experiencing intermittent winter ice cover (Sharma et al. 2019), we expect those lakes to have increased light penetration and potentially more primary production (Weyhenmeyer 2001), including cyanobacteria. Climate change is also shifting the type of precipitation lakes receive, particularly in winter. For example, rainfall on snow-covered ice causes white ice conditions, leading to decreased light penetration through ice and may favor cyanobacterial species adapted to low quantity and quality light conditions (Reuter and Müller 1993). Although cyanobacteria will not thrive in all conditions, their ability to tolerate a wide range of environmental conditions will allow them to persist under variable light conditions in the current climate and under future conditions.

Climate change will also alter external and internal nutrient loading to lakes. At northern latitudes, thawing permafrost will increase allochthonous nutrient inputs through overland flow (Thompson et al. 2012) and through nutrients released from the thawed permafrost itself (Przytulska et al. 2017). Shifts in types of precipitation from snow to rain in warming regions can also lead to increased nutrient loading via runoff, particularly during winter when loading from streams and tributaries may be reduced due to freezing conditions. Furthermore, oxygen depletion under ice can result in bottom-water anoxia and subsequent internal loading of phosphorus (North et al. 2015; Orihel et al. 2017), providing nutrients to fuel cold-water cyanobacterial blooms. Increased nutrient inputs in the absence of changes in temperature may have a positive impact on phytoplankton growth during winter months, but additional work evaluating the effect of nutrients increases at low water temperatures is needed to fully understand the magnitude of those changes.

Although we describe some potential implications of climate change on cold-water cyanobacterial blooms, the current lack of understanding of processes underpinning cold-water cyanobacterial blooms limits our ability to predict how climate change will impact these types of blooms. Our ability to understand cyanobacterial blooms and how they may change in the future hinges on understanding the mechanistic processes that favor cyanobacteria over other phytoplankton taxa under cold temperature conditions.

Future work

Most lakes in the world are located in geographical regions where water temperatures remain < 15°C for at least half of the year (Wetzel 2001). Establishing a baseline for the occurrence and frequency of cold-water cyanobacterial blooms is critical to documenting how they are changing with increasing surface water temperatures and changes to stratification in a future climate and understanding potentially unexpected public and wildlife health implications. Expanding monitoring efforts to year-round data is costly and logistically challenging (Block et al. 2019), but summer-only sampling does not capture changes in phytoplankton phenology. The general lack of flexibility in monitoring by government agencies is being recognized and has been overcome with dedicated "winter blitzes," as has recently occurred on the Laurentian Great Lakes in winter 2021/2022 (Ozersky et al. 2021). Other programs have leveraged citizen science to track and report cyanobacterial blooms including the Bloomin' Algae app in Europe (2019), as well as the Bloomwatch App (2016) and the Cyanoscope program (2016), administered by the U.S. EPA. European water quality monitoring is largely driven by the EU Water Framework Directive (EC 2000; Kallis and Butler 2001) and allows member states to determine the frequency of monitoring themselves as long as ecological status can be determined, leading to wide variation in phytoplankton monitoring, even within European ecoregions. Including standardized, systematic monitoring of phytoplankton and other water quality parameters in winter would provide a more holistic understanding of phytoplankton communities and lake ecology as a whole. Automated lake monitoring strategies, which include instruments for the high frequency, automated quantification of phytoplankton (using underwater microscopes or flow cytometers on lake platforms like LéXPLORE) allow one way forward to obtain continuous data on lake phytoplankton across all seasons (Marcé et al. 2016; Wüest et al. 2021; Merz et al. 2021). Furthermore, experimental mesocosm studies will help to mechanistically understand the effects of environmental drivers and variability for cyanobacterial bloom formation, including the winter season, and support ways of mitigation by testing nature-based solutions (Gerhard et al. 2022).

The use of other emerging technologies, such as Earth Observations, which apply satellite, aerial, or drone imagery for monitoring phytoplankton blooms, has been increasing due to the global availability of data (Ho et al. 2019). The use of Earth Observations for monitoring phytoplankton is likely to increase in the next few years, including high latitude areas, especially with the development of new sensors and new platforms such as nanosatellites (Kuhn et al. 2021). The ongoing development of satellite hyperspectral sensors by different space agencies will allow scientists to retrieve Chl *a* information and continue to develop methods to differentiate phytoplankton groups (Ogashawara 2021). A recent study using satellite imagery to detect cyanobacterial blooms in

U.S. lakes revealed that there is a summer bias, indicating that cyanobacterial blooms are being missed with an open water (ice-off) only monitoring approach (Coffer et al. 2021). These approaches also suffer from a blind spot in winter due to increase of the albedo and cloud cover, ice cover, and are unable to capture metalimnetic blooms or DCLs.

Conclusions

The current paradigm regarding temperature and cyanobacterial blooms is that "blooms like it hot" (Paerl and Huisman 2008). The direct and indirect effects of temperature on promoting cyanobacterial blooms is well-documented; however, ample data exist that provide strong evidence that cyanobacterial blooms can also occur in cold water temperatures, including ice-covered conditions. Consequences of cold-water cyanobacterial blooms for lake ecology and biogeochemical cycles remain largely unstudied but may have profound implications for sustainable lake management and human or environmental health risk assessment. In this paper, we documented common occurrences of these blooms and proposed mechanisms and physiological adaptations that can contribute to cold-water cyanobacterial blooms. We also explored how future climate conditions may affect these blooms and identified key knowledge gaps to direct future research on cold-water cyanobacterial blooms. This work is an important step toward understanding the full scope of environmental conditions that lead to cyanobacterial blooms, and while blooms certainly like it hot, some blooms also like it cold.

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