Blue Waters, Green Bottoms: Benthic Filamentous Algal Blooms Are an Emerging Threat to Clear Lakes Worldwide

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Nearshore (littoral) habitats of clear lakes with high water quality are increasingly experiencing unexplained proliferations of filamentous algae that grow on submerged surfaces. These filamentous algal blooms (FABs) are sometimes associated with nutrient pollution in groundwater, but complex changes in climate, nutrient transport, lake hydrodynamics, and food web structure may also facilitate this emerging threat to clear lakes. A coordinated effort among members of the public, managers, and scientists is needed to document the occurrence of FABs, to standardize methods for measuring their severity, to adapt existing data collection networks to include nearshore habitats, and to mitigate and reverse this profound structural change in lake ecosystems. Current models of lake eutrophication do not explain this littoral greening. However, a cohesive response to it is essential for protecting some of the world's most valued lakes and the flora, fauna, and ecosystem services they sustain.

Keywords: attached filamentous algae, periphyton, global change, littoral, eutrophication

An alarming form of nearshore degradation is occurring in clear lakes around the world: Littoral habitats are greening in the absence of established indicators of eutrophication. The littoral zone is the nearshore habitat where light reaching the lake bottom supports aquatic vegetation and algae. Proliferations of long filamentous algae are increasingly carpeting the littoral zones of lakes that, on the basis of low water column nutrient concentrations and low phytoplankton biomass, are categorized as oligotrophic (box 1, figure 1). These filamentous algal blooms (FABs) represent a structural and functional shift away from the low-growing, often cryptic attached algae that typically form the nutritious base of littoral food webs (Vadeboncoeur and Power 2017). Littoral zones capture and transform nutrients entering lakes from the surrounding landscape (Perillon et al. 2017). They also harbor most of the biodiversity in lakes and are an essential energy source for lake food webs (Vadeboncoeur et al. 2011). Unfortunately, littoral zones are among the least studied habitats in lakes (Vander Zanden and Vadeboncoeur 2020). Given the apparent increase in FABs in oligotrophic lakes, there is a need for a concerted scientific effort to understand the drivers of littoral greening and to develop a cohesive strategy to monitor and respond to this emerging threat.

Very clear lakes usually have high water quality (i.e., low concentrations of the nitrogen [N] and phosphorus [P] necessary for the growth of phytoplankton). The resulting low phytoplankton biomass contributes to higher penetration of light to the bottom. Under conditions of abundant light and low levels of water-column nutrients, benthic algal assemblages are often low growing and relatively inconspicuous (Lowe 1996, Hawes and Smith 1994). Over the past decade, atypical proliferations of benthic filamentous algae, composed of long chains of cylindrical cells attached end to end, have been reported in the littoral zones of clear lakes throughout the world (Timoshkin et al. 2016, Lu et al. 2019, Naranjo et al. 2019, Oleksy et al. 2020). Unfortunately, we are unable to correlate the increased awareness of these

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Box 1. FABs in a small, oligotrophic New Zealand alpine lake.

Sediment nutrient availability and differences in macroinvertebrate densities may provide clues to differences in littoral zone structures of two adjacent subalpine (less than 600 m above sea level) New Zealand lakes (figure 1). (a) Lake Emma has low benthic algal biomass composed of thin diatom biofilms and cyanobacteria. (b) In contrast, the bottom of Māori Lake has dense growths of the green algae, *Spirogyra spp.* (Stewart et al. 2021). Water column total phosphorus (TP) concentrations in Lake Emma (a) are higher than in the filamentous algal bloom (FAB) afflicted Māori Lake (b). However, pore water dissolved reactive phosphorus (DRP) and sediment-associated TP are higher in Māori Lake (b) than in Lake Emma (e.g., potentially bioavailable sedimentary phosphorus (626 versus 440 milligrams of P per kilogram; Waters et al. 2020). Catchment land-use and the deposition of nutrient-enriched sediments may be contributing to FABs in Māori Lake. Furthermore, comparatively low densities of the New Zealand mud snail (*Potamopyrgus antipodarum*) in Māori Lake (Stewart et al. 2019, 2021) may allow *Spirogyra* to flourish. On the basis of a weight of evidence, we suggest that sediment nutrient enrichment has contributed to *Spirogyra* proliferations in Māori Lake with possible interactive effects of release from grazing.

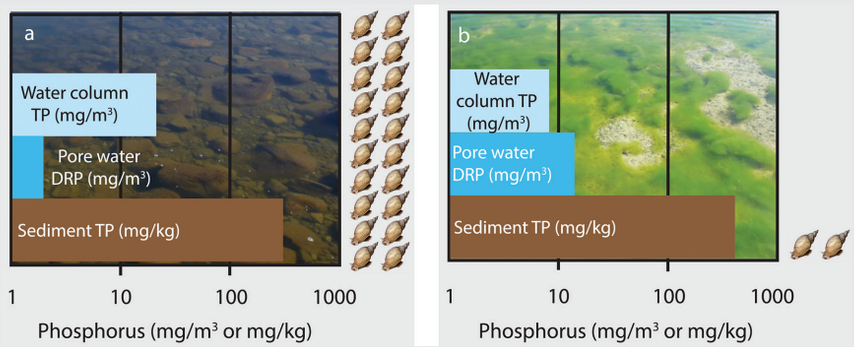

Figure 1. Two remote New Zealand lakes with contrasting grazer densities. (a) Lake Emma and (b) Māori Lake. The bars show phosphorus concentrations in the sediments, the pore water and the water column. Each snail to the right of the graphs represents 1 grazer per square meter.

blooms with an actual increase in occurrence because lake littoral zones are not routinely monitored (Strayer and Findlay 2010, Poikane et al. 2016, Vander Zanden and Vadeboncoeur 2020). With a few notable exceptions (e.g., the Laurentian Great Lakes, Lake Baikal, Lake Tahoe), the increased abundance of attached algae is largely anecdotal or has been inferred using paleolimnological approaches (e.g., Lu et al. 2019, Oleksy et al. 2020).

These atypical proliferations occur on both hard and soft substrata (e.g., rocks, mud, sand, and macrophytes), can be dominated by a single taxon, and achieve biomass densities many orders of magnitude higher than the species they replace (Nozaki 2001, Higgins et al. 2003, Timoshkin et al. 2018, Gladyshev and Gubelit 2019). Sometimes the algae form dense carpets over the lake bottom or fill the water column with an amorphous cloud of filamentous algae (boxes 1–4; figures 1–4). These dense accumulations of algae can be washed ashore, resulting in extensive windrows of rotting algae (box 3) that clog fishing nets, sometimes harbor toxins, and accumulate harmful bacteria (Hudon et al. 2014). Many FABs are formed by green algae in the genera *Spirogyra*, *Zygnema*, and *Cladophora* (Nozaki 2001, Timoshkin et al. 2016, Schneider et al. 2017, Oleksy et al. 2020). However, proliferations can also be formed by filamentous cyanobacteria, especially *Microcoleus* (Wood et al. 2020) and *Microseira wollei* (formerly *Lyngbya wollei*; Hudon et al. 2014, McGregor and Sendall 2014). Regardless of taxonomic composition, unusually dense accumulations of filamentous algae are forming and persisting in the high light, nearshore areas of some of the most iconic clearwater lakes in the world. Often, we do not understand why.

Ironically, the largely successful research effort to understand and mitigate the most widespread water quality problem, eutrophication, complicates our response to nearshore FABs. Lake eutrophication is a global problem that is characterized by high phytoplankton biomass (>8 micrograms [μg] per liter [L] of chlorophyll; Wetzel 2001, Poikane et al. 2019) and high concentrations of P and N in the water column (for most criteria total P >30 μg per L and total N >600 μg per L). FABs are increasingly common in littoral habitats of lakes that fall within the "oligotrophic," or low nutrient, category. Lake managers and limnologists alike are apt to assume that nutrient pollution is the cause of the luxuriant, prolific growth of filamentous algae, but low phytoplankton biomass and low total nutrient concentrations in the lake water means that FABs fall outside current

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conceptual models of lake eutrophication (Timoshkin 2018). Furthermore, limnologists traditionally characterize water chemistry throughout the water column from samples collected above the deepest part of the lake, and littoral habitats are rarely monitored (Strayer and Findlay 2010, Vander Zanden and Vadeboncoeur 2020). Monitoring programs that do include littoral algae often prioritize metrics of diatom taxonomic composition rather than benthic algal biomass (DeNicola and Kelly 2014, Poikane et al. 2016, but see Izhboldina et al. 2017). In many countries, water quality managers and the public are urgently seeking information on how to monitor and manage benthic FABs. Current limnological paradigms do not provide this.

In this article, we present what is known and unknown about benthic FABs in clear lakes, with the goal of providing a foundation for future research. First, we provide context for our hypotheses by describing the successional development of an attached algal assemblage (figure 5). Our hypotheses address changing environmental conditions at different spatiotemporal scales (figure 6) and include nutrient pollution (figure 7), climate-driven changes in lake hydrodynamics (figure 8), and food web perturbations (boxes 1 and 4). Finally, we identify unanswered questions and make suggestions for identifying, monitoring and responding to FABs. Improving our understanding of this emerging threat is essential for protecting some of our most valued lakes and the flora, fauna and ecosystem services they sustain.

Filamentous algal blooms are a late successional stage in benthic algae

In lakes, biofilms dominated by algae develop on submerged surfaces that receive sufficient light for photosynthesis. Common substrata are unconsolidated sediments (sand and mud), rocks, and macrophytes. In nutrient-poor, clear lakes, these biofilms are usually composed largely of low-growing (adnate) and upright (stalked) diatoms, mixed with large-celled filamentous taxa (Lowe 1996). Filamentous green algae such as *Ulothrix* and *Cladophora* have strong holdfasts and can form dense turfs, several centimeters thick, in rocky, well-lit habitats. Thin (approximately 1 millimeter) biofilms of cyanobacteria in the genera *Lyngbya* and *Calothrix* are typical in deeper, low-light habitats (Lowe 1996). However, researchers are increasingly reporting abnormal, explosive growth of filamentous algae in oligotrophic lakes that lack an historical record of such proliferations. We are using the term FAB to refer to atypical proliferations of filamentous algae that cover extensive portions of the lake bottom in the littoral zone and sometimes fill the water column (boxes 1–4). FABs can be composed of taxa that were previously present but not abundant in the algal assemblage, or they can be dominated by nonnative taxa (box 3). Regardless of taxonomic composition, the accumulation of biomass represents a late stage of attached algal succession.

Development of algal assemblages generally progresses along a predictable sequence of increasing biomass and vertical complexity, coupled with taxonomic shifts. After bare surfaces become coated by early bacterial colonizers (Azim and Asaeda 2005), low-growing algae (e.g., tightly attached diatoms) become established, followed by algal cells with more pronounced upright structure (e.g., vertically oriented and long-stalked diatoms). If grazing rates are low and the substratum is sufficiently stable or protected from waves, filamentous algae may eventually dominate the algal assemblage. The vertical development of the biofilm is attributed to competition for space, light, and nutrients (Azim and Asaeda 2005), as well as to the resistance of some mature filamentous taxa to grazing (Steinman 1996).

Initially, algal biomass on bare substrate increases slowly, because cells accrue primarily via colonization and are dependent on the water column or sediment pore water for nutrients (figure 5a, 5b). Abundance and biomass then increase exponentially, and recycling nutrients within the biofilm becomes increasingly important (Borchardt 1996). As biomass accumulates, gradients in dissolved oxygen and pH between the biofilm and the substrate may increase P flux from the sediments to the biofilm (figure 5a, 5c; Wood et al. 2015). Eventually, resource scarcity, grazing or pathogens reduce biomass accumulation, leading to steady-state conditions in which losses balance growth (figure 5a). As long fronds of filamentous algae extend into the water column, the cells at the base of the macroalgal turf experience impaired physiological health (Azim and Asaeda 2005) and light limitation through self-shading (Dodds et al. 1999). Weakened basal cells can lead to rapid detachment and algal sloughing (figure 5a, 5d; Stevenson 1996). Filamentous algae with high drag are particularly susceptible to hydrodynamic detachment (Stevenson 1996). Substrata denuded of attached algae are available for another cycle of colonization or regrowth, biofilm accrual, and sloughing (figure 5a).

Anomalous FAB proliferations have occurred in remote lakes in China (Lu et al. 2019); New Zealand (box 1); in the western United States (box 2); in parts of the shorelines of Lake Baikal, Russia (box 3); and in the Laurentian Great Lakes (box 4). In the Laurentian Great Lakes, *Cladophora* blooms were symptomatic of the early phases of eutrophication, and nutrient abatement was an early management tool (Higgins et al. 2008). Perhaps the recently reported proliferations in other parts of the world are, similarly, the first stages of eutrophication and presage accumulation of nutrients in the water column (Kann and Falter 1989, Lambert et al. 2008). Alternatively, global changes in climate, nutrient availability, hydrology, invasive species, and grazing pressure may interact to shift the dominance of littoral algae in oligotrophic lakes from low-growing taxa to benthic FABs (figure 6). Below, we discuss the changes in abiotic factors that may be promoting FAB development. Following this, we present three (nonexclusive) hypotheses explaining the emergence of FABs in clear lakes: enhanced nutrient loading to or through the catchment (figure 7), alterations of lake thermal regime or hydrodynamics (figure 8), and shifting biotic interactions including decreased grazing, enhanced consumer-mediated nutrient cycling, and altered food webs.

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Box 2. FABs in Lake Tahoe: Climate driven delivery of groundwater nutrients affects FAB development.

Known for its cobalt blue waters and offshore water clarity, Lake Tahoe's nearshore environment has experienced increasing temperatures, declines in native biodiversity, the establishment of nonnative species, and extensive littoral greening on the east and west shores (figure 2; Ngai et al. 2013). Along the southeast shore, FABs have been reported during summer since at least 2008 in Marla Bay (a). On the west shore, where FABs have been intensively studied, they form in winter (b) when watershed recharge, wave action, and seasonal declines in lake level interact to drive nutrient fluxes from the groundwater to the littoral zone (see figure 2 in Naranjo et al. 2019). Winter rain events recharge the groundwater causing nutrient-rich groundwater to discharge into nearshore benthic habitats. Phosphorus and nitrate in the groundwater stimulate attached algae during winter, accelerating biomass accumulation. Benthic algae photobleach in spring, followed by sloughing facilitated by wave action, which causes a decline in biomass despite abundant groundwater nutrients. This suggests other factors (e.g., UV radiation exposure, wave action) may control periphyton biomass during spring.

Figure 2. (a) On the southeast shore of Lake Tahoe in Marla Bay, a benthic FAB composed of Zygnema has occurred sporadically in summer since 2008 when this photo was taken. Photograph: Elena Wave. (b) On the west shore of Lake Tahoe, a FAB develops because of seasonal variation in groundwater inputs of nitrogen and phosphorus that are driven by hydroclimate. Attached algal biomass, as chlorophyll a, is correlated with groundwater nutrient concentrations. This algal biomass is low in November, but a robust biofilm develops and persists through the winter. In spring, the algae are senescing. By June, filamentous algae are bleached and chlorophyll is again low. Photographs: Naranjo and colleagues (2019).

We discuss each hypothesis in turn, recognizing that several may be occurring and interacting.

Abiotic changes may promote filamentous algae blooms

Light, temperature, and nutrients have strong direct effects on the growth of attached filamentous algae, irrespective of the life history of individual taxa or the successional stage of a biofilm (figures 5 and 6). High light availability is a key requirement for FAB development, but at this time, we do not know the lower limit of light intensities at which FABs are likely. Similarly, we know that algal growth rates increase with increasing water temperature but also know that temperatures higher than the metabolic optima of

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individual taxa cause metabolic stress and mortality (Lester et al. 1988). Our current understanding suggests that the filamentous cyanobacteria and green algae that contribute to littoral greening are generally more tolerant of and stimulated by increases in temperature than the low-growing, diatom-dominated assemblages that they replace (Lester et al. 1988, DeNicola 1996). However, some FAB taxa (e.g., *Ulothrix zonata*; Graham et al. 1985) also tolerate or prefer cold conditions. Filamentous algae increase in biomass during winter in Lake Tahoe (box 2) and in Lake Baikal, where *Spirogyra* grows prolifically in late summer but persists through the winter when water temperatures are at least 4 degrees Celsius (°C) in the most polluted areas (Timoshkin et al. 2018).

Inorganic and total N and P concentrations are key indicators in water quality assessments because these two nutrients often limit algal growth in lakes. However, inorganic N and P concentrations are poorly correlated with trophic status, because they turnover rapidly when demand is high (Dodds 2003). Human activities such as sewage management and agriculture add N and P into the surface water (lakes, rivers, and wetlands) and into the larger subsurface pool of groundwater. Phytoplankton in lakes take up these nutrients directly from the water column, which leads to high total N and total P values in water quality metrics. In contrast, the dense growth of attached algae can strip dissolved N and P from the water column and promotes the continuous recycling of nutrients within algal mats (Borchardt 1996). Furthermore, attached algae can obtain bioavailable nutrients directly from sediment pore water and groundwater (Hagerthey and Kerfoot 1998). Sediment pore water occupies the interstices of sediment particles on the lake bottom and is the interface between the groundwater and the lake water column. The concentration of nutrients in the sediment pore water is often several orders of magnitude higher than the water column (Wetzel 2001, Waters et al. 2020). Nutrient flux between the pore water and the water column is mediated by the magnitude of the concentration gradient, redox potential, sediment microflora, hydrology, and turbulence. Nutrient recycling within algal biofilms and reliance on sediment pore-water nutrients can decouple attached algal growth rates from water column nutrient availability. Established water quality networks routinely monitor surface water (e.g., river and lake water column) nutrient concentrations but not the groundwater and pore-water nutrient pools that are most accessible to attached algae (Hagerthey and Kerfoot 1998, Rosenberry et al. 2015). The widespread focus on surface water nutrient concentration limits our ability to understand FABs with current models of eutrophication (Timoshkin 2018).

Nitrogen-fixing filamentous cyanobacteria and diatoms with N-fixing endosymbionts are often a large component of attached algal assemblages in clear, low-nutrient lakes with low attached algal biomass (Higgins et al. 2003, Diehl et al. 2018). Under low-nutrient conditions, experimental addition of both N and P increase benthic algal biomass and often shift species composition (Cooper et al. 2016, Ozersky et al. 2018). Nutrient uptake kinetics are a function of cell size, and small taxa dominate under low-nutrient conditions (Reynolds 1989). Filamentous green algal cells are larger (10–1000 times larger by volume) than those of diatoms and cyanobacteria that often dominate littoral algal assemblages. Filamentous green algae have a higher nutrient demand, especially for nitrate and ammonium (John and Rindi 2015), than the smaller, low-growing taxa that they replace. The recent emergence of FABs in clear lakes may reflect increases in nutrient loading, especially increases in N relative to P. Although C is not often thought to limit algal growth, some studies suggest that dissolved inorganic carbon stimulates the growth of filamentous green algae. For example, additions of free carbon dioxide (CO_2) to a soft-water lake caused a two to fortyfold increase in *Zygnema* biomass relative to controls (Anderson and Anderson 2006). CO_2 supplementation to outdoor tanks caused biomass productivity of *Oedogonium* to increase by 2.5 times in comparison to controls (Cole et al. 2014). The effects of changing CO_2 availability on filamentous algae warrant more research. In the following sections, we explore how regional and global changes may be facilitating the proliferation of filamentous algae in lake littoral zones.

Hypothesis 1: Enhanced nutrient loading to or through catchments promote FABs

Changes in climate, land use, and vegetation may be increasing loading of nutrients into the littoral zones of oligotrophic lakes (Rosenberger et al. 2008, Sinha et al. 2017, Kelly and Schallenberg 2019, Lu et al. 2019). Elevation and landscape position (whether a lake is situated at the top or bottom of a catchment) affect the relative rate of transport of nutrients to lakes by surface flow (especially rivers), shallow subsurface flow, and groundwater (Webster et al. 1996). Basin shape (morphometry) affects the relative distribution of light on surfaces in lakes as well as the movement of nutrients among groundwater, sediment pore water, and water column pools. Landscape position and lake morphometry interact to determine whether sediment nutrients are more accessible to attached algae or phytoplankton. Mountain lakes have small catchments and, historically, limited exposure to point-source anthropogenic nutrients owing to their remote location. In deep (average depths larger than mixing depths), steep-sided basins, particulate nutrients eventually sink and are largely unavailable to phytoplankton because they are sequestered in the sediments below the photic zone. FABs have been reported in remote lakes with high landscape position and steep-sided, deep lakes (Lu et al. 2019, Oleksy et al. 2020). Where FABs are linked to anthropogenic nutrients, groundwater nutrient pollution can be the cause of littoral greening (boxes 2 and 3; Timoshkin et al. 2018), and basin geomorphology is a strong determinant of groundwater dynamics. We explore how changes in groundwater nutrients and nutrient availability at the catchment scale may be promoting the luxuriant greening of the littoral

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Box 3. New and historical FABs in Lake Baikal.

Lake Baikal in Siberia (figure 3) is renowned for its unparalleled species richness and endemism. Since 2010, this biodiversity has been threatened by FABs formed by the green algae *Ulothrix zonata* and *Spirogyra* and by the cyanobacterium *Tolypothrix*. *Ulothrix zonata* has historically grown around the entire shoreline of the lake (a), but in the last decade its biomass has increased up to five times in some areas. New FABs dominated by a nonnative *Spirogyra* (b) develop in late-summer–autumn near human settlements (Timoshkin et al. 2016, 2018) and now grow year-round to depths up to 20 meters (m) in areas experiencing continuous, intensive nutrient pollution (Volkova et al. 2018). These massive FABs strongly suppress native benthic communities, clog the nets of fishers, and foul beaches (c). Excess N and P from untreated human sewage stimulate the explosive growth of *Spirogyra* (Ozersky et al. 2018). In contrast, *Tolypothrix* FABs (d), appear to be stimulated by nutrient release triggered by forest fires, when nutrients flow from the land into the interstitial water of the splash zone.

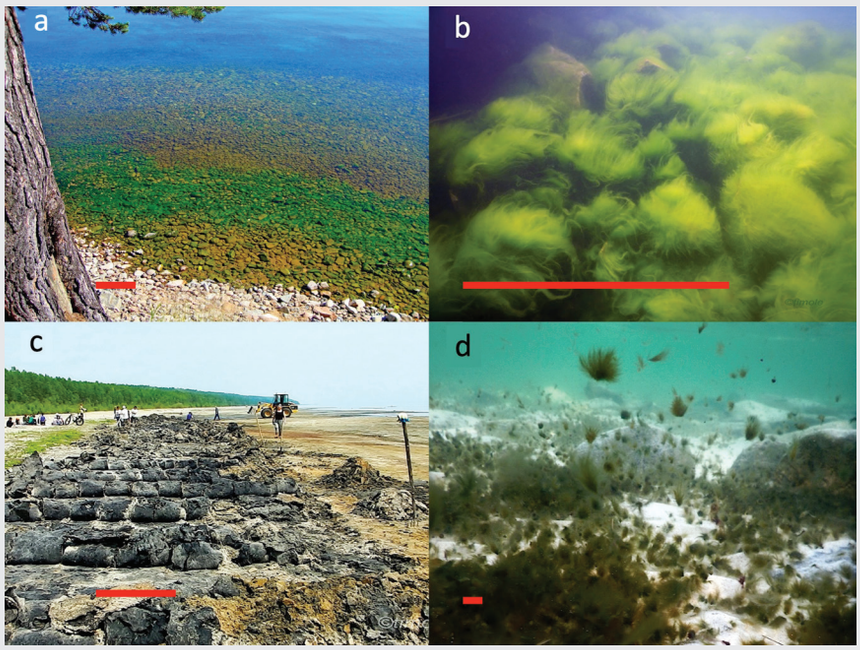

Figure 3. (a) Ulothrix, a native benthic alga, whose biomass has increased markedly in areas experiencing nutrient pollution (Bol'shie Koty, August 2011). (b) Spirogyra covering rocks at 2.5 m (Peschanaya Bay, September 2016). (c) Beach fouled with washups of Spirogyra, rolled and awaiting removal, (Senogda Bay, June 2016). (d) Tolypothrix in nearshore waters a year after a local forest fire (Bolshoy Ushkany Island, September 2016). The red scale bars in panels (a)–(c) represent 1 m; in panel (d), it represents 1 centimeter. floating Tolypothrix colonies in d) are 0.5–1 centimeters in diameter. Photographs: Oleg Timoshkin.

zones of clear, deep lakes and clear lakes with high landscape position.

Groundwater nutrient supply to filamentous algal blooms. Anthropogenic nutrient pollution causes nuisance and noxious algal blooms. However, the frame of reference for the persistent problem of cultural eutrophication is, in the minds of scientists and the public, largely limited to nutrient pollution of surface water and nuisance blooms of phytoplankton (Schindler 2006). In human-dominated landscapes, nutrients from human waste and agricultural fertilizers are transported to lakes largely by surface waters, especially rivers. Agricultural and urban nutrient pollution often cause surface-water nutrient concentrations to exceed those of the groundwater (figure 7a), even in areas with shallow groundwater pollution (Rixon et al. 2020). Nutrients accumulate in the sediment pore water owing to successive cycles of settling and remineralization of particulate nutrients in the lake. Nevertheless, high pore-water concentrations will not necessarily promote FABs in eutrophic lakes because excess water-column nutrients transported from the watershed by surface water are readily converted into

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phytoplankton biomass, which then reduces light availability to attached algae (Vadeboncoeur et al. 2008). Benthic filamentous algae thrive under high light conditions (Donahue et al. 2003). Only when groundwater nutrient concentrations are relatively high and water column nutrient concentrations are low is nutrient pollution likely to promote benthic FABs rather than phytoplankton (figure 7b; Timoshkin et al. 2018, Naranjo et al. 2019).

Groundwater nutrient pollution is directly linked to the occurrence of FABs in small lakes situated high in landscapes as well as the shorelines of large deep lakes, such as Lake Baikal (box 3; Timoshkin et al. 2018) and Lake Tahoe (box 2; Naranjo et al. 2019). Malfunctioning septic tanks and unlined cesspools in exurban lake districts can contaminate groundwater with nutrients (Timoshkin et al. 2018). The speed and pathways by which water moves from the groundwater to the lake determine the susceptibility of littoral zones to groundwater pollution. Catchments with shallow subsurface critical zones (Hahm et al. 2019)—that is, thin, poorly developed inorganic soils and underlying bedrock with little water holding capacity—cannot mitigate the transport of nutrients from the groundwater to the lake except through uptake by vegetation. Lakes perched high in the landscape are often in areas of mineral soil, and receive most of their water through direct precipitation or groundwater (Webster et al. 1996). In the absence of anthropogenic sources, groundwater nutrient concentrations are low. However, any new nutrient influx into the catchment (e.g., through atmospheric deposition or through point sources such as septic tanks) can be conducted rapidly to and through the shallow groundwater with minimal uptake, until nutrients emerge at the sunlit sediment–water interface of a littoral zone (Timoshkin et al. 2018). Under these circumstances, attached algae have the first opportunity, before phytoplankton, to sequester nutrients entering through littoral sediments (Rosenberger et al. 2008). Rapid uptake of nutrients by benthic algae and plants will reduce nutrient concentrations as groundwater traverses the sediment–water interface (Dodds 2003). This uptake, combined with dilution, leads to a decreasing gradient of nutrient concentrations from the groundwater to the pore water to the overlying water (figure 7b). Phytoplankton biomass will remain low and the water relatively clear because the lake water itself has low nutrient concentrations. Groundwater pollution has caused robust growth of FABs in Lake Baikal and Lake Tahoe. This problem may be widespread if new nutrient sources are becoming available in the catchments of remote, undeveloped lakes.

Changes in nutrient transport within catchments. The rates and pathways of precipitation and nutrients flowing from the land surface to lakes depend on the properties of the catchment's critical zone (Lin 2010), which extends downward from the top of the vegetation's canopy to the top of the unweathered bedrock. Water travels rapidly along shallower surface and subsurface pathways and much more slowly through the deep groundwater path. Climate change is transforming critical zone dynamics. Across the globe, mountain glaciers are receding, exposing fresh rock and glacial till to weathering, potentially liberating previously unavailable P. In addition to reduced ice cover, high-intensity rainfall events are increasingly frequent and are often interspersed with drought. Intense rains deliver nutrient-rich sediments to nearshore habitats (Hayhoe et al. 2007, Sinha et al. 2017, Casson et al. 2019). Droughts are stressing terrestrial vegetation, leading to weakened root networks and increased fire frequency, which both increase erosion. Fire also mobilizes nutrients, especially P, because nutrient-rich ash is transported to lakes (McCullough et al. 2019). Targeted research is needed to determine whether increased erosion, increases in fire-mobilized nutrients, and changes in the timing and magnitude of water delivery via surface runoff and groundwater flow to lakes are causing the emergence of FABs in remote lakes such as those in the western United States (Naranjo et al. 2019, Oleksy et al. 2020) and China (Lu et al. 2019).

Increases in atmospheric nutrient delivery to catchments. Nutrient pollution of groundwater and surface waters of remote lakes may be increasing because of increased atmospheric delivery of anthropogenic nutrients to catchments. Over recent decades, aeolian transport of bioavailable N and P-rich dust has increased markedly worldwide (Brahney et al. 2015). Humans have more than doubled bioavailable N cycling on Earth (Vitousek et al. 1997). Atmospheric transport carries reactive N from human-dominated landscapes (Camerero and Catalan 2012, McCullough et al. 2019) to remote watersheds. Phosphorus-rich dust carried by wind can fertilize ecosystems half a world away (Chadwick et al. 1999), and water column TP concentrations are increasing in lakes and streams throughout the United States (Stoddard et al. 2016). This continental-scale loss of oligotrophic inland waters in North America has been associated with a 40% postindustrial increase in global atmospheric P transport (Brahney et al. 2015). The global increase in atmospheric transport of N and P is delivering new nutrients to lakes throughout the world (Camerero and Catalan 2012). Research is needed to establish whether increased atmospheric transport is driving the occurrence of FABs in lakes that hitherto have experienced little direct human activity.

Hypothesis 2: Altered lake stratification or hydrodynamics favor FABs

Climate-driven changes in lake stratification, wind waves, and lake level (Woolway et al. 2020) can affect the physical stability of the lake substrate, shear stress at the substrate surface, water temperature, and distribution of nutrients. In the present article, we evaluate how climate-driven changes in lake stratification and hydrodynamic processes (waves and lake level) may promote FABs by creating a high light, warm environment that favors filamentous algae and by enhancing nutrient flux from the groundwater, pore water, and the hypolimnion to benthic substrates.

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Box 4. Cladophora in the Laurentian Great Lakes: Nutrients and invaders.

Localized blooms of *Cladophora glomerata* L. (Kütz) in shallow, nutrient-rich portions of the Laurentian Great Lakes (e.g., western basin of Lake Erie; figure 4) occurred as early as the mid-nineteenth century. *Cladophora* FABs in Lakes Erie, Ontario and Michigan became problematic in the 1950s and were linked to external phosphorus (P) loading (Higgins et al. 2008). P load abatement programs implemented in the 1970s successfully reduced *Cladophora* FABs. Concern over FABs faded (Auer et al. 2010), but by the mid-1990s blooms occurred across the lower Great Lakes despite no increase in P concentrations (Higgins et al. 2008). What had changed?

The resurgence of Great Lakes *Cladophora* FABs is linked to the invasion and spread of dreissenid (zebra and quagga) mussels. Dreissenid establishment may facilitate FABs by increasing water clarity, altering littoral nutrient cycling, and providing substrata for algal attachment (Hecky et al. 2004, Francoeur et al. 2017). Dreissenids stimulate the growth of FABs by moving nutrients from the water column to the benthic littoral zone via conversion of their food (filtered plankton) into fecal and pseudofecal production. Consequently, they decouple water column nutrient concentrations and water clarity from external nutrient loading from the watershed. For example, Lake Michigan experiences extensive *Cladophora* FABs (Higgins et al. 2008) despite water column P concentrations indicative of ultraoligotrophy. The ongoing expansion of dreissenids and other invasive bivalves (golden mussels, Asian clams) means that FABs may become a problem in more lakes, even in the absence of increased nutrient loading.

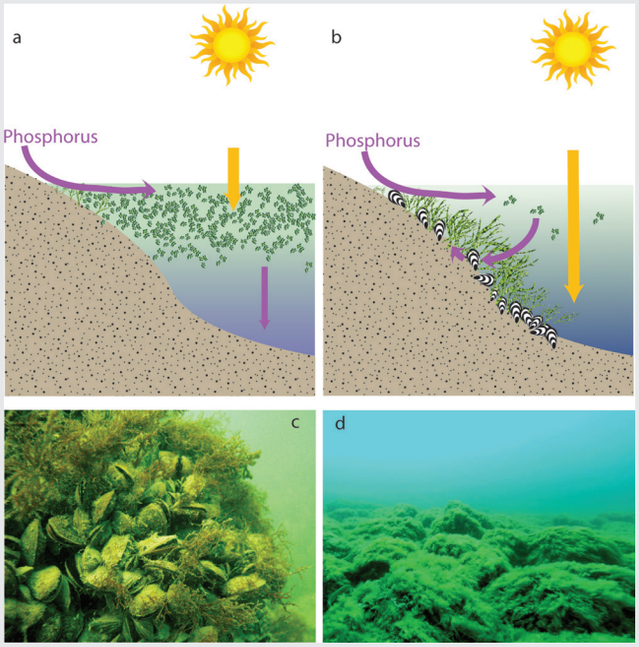

Figure 4. Dreissenid-mediated stimulation of Cladophora FABs in the Laurentian Great Lakes: (a) Before the spread of invasive dreissenid mussels in the 1990s, P loading from the landscape resulted in relatively high phytoplankton biomass, which reduced light penetration and restricted Cladophora to shallow littoral habitats. Phosphorus was deposited into deep sediments when phytoplankton died. (b) The spread of dreissenids caused water clarity to increase because they efficiently filtered phytoplankton causing an increase in light penetration, which allowed Cladophora to colonize greater depths. Dreissenid mussels also increase nutrient availability to Cladophora by translocating particulate nutrients (in phytoplankton) from the water column to the littoral sediments. The progressive colonization of littoral soft substrates by dreissenid mussels created additional substrate for Cladophora attachment enabling its expansion to areas it could not previously inhabit. (c) Cladophora attached to dreissenid mussels in Lake Michigan. (d) Extensive Cladophora bloom in the rocky littoral zone of Lake Michigan. Photographs: Harvey Bootsma.

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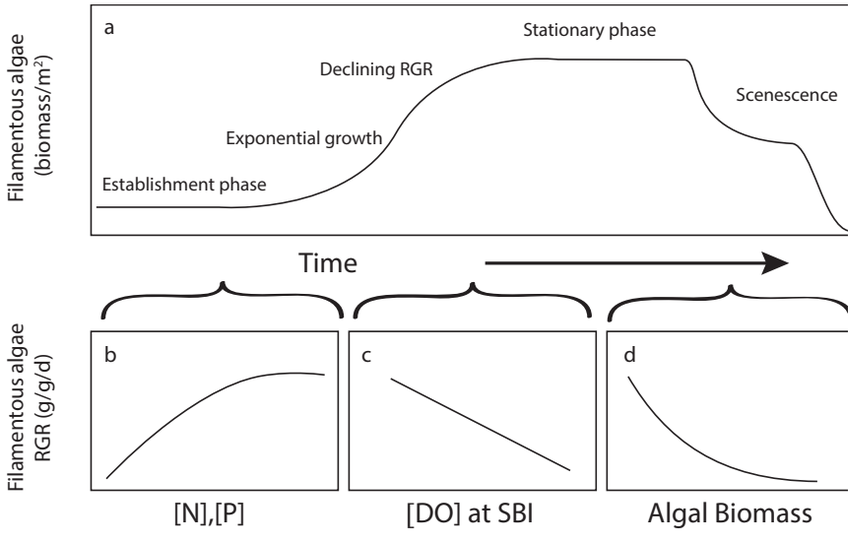

Figure 5. (a) Phenology of the development of a filamentous algal mat. In the absence of grazing, algal biomass develops on bare substrata following a predictable progression over time with different environmental factors (b, c, d) affecting relative growth rate (RGR, g/g/d) at different stages of assemblage development. (b) Early in biofilm development, RGR increases with increasing availability of nitrogen (N) and phosphorus (P) concentrations in the overlying water or inflowing groundwater. As biomass accumulates, RGR slows and nutrient recycling within the biofilm becomes more important. (c) In thicker biofilms, photosynthesis generates high oxygen concentrations during the day and at the surface of the mat, whereas respiration depletes oxygen at night and deep in the mat. Low dissolved oxygen at the interface between the substratum and the biofilm (SBI) increases the flux of inorganic P to the algae (Wood et al. 2015), potentially increasing growth rates. (d) As biomass continues to accumulate, cells at the base of the mat are shaded by cells at the surface. Light limitation causes basal cells to senesce, and the resultant weakening of attachment to the substrate can lead to successive episodes in which filamentous algae are dislodged and dissipated by wave action. Direct consumption of benthic algae by grazers can strongly affect the trajectory of algal development, reducing biomass accumulation and altering taxonomic composition.

Creation of a favorable FAB environment. Climatic warming strengthens and prolongs summer stratification (Adrian et al. 2009) and reduces the amount and duration of winter ice cover (Sharma et al. 2019). FABs have been particularly evident in clear temperate lakes that undergo seasonal cycles of thermal stratification and mixing. Stronger, longer thermal stratification tends to prolong the growing season for attached algae while having minimal direct effects on the hydrodynamic processes that deliver nutrients (see below). Prolonged stratification can increase water clarity in small to medium size lakes (at most 500 square kilometers; Schindler et al. 1996) by depriving offshore phytoplankton of nutrients. Over the growing season dead organisms sink, progressively sequestering epilimnetic nutrients in the hypolimnion. Stronger and more persistent stratification during the growing season (Adrian et al. 2009) prolongs this depletion of epilimnetic nutrients. The resulting lower phytoplankton biomass, in turn, increases light penetration in the water column. In some regions, reductions in rainfall reduce loading of terrestrial dissolved organic matter (Schindler et al. 1996), resulting in increased water clarity.

Attached filamentous algae thrive under the high-light conditions not only because of increased availability of a limiting resource (light) but because the lake bottom and shallow littoral waters are warmed when they intercept radiation. For example, in Lake Ontario, rapid warming in spring causes more pronounced temperature gradients between the littoral zones and offshore waters. Differential heating of the littoral zone relative to offshore water in spring can also lead to a thermal bar, which is an isothermal band of 4°C water that prevents mixing of nearshore and offshore water (Rao et al. 2004) and can trap nutrients in the littoral zone (figure 8a). The number of beach closings due to *Cladophora* blooms was positively correlated with the magnitude of this thermal gradient (Vodacek 2012), suggesting that warmer spring temperatures—and possibly springtime nutrient flows into nearshore waters—may facilitate FABs.

Hydrodynamic changes associated with climate change may also facilitate FABs by promoting or maintaining algal attachment to the substrate and by increasing habitat available for colonization. Climate change alters the frequency and intensity of wind waves, which erode shorelines, leaving behind coarse-grained substrates that foster the attachment and growth of filamentous algae. The effect of wind waves depends on the development stage of the algae. Waves increase nutrient delivery to attached algae (Stevenson 1996), but intense wind waves slough late successional stages of FABs from the benthos. Therefore, FABs are usually most profuse in protected, quiescent waters or below the effect of strong wave action (Gladyshev and Gubelit 2019). Rising lake levels may provide new colonization space for benthic filamentous algae, whereas falling lake levels open up deep, often nutrient-rich habitats that were previously too dark to support filamentous algal growth (figure 8b). Ice scour dislodges benthic filamentous algal growth and holdfasts from the substrate in late winter or early spring in nearshore habitats. Climate-induced reductions in the extent, thickness, and duration of ice cover (Sharma et al. 2019) are almost certainly reducing overwinter mortality of filamentous algae, contributing to rapid establishment of filamentous algae in the spring.

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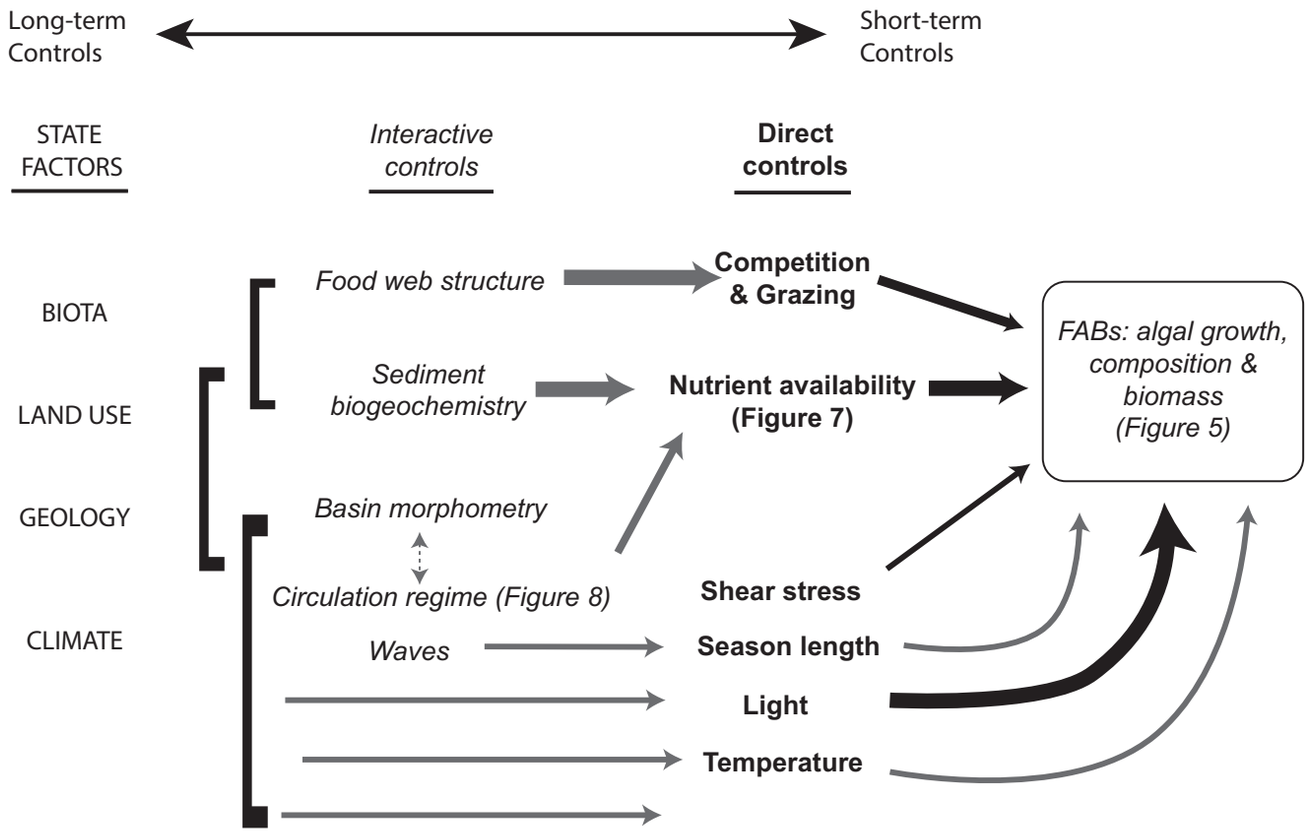

Figure 6. Regional biota, geology, land use, and climate are state factors that affect lake morphometry, circulation, biogeochemistry and food webs. These elements of lake ecosystem structure and function interact with strong direct controls (black arrows) to determine attached algal growth, biomass and composition. Long-term, widespread changes in climate and biota may be altering the strength of direct controls on the development of attached algal assemblages in lakes, making filamentous algal blooms more likely. Thickness of arrows represents relative strength of controlling factors. Specific controls on benthic algae are illustrated in greater detail in Figures 5, 7, and 8.

Enhancing nutrient flux from groundwater, pore water, and the hypolimnion to the benthic substrate. Fluctuations in lake level will become more common and pronounced as precipitation events and droughts increase in frequency with climate change (Hoegh-Guldberg et al. 2018). Lake level fluctuations increase delivery of nutrients to the nearshore substrate by enhancing groundwater flow (Naranjo et al. 2019), nutrient mineralization rates (Birch 1964, Jarvis et al. 2007), and shoreline erosion. When lake levels fall, hydraulic gradients enhance the flow of groundwater into and through the littoral substrates (figure 8b). In Lake Tahoe (in the United States), groundwater discharge increased when lake levels dropped, and groundwater nutrients stimulated filamentous algal growth (box 2; Naranjo et al. 2019). Irrespective of groundwater nutrient concentration, groundwater discharge can stimulate benthic algal growth by transporting nutrient-rich sediment pore water into the littoral zone (Perillon et al. 2017). Rising lake levels may promote attached algal growth because inundation of terrestrial organic matter mineralizes and moves nutrients from soils into the littoral zone (Steinman et al. 2012), a phenomenon known as the Birch effect (Birch 1964). Finally, shoreline erosion resulting from lake level fluctuations can deliver P-rich sediments to the littoral zone, stimulating attached algal growth (Hambright et al. 2004).

Wind waves, internal waves, and surface seiches (supplemental table S1) also drive the flow of nutrient-rich water through nearshore sediments (Precht and Huettel 2003, Kirillin et al. 2009, Roberts et al. 2019). In addition, wind-driven upwelling can transport nutrient-rich water from the hypolimnion into the littoral zone (figure 8c; Corman et al. 2010). Nutrient delivery by these hydrodynamic processes, however, is less likely to be important for sustaining FABs than those processes mentioned previously because waves, seiches, and upwellings are of relatively short duration (supplemental table S1). Nevertheless, increases in the frequency or duration of any of these wind-driven processes would accelerate the delivery of nutrient-rich groundwater through the sediment–water interface, making nutrients more accessible to attached algae.

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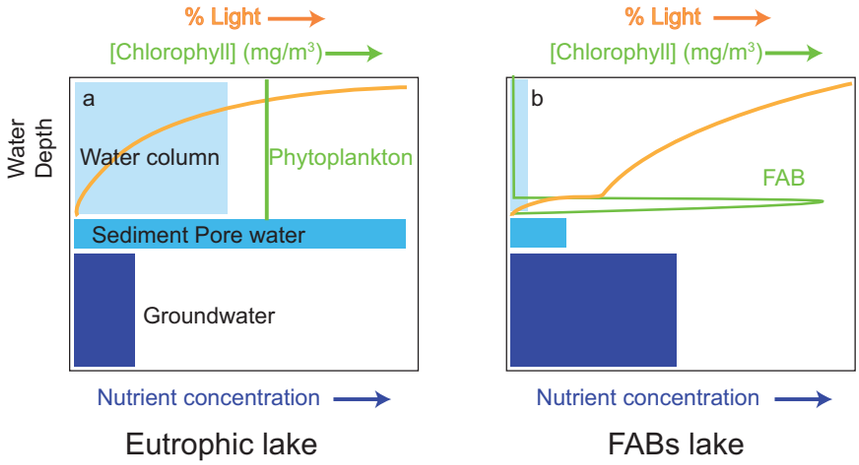

Figure 7. Hypothetical distribution of chlorophyll (green line), and light (gold line) in the nearshore, well-mixed waters of a eutrophic lake (a) and a lake experiencing filamentous algal blooms (FABs; b). The width of the blue boxes represents the hypothetical relative concentration of nutrients in the water of the mixed epilimnion, sediment pore water, and groundwater in the two types of lakes. Although these relative concentrations were based on limited data from the eastern United States, sediment pore–water nutrient concentrations can be orders of magnitude higher than in the lake water column. (a) Eutrophication typically involves high water column nutrient concentrations and high phytoplankton biomass (high chlorophyll in the water column) in the nearshore. Phytoplankton in the water rapidly attenuate light, limiting the growth of attached algae even when pore-water nutrients are relatively abundant. (b) Higher nutrient concentrations in the groundwater or pore water than in the water column may be a prerequisite for FAB development. These conditions limit phytoplankton biomass in the water column. Unlike in the eutrophic lake, ample light penetrates to the lake bottom, but is then attenuated within a few centimeters of the surface of the FAB. Relatively high light and high nutrients at the sediment water interface promote littoral FAB development.

Hypothesis 3: Shifting biotic interactions can favor filamentous algae

Biotic interactions can affect the development of FABs directly or indirectly. Herbivorous zooplankton indirectly facilitate the establishment of benthic vegetation, including FABs, because they improve water clarity by consuming phytoplankton (Scheffer et al. 1993, Barnes and Wurtsbaugh 2015). Similarly, filter-feeding invasive dreissenid mussels are linked to the widespread resurgence of FABs (primarily of *Cladophora*) since the mid-1990s in the Laurentian Great Lakes (box 4; Higgins et al. 2008). Grazing by dreissenids removes phytoplankton and detrital particles from the water column, improving water clarity (Higgins and Vander Zanden 2010) and extending the maximum depth and area suitable for *Cladophora* growth (Winslow et al. 2014, Kuczynski et al. 2020). Furthermore, waste released by dreissenids on the lake bottom provides nutrients that enhance *Cladophora* growth and biomass (Auer et al. 2010).

Benthic grazers that scrape or gather benthic algae from surfaces exert direct, top-down control by consuming benthic algae, and it is this type of grazer to which we subsequently refer throughout the remainder of this section. Highly nutritious attached algae (e.g., lipid-rich diatoms), although they are often cryptic as adnate veneers of low biomass, are preferred by many benthic grazers, whose efficient feeding limits accumulation of algal biomass. Diatoms can maintain high rates of productivity under intense grazing because grazers indirectly benefit the unconsumed algae by reducing self-shading and increasing nutrient recycling (Steinman 1996, Vadeboncoeur and Power 2017). The resultant decoupling of primary productivity rates and attached algal biomass is characteristic of strong top-down control. There is overwhelming experimental evidence of strong top-down control in benthic aquatic habitats (Hillebrand 2009): When grazers are excluded, filamentous chlorophytes dominate benthic algal assemblages in lakes and rivers (Power 1990). The occurrence and persistence of FABs may be driven by a widespread weakening of top-down control caused by a phenological mismatch between algae and grazers (Dell et al. 2014) or by reductions in total densities of critical herbivores. Targeted research on grazers and FABs remains rare, but in the present article, we apply extensive general knowledge of grazer control of benthic algae to inform future research on FABs.

Phenological asymmetries that alter the cost, benefit or timing of consumption. Top-down control is most effective during the early, exponential growth phase of algae when grazers can consume new algal biomass almost as quickly as it is produced. Environmental factors that increase growth rates of algae or reduce the consumption rate of individual grazers can allow algal escape from grazer control during early successional stages (Steinman et al. 1987). As we discussed above, anthropogenic nutrient pollution, the removal of riparian vegetation, and long-term increases in global temperatures may be reducing overwinter mortality of algae and promoting the rapid growth of filamentous algae early in the growing season. These changes in mortality and growth may narrow the window during which consumers can control benthic algal biomass.

Warmer spring temperatures accelerate the growth and development of grazers as well as algae. For animals, warmer developmental temperatures can result in faster growth, smaller adult body size (Sentis et al. 2017), and more generations per year. In addition, warmer temperatures help vertebrate grazers digest algae more efficiently

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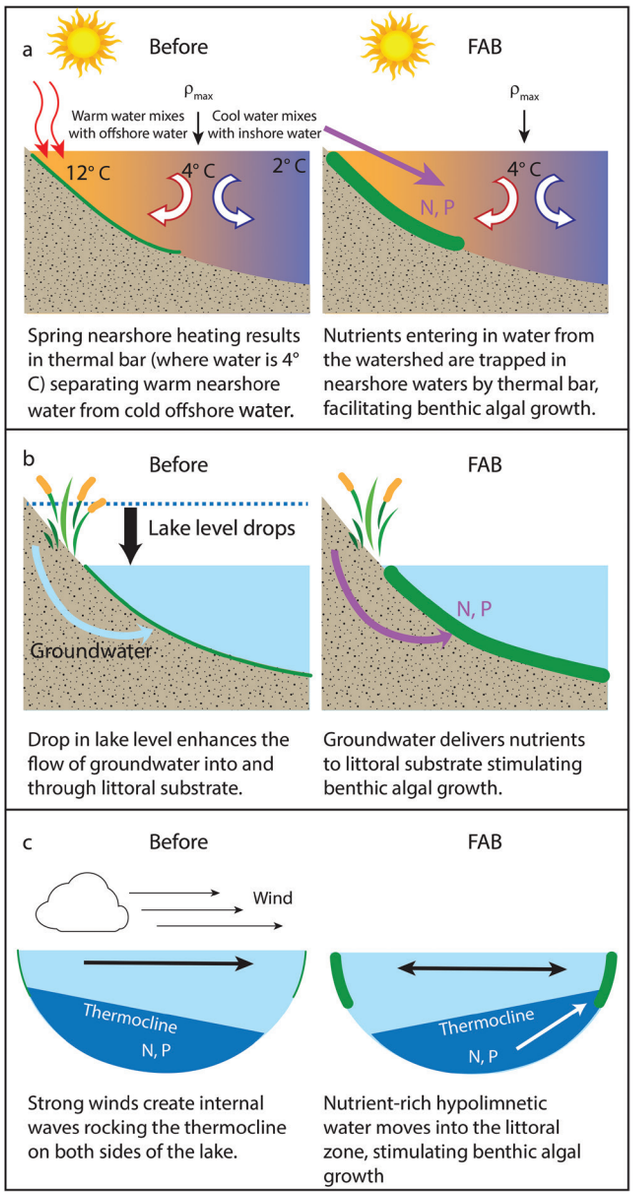

Figure 8. Hydrodynamic processes (left column) that potentially promote filamentous algal bloom (FAB) development (right column) by delivering nutrients to the substrate of the littoral zone of lakes. These processes include (a) heating of nearshore water in spring, which creates a thermal bar (where water density is maximal, ρmax) causing entrapment of nutrient-rich water entering from the watershed; (b) a decline in lake level resulting in a hydraulic gradient that favors flow of groundwater into the substrate of a lake's littoral zone; and (c) wind-induced tilting of the thermocline, leading to an internal wave that moves nutrient-rich hypolimnetic water into the littoral zone of a lake

(Carriera et al. 2016). Therefore, high temperatures early in the season are likely to benefit both resource and consumer (Kazanjian et al. 2018). However, if, as the season progresses, daily average temperatures exceed grazer tolerances, grazer assemblages can collapse, allowing filamentous algae to flourish (Werner et al. 2016). The complexity of temperature effects is illustrated in a comparison of geothermally heated streams; benthic invertebrate production was positively correlated with temperature, because algal primary production increased with increased annual stream temperature (Junker et al. 2020). Despite the positive effect of temperature on invertebrate production, attached algal biomass increased a hundredfold across the 25°C temperature gradient among streams, suggesting a weakening of top-down control with increasing average temperature.

Declining grazer densities. Benthic grazers can prevent the successful establishment of new algal filaments, but many grazers avoid or are unable to consume mature filaments of green algae (Dodds and Gudder 1992). Therefore, a reduction in grazing pressure can rapidly shift an assemblage to dominance by filamentous algae (Power et al. 2008). We review two potential drivers of current grazer decline that may release FABs: Changes in abiotic variables are making the littoral zone more physically challenging for grazers, and chemical (e.g., pesticides) or biological (e.g., nonnative predators) control of grazers is intensifying.

Small grazers with limited mobility can be extremely sensitive to dissolved oxygen concentrations and pH gradients at the sediment–water interface. Caddisfly larvae, mayfly larvae and snails are abundant, efficient grazers that exert strong top-down control on attached algae in temperate and boreal latitudes (Steinman 1996). Regional lake acidification late in the twentieth century caused widespread reductions in grazers, and a concurrent increase in filamentous algal biomass in the littoral zones of acidified lakes (Schindler 1990), but new research is needed to test whether current increases in attached algal biomass are linked to declines in grazer densities. For example, as was noted above, extreme weather events and watershed deforestation are increasing sediment loading to littoral habitats (Hambright et al. 2004). In tropical Lake Tanganyika, sediments compromised the growth and feeding activity of algivorous fish, leading to a positive correlation between sediments and attached algal biomass (Munubi et al. 2018). In addition to directly (Wagenhoff et al. 2013) and indirectly (Munubi et al. 2018) promoting filamentous algal growth, sediments fill interstitial spaces, reducing total habitat and promoting hypoxia in sediments. Filamentous algal proliferations themselves can create adverse environmental conditions for zoobenthos (Arroyo et al. 2012). High photosynthetic rates of filamentous algae during the day combined with high respiration at night produce extreme diurnal fluctuations in pH and dissolved oxygen (Wood et al. 2015). If FABs create adverse conditions for grazers, their occurrence may cause long-term declines in grazer recruitment and survival.

Grazer densities may be decreasing, independent of changes in abiotic conditions or consumer-resource dynamics in littoral zones. An estimated 70% of caddisfly taxa and 40% of mayfly taxa, two keystone grazers in lakes, have declined in density over the past 50 years (Sánchez-Bayo

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and Wyckhuys 2019). The cause of this decline is unknown, but the widespread use of pesticides in agriculture and their atmospheric transport to remote lakes (Bradford et al. 2010) are implicated (Yamamuro et al. 2019). The use of neonicotinoids in rice paddies has drastically reduced the abundance of generalist benthic invertebrates—and, consequently, fish yields—in brackish lakes in Japan (Yamamuro et al. 2019). Amphibian densities are declining globally because of chytrid fungus (Ranvestel et al. 2004, Lips 2016) and agricultural herbicides (Hayes and Hansen 2017). Larval amphibians exert top-down control on algae (Ranvestel et al. 2004, Mallory and Richardson 2005), and benthic algal biomass more than doubled after a disease-driven decline in tadpoles in a tropical stream (Whiles et al. 2013). Given the strong evidence of widespread declines in aquatic grazers (Lips 2016, Sánchez-Bayo and Wyckhuys 2019, Yamamuro et al. 2019), there is an urgent need to document these declines in specific lakes and evaluate their potential link to changes in benthic algal biomass and FABs.

Finally, changes in the abundance of top predators may have caused a decline in grazer densities. For example, an increase in FABs in historically fishless high-elevation lakes in the western United States may be related to a trout stocking program initiated in the 1800s (Knapp et al. 2001). Fish introductions reduced the average size of zooplankton, reduced zoobenthic invertebrate densities, and exterminated native frog populations (Knapp et al. 2001). More research is needed to document how top-down control acting alone or in combination with anthropogenically driven changes to climate and nutrient deposition may be linked to the appearance of FABs.

Charting the way forward

Our review suggests that environmental stressors promoting FABs can scale from point source nutrient pollution (Timoshkin et al. 2016, 2018) and local introductions of nonnative species up to and possibly including regional and global changes in precipitation, wind, temperature, and airborne nutrients (Brahney et al. 2015, Woolway et al. 2020). These stressors lead to proliferations of filamentous algae in lakes that otherwise appear minimally affected by human activity. Our ability to forecast the occurrence and ecological consequences of FABs is hampered by the limited research on littoral zone processes and the lack of a consistent framework for detecting ecological change in nearshore habitats (Strayer and Findlay 2010, DeNicola and Kelly 2014). The international scientific and management communities have an opportunity to develop FAB monitoring protocols and research approaches that integrate the effects of variable stressors and cumulative anthropogenic impacts on lake littoral zones. Our recommendations include establishing criteria that allow the public and scientists to identify FABs and report their occurrence, standardizing methods for monitoring attached algae and incorporating these methods into existing lake monitoring programs or research initiatives, and integrating attached algae into current models of lake trophic status and food webs (Vander Zanden and Vadeboncoeur 2020).

Around the world, members of the public, managers, and scientists are noticing and reporting FABs in littoral zones with increasing frequency. We are unable to unequivocally link this increased reporting to increases in occurrence owing to minimal monitoring of littoral zones, but the increased awareness by the public is informative. People feel that FABs are undesirable and diminish the recreational quality of water bodies (Suplee et al. 2009). The public has consistently identified riverine FABs depicted in photographs as "undesirable," especially when algal dry biomass exceeded 115 grams per square meter (Suplee et al. 2009). Public sensitivity to green lake bottoms could help document the spatial extent and temporal frequency of FABs through community-science platforms such as iNaturalist.org. Documenting the frequency, extent, and duration of FABs in lakes is a crucial first step to responding to this threat to lake ecosystems.

Standardized methods for describing and quantifying FABs (e.g., taxonomic identification, percentage biomass cover) are essential for assessing the occurrence of FABs within and across lakes (DeNicola and Kelly 2014, Poikane et al. 2016). New Zealand's National Institute of Water and Atmospheric Research Stream Periphyton Monitoring Manual and the European Union's Water Framework directive provide templates for developing monitoring protocols for attached algae at flexible spatial and taxonomic scales (Biggs and Kilroy 2000, Poikane et al. 2016). Scientists at Lake Baikal have proposed a universal scheme for monitoring littoral plants and animals inhabiting different benthic landscapes (Timoshkin et al. 2005). Use of existing technologies, such as remote sensing and the in situ deployment of high-frequency or event-triggered sensors, could supplement standardized monitoring and contribute to our understanding of the spatial distribution of FABs and their effects on water quality. Research networks, agencies, community scientists, and limnologists can incorporate standardized monitoring of the littoral zone into existing efforts. For example, lake observation networks (e.g., the European Water Framework Directive, the US Environmental Protection Agency Lakes Assessment, the US Long Term Ecological Research Network, the Global Lake Ecological Observatory Network) are already collecting data essential for understanding lake processes that promote FAB development, but these data could be leveraged more effectively (DeNicola and Kelly 2014).

We know much less about the determinants of benthic algal structure and function in lakes than we do about controls of phytoplankton dynamics in open water (Lowe 1996, Cantonati and Lowe 2014, Schneider et al. 2017). We need more basic research on attached algal dynamics, with a specific focus on the poorly understood and undesired outcome of FABs. FABs may be early indicators of changes in lake trophic status associated with nutrient loading in clear lakes, but models of eutrophication have struggled to

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incorporate both pelagic and benthic processes (Schindler 2006, Vadeboncoeur et al. 2008). Although scientists and managers recognize that ecosystem processes differ between the littoral and open water zones of lakes, conceptual models of lake eutrophication are still focused on the open water zone and water column metrics. To accommodate FABs and other emerging responses to global change, the concept of eutrophication should expand beyond water column nutrients and phytoplankton biomass to include cross-habitat links, groundwater pollution, and food web perturbations (Hecky et al. 2004, Vander Zanden and Vadeboncoeur 2020).

Limnologists can broaden research programs to provide management recommendations aimed at mitigating FABs and their ecological and social consequences. The public and lake managers view FABs as a response to nutrients alone (Suplee et al. 2009, Jakus et al. 2017), but FABs are likely a common response to multiple and interacting stressors. Management strategies necessary for mitigating their occurrence in lakes must accommodate this complexity (Schindler 2006, Poikane et al. 2019). Addressing groundwater nutrient pollution may prove more tractable than the management of climate-driven hydrodynamic changes or reducing the impact of invasive species, but creative system-specific approaches that reduce the consequences of multiple stressors can reduce the magnitude, frequency, and negative effects of FABs.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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