



Predicting algal blooms: Are we overlooking groundwater?

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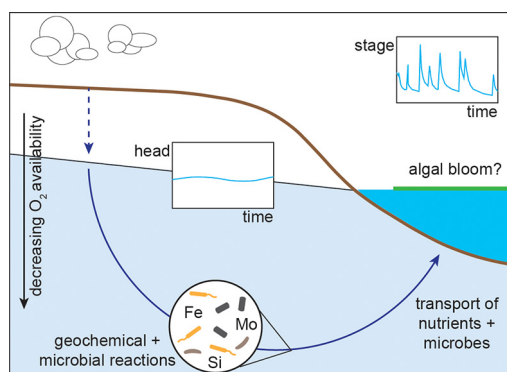
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HIGHLIGHTS

- Long residence times cause groundwater to be distinct from surface water.
- Groundwater can modulate algal blooms through control of in-stream water chemistry.
- Redox state of the subsurface influences how groundwater controls algal growth.
- Extent of water-rock interactions influences how groundwater controls algal growth.
- Stability of groundwater discharge influences how groundwater controls algal growth.

GRAPHICAL ABSTRACT



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ABSTRACT

Significant advances in understanding and predicting freshwater algal bloom dynamics have emerged in response to both increased occurrence and financial burden of nuisance and harmful blooms. Several factors have been highlighted as key controls of bloom occurrence, including nutrient dynamics, local hydrology, climatic perturbations, watershed geomorphology, biogeochemistry, food-web control, and algal competition. However, a major research gap continues to be the degree to which groundwater inputs modulate microbial biomass production and food-web dynamics at the terrestrial-aquatic interface. We present a synthesis of groundwater related algal bloom literature, upon which we derive a foundational hypothesis: *long residence times cause groundwater to be geochemically and biologically distinct from surface water, allowing groundwater inputs to modulate algal bloom dynamics (growth, decline, toxicity) through its control over in-stream water chemistry*. Distinct groundwater chemistry can support or prevent algal blooms, depending on specific local conditions. We highlight three mechanisms that influence the impact of groundwater discharge on algal growth: 1) redox state of the subsurface, 2) extent of water-rock interactions, and 3) stability of groundwater discharge. We underscore that in testing hypotheses related to groundwater control over algal blooms, it is critical to understand how changes in land use, water management, and climate will influence groundwater dynamics and, thus, algal bloom probabilities. Given this challenge, we argue that advances in both modeling and data integration,

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including genomics data and integrated process-based models that capture groundwater dynamics, are needed to illuminate mechanistic controls and improve predictions of algal blooms.

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1. Introduction

Algal blooms (ABs) within inland freshwater rivers, streams, lakes, and lagoons (Andres et al., 2019) are estimated to cost the United States upwards of \$2.4 billion annually (Wurtsbaugh et al., 2019). An increase in the frequency, duration, and magnitude of bloom events, particularly harmful ABs, has driven research efforts towards improving our ability to understand and predict their occurrence (e.g. Ho and Michalak, 2015; Otten et al., 2015, 2016; Pace et al., 2017). Research efforts have largely focused on surface processes, particularly harmful sources (Carpenter et al., 1998) and availability (Paerl et al., 2016; Schindler et al., 2016), and watershed transport (Abbott et al., 2018; Moatar et al., 2017).

The importance of groundwater contributions has been discussed in the literature, although rather scarcely, and typically only from a limited perspective focused on nutrient budgets. Paerl (1997) suggested that groundwater inputs and atmospheric deposition from urban, industrial, and agricultural sources may have resulted in the expansion of harmful algal blooms in coastal and offshore waters. There has also been an understanding that submarine groundwater discharge can cause eutrophication in near coastal waters (Smith and Swarzenski, 2012) and lakes (Meinikmann et al., 2015) from groundwater-derived nutrient and solute loadings such as nitrogen (N) and phosphorus (P) (Sawyer et al., 2016). Nonetheless, the role of groundwater beyond simplistic nutrient delivery mechanisms has not received much attention. Few studies have investigated the role of groundwater and groundwater/surface water interactions (GWSWI) in the development of ABs in terrestrial waters. Our goal is to reassess the current state of research on

groundwater's role in algal bloom development, to reinvigorate and direct research in this area. We highlight that recent research suggests that the role of groundwater is not limited to the delivery of N and P, and in fact that groundwater may play multiple important roles in controlling AB production in terrestrial aquatic ecosystems. Our hope is to prompt intrigue across scientific fields as to the diverse roles groundwater can have in governing AB dynamics.

Different causes for ABs have been reported for different systems. Algal abundance may be high if nutrient availability within a water body is also high, such as high N and P concentrations in agricultural runoff. In contrast, if other primary producers such as macrophytes or phytoplankton are present to compete for nutrients and light, the same abundance of nutrients in this alternate steady state may not be able to support a bloom (Scheffer et al., 1993). In addition to nutrient and light availability, bloom emergence also depends on watershed hydrodynamics, geomorphological, biogeochemical, food-web, and climate dynamics which shape critical in-stream pathways (Lobera et al., 2017; Nogaro et al., 2013; Power et al., 2015; Walsh et al., 2016). All of these mechanisms have been considered at some level of scientific inquiry yet no models exist that include all of these possible mechanisms. Process-based models that consider multiple, interacting processes are needed. The development of such a model would help better understand the role of integrated hydrologic inputs from shallow soils and deeper aquifers in regulating AB formation (Andres et al., 2019).

A major research gap in predicting terrestrial-aquatic controls on AB probability is understanding the role of groundwater inputs in modulating microbial biomass production and food-web dynamics through controlling nutrient dynamics. In this paper, we consider the

mechanisms through which GWSWI may regulate ABs considering what has been explored to date as well as identifying critical gaps in knowledge where future research is needed.

1.1. Evidence of groundwater's role in algal growth

Several lines of evidence indicate that groundwater can play a key role in the regulation of ABs. These lines of evidence, and the subsequent hypotheses that we present in the following sections, are related to differences in physical and geochemical properties of groundwater and surface water. These do not reflect all of the possible mechanisms through which groundwater may regulate algal growth, but highlight the potentially more prevalent mechanisms. The differences in physical and geochemical properties of groundwater and surface water are predominantly driven by the differences in residence time, where residence times for surface water systems are often measured in hours or days (e.g., Jones et al., 2017) and groundwater flow systems of the same spatial scale are often measured in years or decades (e.g., Gleeson et al., 2016). Stemming from the contributing and subsequent differences in geochemical and physical properties, evidence that relates to groundwater's role in algal growth can be summarized by highlighting the importance of groundwater's role in the hyporheic zone dynamics, GWSWI, nutrient budgets and ratios, and food-web habitats.

1.1.1. Hyporheic zone dynamics and groundwater-surface water interactions

The hyporheic zone is the area of mixing between groundwater and stream water (Figure 1). Groundwater inputs to this zone help determine what redox processes occur there and nutrient, microorganism (microbes, bacteria, and invertebrates), and element delivery to streams (Marmonier et al., 2012). Research has only recently identified the role of subsurface flow paths through the hyporheic zone as a major contributor to benthic and in-stream algal stability, and the controls of these flow paths over water biogeochemistry is rarely recognized in models predicting ABs (Krause et al., 2017; Larsen and Woelfle-Erskine, 2018). GWSWI provides pathways for both nutrient consumption as well as nutrient supply to surface waters (Fox et al., 2016; Malzone et al., 2016), which can decrease and increase ABs, respectively. Most importantly, the seasonal variability of stream flow conditions and the timing of when streams shift from dominantly gaining to losing can

dictate when and where Fe, N, and Si in-stream stoichiometry are in excess or limiting through hyporheic bacterial conditions that feedback on flow and nutrients (Newcomer et al., 2016), and could be a primary factor in determining algal taxonomic dominance (Myllynen et al., 1997).

The mechanisms by which GWSWI can impact surface water concentrations of nutrients, in-stream periphyton, and phytoplankton dynamics is directly related to the magnitude, residence time, and degree of vertical hydrological exchange (Doering et al., 2013). Vertical exchanges between shallow subsurface and deeper groundwater can amplify the delivery of nutrients, microbial matter, and solutes, impacting the chemistry of downstream river segments (Gomez-Velez et al., 2017; Grant et al., 2018; Krause et al., 2017; Li et al., 2020; Newcomer et al., 2018). In particular, vertical exchanges mediate the interactions and feedbacks between nutrient and algal communities by maintaining or removing Fe, Si, N, C, P, Se, and Hg, which are essential micronutrients/metals that support growth and maintenance of various algal taxa and community assemblages (Gobler et al., 2013; Larsen and Woelfle-Erskine, 2018; Mangal et al., 2019). For example, microbial uptake and methylation of Hg in the hyporheic zone has also been associated with certain types of benthic algal organic matter (Mangal et al., 2019). Vertical hydrologic exchanges also support nutrient recycling (such as N), maintain clean bed sediments, and support diverse microbial assemblages (Marmonier et al., 2012; Nogaro et al., 2013), which play an important role in mediating water quality and biogeochemical cycles down watershed gradients (Harvey and Gooseff, 2015; Kim et al., 2017; Kolbe et al., 2019; Musolf et al., 2015) towards downstream land-water interfaces (e.g., Great Lakes). What we recognize from the multitude of studies exploring factors contributing to AB is that the first step towards prediction of ABs is to appropriately represent chemical and hydrological mechanisms in models, including the ability to represent vertical hydrological exchanges across terrestrial-aquatic interfaces, thus representing both the shallow and deep subsurface.

1.1.2. Nutrient budgets and ratios

Watersheds can control the nutrient ratios through several mechanisms, including surface runoff, as well as hyporheic denitrification, oxyhydroxide transport by groundwater to surface water, and weathering of minerals containing Se, Fe, Si, and Mn (Dekov et al., 2014; Gobler et al., 2013; Lewitus et al., 2012; Wall et al., 1998). For example, diatoms require a molar Si:N:P ratio of 16:16:1. When Si becomes scarce,

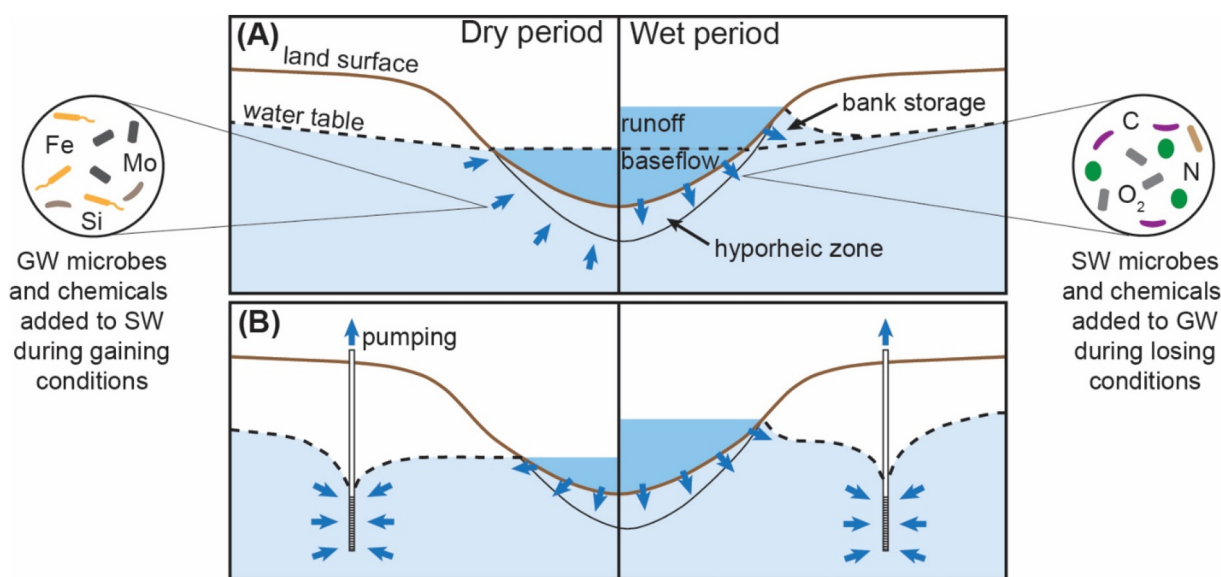


Fig. 1. a) Proportion of gaining to losing conditions can support different stable steady states of ABs through delivery of chemistry, microbes, and invertebrate assemblages important for food-web stability; b) potential effects of groundwater pumping on stream conditions. Groundwater pumping can shift streams to dominantly losing. During both dry periods and wet periods, distinct microbiological and nutrient conditions enter the surface water or enter the groundwater. Delivery of these unique microbiomes to surface waters can change the fundamental biological, physical, and chemical conditions modulating bloom dynamics.

diatom size is altered and a regime shift towards nonsilicious dinoflagellates may occur (Officer and Ryther, 1980). It has been hypothesized that Si limited conditions (Turner and Rabalais, 1991) have led to increased blooms of toxic dinoflagellates compared to conditions of higher N and P loads (Dortch and Whitedge, 1992). Iron and Copper concentrations (Fe, Cu) also directly modulate the Si:N ratios within diatoms which regulate the toxicity of the bloom (Rue and Bruland, 2001). Similarly, biomass and toxin production by cyanobacteria such as *Microcystis* spp. are thought to be controlled by the form and stoichiometry of N and P (e.g., Andersen et al., 2020; Paerl et al., 2016).

Phosphorus and nitrogen concentrations in groundwater and surface water often differ significantly so that groundwater contributions may promote algal growth by increasing nutrient supply, suppress algal growth by diluting nutrient concentrations, or may promote specific algal taxa by altering nutrient stoichiometry (Anderson et al., 2002). The differences in water chemistry between surface water and groundwater arise from the differing biogeochemical mechanisms and anthropogenic inputs.

Nitrate is often the most abundant form of ionic nitrogen in both surface water and groundwater (e.g., Howarth et al., 1996; Lewandowski et al., 2015). Nitrate is highly soluble and available for microbial transformation to gaseous forms in the presence of an electron donor such as organic carbon (Rivett et al., 2008). Because of this, nitrate often enters aquatic systems with watershed runoff and advects into both surface water and groundwater pools. If conditions support denitrification along the flow path, nitrate concentrations decrease before groundwater recharge occurs. If not, high concentrations of nitrate can persist in groundwater for long periods of time in systems with low electron donor supply (Rivett et al., 2008).

Groundwater P concentration is dependent on geology and long-term patterns in watershed land use (Powers et al., 2016; Sharpley et al., 2013). Along the coasts of the Great Lakes for example, approximately $\frac{1}{3}$ of the coastlines are vulnerable to groundwater inputs of P and N (Knights et al., 2017). Many soils are naturally deficient in P and the primary source of P is often anthropogenic activities such as fertilizer and manure application. Long term anthropogenic activities in urban and agricultural watersheds have led to a gradual accumulation of legacy P in soils that would otherwise be low in P (Sharpley et al., 2013). In many of these regions, legacy P has exceeded soil sorption capacity and under the right conditions is released in a dissolved form (Haygarth et al., 2014; Powers et al., 2016). Dissolved P can be transported into groundwater where it persists, resulting in groundwater being substantial sources of legacy phosphorus to surface water bodies (Holman et al., 2008; Schilling et al., 2020).

1.1.3. Food-web habitats

Hydrodynamic conditions, such as groundwater flow and GWSWI, can have an important co-evolutionary role in the stability, re-assembly, and number of trophic levels (Diffenbaugh et al., 2015; Gray et al., 2015; Marks et al., 2000; Waliser and Guan, 2017). Disturbances such as atmospheric rivers, fires, droughts, hurricanes, and floods can influence the physical hydrodynamic conditions (such as runoff, groundwater flow, and GWSWI), potentially shifting the steady state of a watershed and the food-web habitats dependent upon it and ability for food-webs to establish. Food-web habitats also include the communities and assemblages of macro and micro fauna/organisms such as instream and groundwater microbes, bacteria, and invertebrates.

Microorganisms play a pivotal role in the functioning of ecosystems through their impacts on biogeochemistry as well as their novel recognition as critical keystone taxa in environments (Banerjee et al., 2018). Even more complexity is introduced when considering algal-bacterial interactions (Sison-Mangus et al., 2016). Microbial community composition has been shown to be a key interacting factor influencing AB conditions (Klindworth et al., 2014; Needham and Fuhrman, 2016). Interactions include the recycling of N, C, and P from decaying algal

organic matter, or provisioning important micronutrients to algae which can promote or inhibit certain AB growth (Kazamia et al., 2012).

Macroorganisms impact biogeochemistry and can also serve as sources of diversity and as transport vectors for microbial populations (Smith et al., 2016). Macroorganisms, including groundwater and surface water invertebrates (e.g. stygofauna and benthic invertebrates) are important as players in food-webs. Stygofauna are a potential source of organic matter from groundwater to surface water, and their activities are thought to mediate the transfer of organic matter through the aquifer system (Smith et al., 2016). Biodiversity of groundwater invertebrates and their function is understudied (Danielopol et al., 2003), but is hypothesized to positively contribute to important ecosystem services such as maintaining functional assemblages important for pollutant degradation. This includes the provision of important services to surface waters supporting algal diversity and stability such as mayflies and nymphs which are grazers of algae (Boulton et al., 2008). Groundwater contributions of these invertebrate assemblages may play important roles in suppressing harmful or nuisance algal dominance conditions because they are consumers of algae.

These collective influences of climatic, hydrological, biogeochemical and micro-macro organisms are demonstrated in the two riverbed examples provided below:

- 1) As a major control on food-web reassembly and trophic interactions, hydrological perturbations within watersheds have been shown to initiate equilibrium or dis-equilibrium conditions at the start of the growing season by changing channel morphology and grazing by invertebrates (Lobera et al., 2017). Riverbed scour, which can be driven by GWSWI, is a well-recognized mechanism supporting this watershed state shift, and has been shown to provide the biogeochemical and geomorphological equilibria to support a shift towards re-establishment of non-toxic food-webs (Junk et al., 1989; Lobera et al., 2017; Power, 2001). Stability and cohesion of riverbeds and riverbanks, which work to prevent scour and erosion, is controlled by the pore water pressure and normal stress of the sediments and streambank materials, which is controlled by groundwater conditions and GWSWI (Simon et al., 2000). Changes in the streambed conditions, potentially driven by changes in both the surface water and groundwater, control the amount and extent of scour and erosion.
- 2) Wet-winter conditions provide a multitude of services, including the recharge of aquifers which supports baseflow to streams during dry seasons. This baseflow plays an important role in stabilizing benthic assemblages (Lavers et al., 2015). Baseflow can also maintain benthic algal productivity and diversity across run-riffle sequences (Peterson and Grimm, 1992), maintain clean bed sediments for diverse microbial assemblages (Nogaro et al., 2013), and initialize benthic periphyton (green-algae, attached primary producers) that support a multi-level food chain and a stable steady state during the growing season (Power et al., 2008). Wet-winter conditions supporting annual benthic riverbed resets are acknowledged to play an important role in stabilizing invertebrate communities through sediment scour and top-predator removal which is a critical top-down food-web control on algae proliferation (Jones et al., 2015). Conversely, lack of winter precipitation events or the occurrence of more extreme precipitation events may provide the hydrological foundation for shifting the balance of these sensitive trophic webs towards cyanobacteria (Power et al., 2015). Dry conditions lower water tables that decrease or eliminate baseflow, produce downward chemical gradients (Dahm et al., 2003), and limit ecosystem services facilitated within hyporheic zones (Newcomer et al., 2018).

2. Possible mechanisms for groundwater control of ABs

A significant difference between surface water and groundwater flow systems is their residence time, where groundwater typically has much longer residence times compared to surface water bodies

(Gleeson et al., 2016; Jones et al., 2017). Our umbrella hypothesis is that: long residence times cause groundwater to be geochemically and biologically distinct from surface water, such that changes in groundwater inputs can alter in-stream environments, including the ability to support or prevent ABs (Figure 1). Mechanisms that create geochemically and/or biologically distinct groundwater include:

- More reduced environment and possible denitrification:** Groundwater, particularly in deeper subsurface systems, has limited interaction with the atmosphere and therefore typically has more reduced conditions compared to surface water (see Hypothesis 1). Where supplies of electron donors are present, the more reduced condition of the subsurface can drive denitrification reactions that are often inhibited under oxic conditions in shallow soils.
- More geochemical and microbial reactions:** Slower groundwater flow increases the contact time with surrounding porous media, allowing more water-rock-microbial interactions (see Hypotheses 2).
- Stability and relative contributions of groundwater:** Variability in the quantity and quality of groundwater fluxes tend to be dampened compared to those at the surface because the long residence time integrates input signals. This makes groundwater more consistent and stable compared to surface waters that are directly impacted by short term and seasonal climatic conditions (see Hypothesis 3).

Hypothesis 1. Reduced state of the subsurface can cause groundwater discharge to control algal growth

Groundwater discharge has the potential to supply aquatic habitats with nutrients and microorganisms that promote development of ABs. The concentration and form of those nutrients depends on the microbial reactions occurring along the groundwater flow paths, which is driven in part by groundwater redox state. Many microbial reactions occur in aquifers (Dahm et al., 1998; Kolbe et al., 2019), however, microbial nitrogen and metal cycling may be of particular relevance to ABs (e.g., Orihel et al., 2016; Paerl et al., 2016).

Subsurface microorganisms can alter nitrogen inputs to aquatic habitats through nitrogen cycling (Figure 2a). Denitrification consumes nitrate in anoxic environments and can produce dinitrogen and a variety of nitrogen species with intermediate oxidation states (e.g., N_2O , NO, NO_2^-). Nitrate reduction can also occur via dissimilatory nitrate

reduction to ammonium (DNRA), which produces ammonium. Anaerobic ammonium oxidation (anammox) can occur where ammonium and nitrite are available. Where groundwater flow transports ammonium to zones that contain oxygen, nitrification can produce nitrate. Thus, the form of nitrogen delivered to surface waters by groundwater discharge depends on which portions of the nitrogen cycle, if any, are occurring within the subsurface.

Where nitrate is transported into streams through anoxic layers within riparian zones, often due to current or historic agricultural use of fertilizers, denitrification can reduce nitrate stream pollution. Tesoriero et al. (2015) asserts that the geologic setting, including the thicknesses of surficial oxygenated aquifers, associated shallow versus deep flow paths, clay content, and organic content, control the extent of denitrification and stream nitrate. These subsurface structures also determine how much groundwater discharges to streams. For example, in rivers draining to the Chesapeake Bay, almost half the water and N are annually derived from groundwater with median residence times of 10 y (Lindsey et al., 2003). ABs therefore rely on application rates of N-containing fertilizer in nearby fields but also on the presence of flow pathways of oxygenated groundwater from deep oxic aquifers where denitrification does not occur (Tesoriero et al., 2013).

Similarly, metal cycling (Figure 2b) has the potential to affect groundwater inputs of several nutrients to aquatic habitats, including P, Fe(II), Si, Mo, and Cu. Iron plays a key role in moderating the growth and dominance of some algal taxa (i.e., cyanobacteria) (Orihel et al., 2016). Iron, Mo, and Cu also play important roles in regulating carbon and nitrogen metabolism within cyanobacteria (Rueter and Petersen, 1987). High carbon dioxide levels combined with silica limitation in surface waters can synergistically increase the toxicity of some blooms dominated by diatoms (Tatters et al., 2012).

Each of these nutrients can be immobilized on (oxyhydr)oxides and other solid-phases through adsorption-desorption reactions (Cornell and Schwertmann, 2003). Reduction of manganese(IV) and iron(III) in anoxic environments produces Mn(II) and Fe(II), respectively, and causes (oxyhydr)oxide minerals to dissolve. Thus, microbial metal reduction can mobilize those nutrients by consuming (oxyhydr)oxide minerals and decreasing the availability of sorption sites. Consistent with this mechanism, studies observed correlations between phosphate and iron(II) concentrations in groundwater beneath agricultural landscapes (Carlyle and Hill, 2001; Schilling et al., 2018; Tomer et al., 2010).

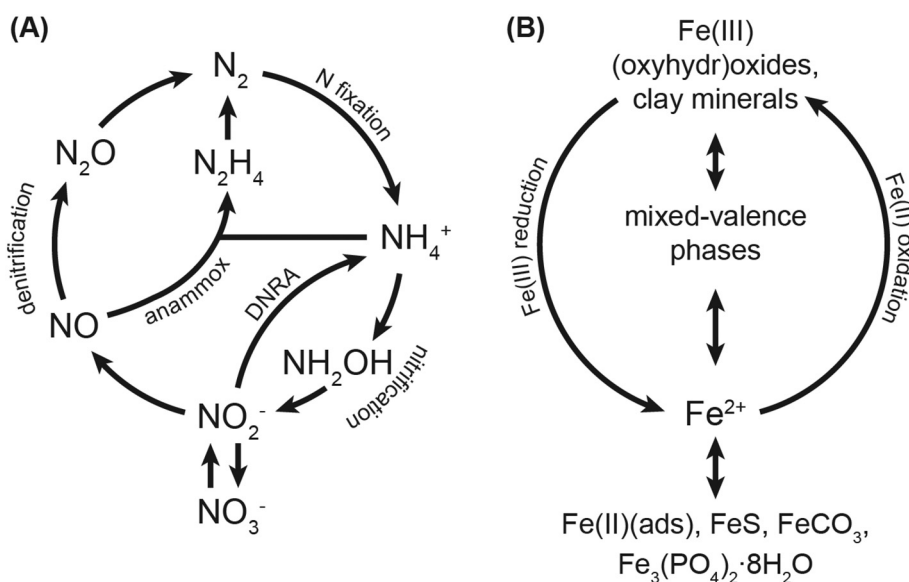
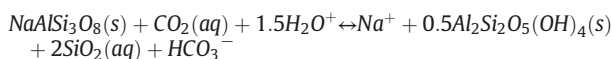


Fig. 2. Microbial (a) nitrogen and (b) iron cycles. The nitrogen cycle diagram (a) is based on Jetten (2008). The iron cycle diagram (b) includes mineral sources of ferric iron, consistent with near-neutral pH environments. The diagram also depicts some potential fates of ferrous iron, including sorption (Fe(II)(ads)), precipitation of mackinawite (FeS), siderite (FeCO₃), and vivianite (Fe₃(PO₄)₂·8H₂O), and formation of mixed-valence phases such as green rust.

These examples illustrate how the redox state of the subsurface can affect the microbial environment, which in turn affects the nutrient content of the groundwater discharging to surface water bodies. The nutrient content of groundwater can be spatially and temporally heterogeneous, depending on which reactions occur (Dahm et al., 1998), increasing the importance of understanding the subsurface environment and groundwater flow paths in predicting AB development.

Hypothesis 2. Extent of water-rock interactions impacts the control of groundwater discharge on algal growth

Chemical weathering, in addition to microbial reactions, influences the nutrient delivery of groundwater discharge to aquatic habitats. Chemical weathering in the subsurface is driven primarily by reaction of minerals with meteoric water and acids, including carbonic and organic acids (Brantley et al., 2011). Those acids are produced primarily by degradation of organic matter and plant respiration (Silverman, 1979). Acid migrating into the subsurface and along groundwater flow paths reacts with minerals and produces solutes (Kump et al., 2000), including alkali Earth metals and silica, as shown in the following example reaction in which albite ($\text{NaAlSi}_3\text{O}_8$) reacts with carbon dioxide and produces kaolinite ($\text{Al}_2\text{Si}_2\text{O}_5(\text{OH})_4$):



Because those reactions consume acid, pH and the alkalinity content of groundwater generally increases as chemical weathering occurs (Carrillo-Rivera and Cardona, 2012). Microbial respiration occurring alongside these chemical weathering reactions can also increase pH because many microbial respiration reactions consume protons (Park et al., 2006, 2009).

Solutes liberated by chemical weathering can serve directly as nutrients for algae, including silica and numerous trace elements. Moreover, by affecting the pH and ionic strength of groundwater, chemical weathering would also affect the sorption of nutrients onto aquifer and hyporheic zone minerals (Cornell and Schwertmann, 2003). For example, phosphorus sorption onto (oxyhydr)oxide is at its maximum at low pH and decreases gradually as pH rises (Cornell and Schwertmann, 2003). This relationship suggests that the ability of phosphorus to sorb may tend to decrease as acid is consumed by weathering reactions.

Factors that determine the extent to which those reactions occur include the residence time of the water in the subsurface and the reaction kinetics of the minerals along the flow paths. Groundwater that has had a longer residence time in the subsurface has had more contact time with minerals, allowing more weathering to occur. Some minerals react relatively quickly with acid and are often found to be in equilibrium with groundwater (e.g., calcite) whereas other minerals react more slowly but still have a significant influence on groundwater chemistry (e.g., plagioclase, biotite, and other primary silicates) (Glynn and Plummer, 2005). Therefore, local geology has a strong influence on the weathering reactions that occur along groundwater flow paths and thus the concentration and form of nutrients that could be delivered to the surface.

Hypothesis 3. Systems with greater proportion of groundwater discharge have greater stability and thus increased probability of supporting ABs

The proportion of groundwater discharge influences the environmental stability of conditions of an aquatic habitat. Groundwater chemistry, temperature, and the direction and magnitude of exchange with surface water significantly affects conditions in those surface water bodies (Winter, 1999). Surface water bodies that receive little groundwater are heavily influenced by climatic conditions and variability. Groundwater discharge can help buffer surface water variability, especially between precipitation events, by providing a relatively steady source of water with a relatively

stable composition and temperature. Therefore, systems receiving a relatively higher proportion of water from groundwater discharge have the potential for greater stability (Figure 1) which may promote stable food-webs and singular AB development (i.e. one taxa becomes dominant).

Hypothesis 3-1. The influence of groundwater on surface water composition and AB development is greater during dry seasons than wet seasons.

Stream water consists of water from different sources and with different histories. Stream water sources include surface runoff, shallow soil water (e.g., perched water table), and relatively deep groundwater. The dominance of shallow versus deep water varies under wet and dry conditions. Disproportionally high DOC and nutrient exports during storms suggest that shallow soil water is a major source and key driver of variable stream concentrations of these constituents (Boyer et al., 1997; Pacific et al., 2010; Seibert et al., 2009; Zhi et al., 2019). For example, under wet conditions when stream water is predominantly derived from shallow soil water, nitrate concentration is often high reflecting the legacy store of fertilizers in soils (Van Meter et al., 2018). Conversely, under dry conditions when streams are often groundwater fed, nitrate concentrations may reflect the extent of nitrate removal and denitrification in the subsurface (Benettin et al., 2020; Kolbe et al., 2019; Thomas et al., 2016). Although, also under dry conditions, stream water may reflect the high concentrations of geogenic species derived from deep groundwater sources (Kim et al., 2014) or reflect the high concentration of wastewater derived nutrients and contaminants if wastewater supplies low-flow conditions (Bowes et al., 2005). The chemistries of deep and shallow groundwater typically differ, with the extent of difference usually defined by the variance of subsurface physical and biogeochemical conditions with depth (Herndon et al., 2018; Sullivan et al., 2016).

Hypothesis 3-2. Groundwater discharge influences the stability of AB conditions in aquatic habitats through maintenance of greater biodiversity.

A growing body of research supports the idea that maintenance of biodiversity is an important tool for habitat stability (Hooper et al., 2005) and control of AB (Glibert, 2017). Natural disturbances (rainstorms, changing flow conditions, fires, etc.) are a few of the ways that biodiversity in stream habitats is maintained through development of heterogeneity within the stream and for opportunities for new species to colonize (Arnon et al., 2015; Stegen et al., 2016). When a greater number of species can take advantage of niche opportunities to control nutrients in streams and groundwater, many potential outcomes exist in terms of species dominance within the stream, often preventing one single dominant species (Cardinale, 2011). An example of this is the greater occurrence of salmon redds in locations with upwelling hyporheic groundwater (Larsen and Woelfle-Erskine, 2018; Neumann and Curtis, 2016), where salmon populations are known to have suppression effects on key AB consumers such as invertebrates (Harding and Reynolds, 2014). While the interplay of the chemical composition of GWSWI and groundwater discharge and other factors controlling biodiversity is complex (Lepori and Hjerdt, 2006) the potential for research delineating key feedbacks and interactions between groundwater discharge and species biodiversity highlights several lines of inquiry: (i) How does groundwater discharge from agricultural areas impact stream biodiversity and AB? (ii) Given algal and microbial species with varying degrees of functional diversity can participate in significant nutrient uptake, can maintenance of algal and microbial biodiversity help control nutrient exports downstream? (iii) Is there a feedback mechanism such that greater groundwater discharge can promote some AB taxa to dominate and potentially limit biodiversity?

3. Looking to the future: potential implications of environmental change on groundwater control of ABs

Many changes to our environment have occurred and are predicted to occur in the future. These environmental changes will affect processes and mechanisms that cause ABs, including the role of groundwater. Most environmental changes are driven by anthropogenic activities, including changes in land use, water management and climate. Here we discuss some implications of the potential changes to groundwater's role in AB development with respect to these changing environmental conditions.

3.1. Land use

Since the 1600s, the dominant change in land use continues to be the conversion of natural watersheds (e.g., forests, shrublands, wetlands) to agriculture (croplands and grazing). Recent studies have demonstrated that agricultural watersheds with the fewest wetlands tend to contribute the highest nutrient loads (Hansen et al., 2018). In addition, the adaption of agricultural management systems, such as the installation of subsurface drain tiles, have increased the rate of water delivery dynamics within the watersheds (Foufoula-Georgiou et al., 2015; Schottler et al., 2014; Zhang and Schilling, 2006). Agricultural lands today are intensively managed landscapes where human energy inputs (farm machinery and chemical use) and human modifications of the landscape (tile drains, ditching, and channel straightening) have greatly amplified nutrient loading and accelerated their delivery to downstream waterbodies (Kumar et al., 2018). Long term stores of high nitrate concentrations (Wang et al., 2012) have been mapped globally (Ascott et al., 2017) and suggest that high nutrient load futures will be a likely long term input to surface water systems. Phosphorus is also projected to represent a likely legacy nutrient source on future algal blooms. Recent studies have shown just how reactive different forms of phosphate are and how they can have multiple sources along with complex retention and remobilization mechanisms (Bingham et al., 2020) and also represent likely legacy effect on future algal blooms. Despite worldwide efforts to reduce watershed inputs of nitrate and quantify legacy nutrient stores, agricultural lands are predicted to expand in the future to try to meet the food demands of an increasing population. An implication of the legacy nutrients and the expansion of agriculture is the promotion of conditions favorable for ABs development for decades to come.

3.2. Water management

The hydrologic conditions and distribution of water throughout most river basins are controlled by reservoirs, and are further modified by surface water diversion and groundwater pumping for irrigation (Barlow and Leake, 2012; Graf, 1999). With changing climate conditions, these management strategies will be optimized to best maintain or augment current water resource availability due to economic, social, and ecologic dependence on consistent and accessible water resources (e.g., Brookfield and Gnau, 2016; Smilovic et al., 2019). As such, water management practices can dominate the hydrologic conditions of managed river basins, and can have implications on AB development.

Reservoirs and surface water contributions/diversions affect the hydrologic conditions of a stream through altered flow rates and surface water levels. This can also affect water exchange with the subsurface and hyporheic flow (Winter, 1999). As a result of these manmade controls over stream levels, hydrologic conditions in the stream do not necessarily reflect climate variability, and algal growth and transport within the system may not be predicted by climate conditions alone (Drenovsky et al., 2010). Drenovsky et al. (2010) found that water availability was a main factor driving microbial composition and biomass, and that biomass was lowest in ecosystems with either the wettest or the driest soils. Additionally, they found that soil water availability

was a better indicator of microbial community composition than precipitation, particularly in agricultural regions where water management is integrated into soil moisture measurements (Drenovsky et al., 2010). In many of Europe's largest rivers, low flow conditions during dry periods are mostly supported by wastewater inputs rather than groundwater baseflow (Bowes et al., 2005) representing a potentially large source of non-groundwater derived nutrients. Therefore, changes to reservoir management and surface contributions/diversions may have significant effects on the prevalence of downstream ABs.

Surface water is not the only system impacted by anthropogenic water management and use. Over the past century, groundwater use in irrigated agriculture caused overexploitation of major aquifer systems around the globe (Scanlon et al., 2012; Siebert et al., 2010). This has also affected surface water as groundwater is primarily discharged to streams and rivers and is often the main component of streamflow (Barlow and Leake, 2012). Groundwater extraction can reduce baseflow to streams, reducing water levels and altering GWSWI and hyporheic flow. Non-stationary effects of climate change, including warmer temperatures and longer droughts, have further exacerbated the problem (Diffenbaugh et al., 2015; Luce and Holden, 2009; Milly et al., 2008; Rood et al., 2005; Seager et al., 2007). During droughts, groundwater is relied upon to compensate for the lack of precipitation and streamflow, and during wet conditions groundwater use is reduced because water is available through precipitation or streamflow diversions. This variability in groundwater pumping causes changes to flux through a streambed, and can convert a gaining stream to a losing stream (Figure 1b; Barlow and Leake, 2012) further depleting streamflow, and increasing the likelihood of low flow conditions. In addition, changes to groundwater pumping can cause variability in hyporheic flowrates and patterns (Boano et al., 2014). As described previously, groundwater discharge to streams and hyporheic flow are important sources of nutrients and thermal energy to streambed and in-stream environments and support the stability and richness of in-stream microbial communities (Barlow and Leake, 2012; Boano et al., 2014). An implication of increased groundwater extraction is a reduction in the delivery of these nutrients and thermal inputs, decreasing the frequency and intensity of ABs (Cho et al., 2016).

3.3. Changing climate

Climate shifts, including the type (e.g., snow/rain dominance), frequency, intensity and duration of precipitation events as well as melt dynamics, are altering GWSWI by changing the ratio of inputs from direct surface runoff, shallow groundwater inputs, and deep groundwater inputs (e.g., Foster and Allen, 2015; Sulis et al., 2012). For example, many of the mid-continent and western mountain ranges in the US have been experiencing a decline in snow pack and/or early melt or rain-on-snow events. This shift toward more rapid melt dynamics and a greater degree of rain-on-snow events is often linked to increases in overland and shallow subsurface flow, compared to slower melt dynamics which support a greater degree of infiltration and deeper subsurface water flow (Meixner et al., 2016; Surfleet and Tullos, 2013; Tague and Grant, 2009). As flow paths become shallower across these systems, a larger proportion of water interacts with decomposing near-surface organic matter and its associated nutrients and can bypass transformation in the subsurface, delivering more nutrients to surface water bodies.

Like changes in snow dominate recharge of groundwater systems, shifts in rainfall patterns and associated changes in groundwater extraction alter both the quantity and quality of water delivered to surface water bodies (Gleeson and Richter, 2018; Kendy and Bredehoeft, 2006). Specifically, increased depth to the water table due to decreased recharge and increased groundwater extraction can change both hydraulic gradients between groundwater and surface water and the depth to which oxygen and acids penetrate the subsurface. This can

control the release of geogenic derived nutrients and or stored anthropogenic inputs (NO₃; Kløve et al., 2014; Puckett et al., 2008).

Overall, the trend in many environments is that the variance in GWSWI is shifting due to changing climate conditions which has both an impact on nutrients that are delivered to surface waters and the oxic/anoxic state by which both the interacting flow paths and surface water bodies experience.

4. Tools for quantifying groundwater's control over ABs

While we have seen significant advancement in tools capable of improving our understanding of groundwater's control over ABs, these tools often remain siloed in the communities/disciplines where they were generated. Below we present a robust, but not exhaustive, exploration of both new and well-established tools for measuring and modeling groundwater's contribution to in-stream conditions. If used in concert, these can reveal key mechanisms by which groundwater can control AB dynamics and help us to advance aquatic and terrestrial numerical models.

4.1. Measurement methods

Recent advances in environmental sensors make them more affordable, robust, and capable of resolving water sources, flow paths, and biogeochemical transformations. Advancements in environmental sensor technology have greatly accelerated the frequency of measurements, increasing temporal and spatial resolution. The current generation of environmental sensors improves upon: 1) detection of traditional tracers of groundwater such as temperature, conductivity, and discharge (Kalbus et al., 2006; Moeck et al., 2017; Schmidt et al., 2006); 2) environmental signatures of water chemistry that may be distinct between groundwater and surface water or effect critical biogeochemical transformations, such as nitrate concentration, dissolved oxygen, algal pigments (Abbott et al., 2016; Pellerin et al., 2016); 3) stable isotopes including water and nutrient isotopes (e.g., ¹⁸O, ²H, ¹⁵N; Sebestyen et al., 2014; Sprenger et al., 2019; Sullivan et al., 2016); and 4) our ability to assess aquifer microbiology (Chapelle et al., 1995; McMahon and Chapelle, 2008). Together, the information gained from the new generation of environmental sensors can be used to define the role that groundwater is playing in harmful AB formation.

4.1.1. Traditional tracers

Newer methods of detecting traditional tracers of groundwater, such as conductivity and temperature, include the use of fiber-optic cables and thermal cameras, and advances in existing technologies such as pressure transducers (Kalbus et al., 2006) and conductivity probes, all allow high resolution monitoring of groundwater-surface interaction. For example, fiber-optic cables strung along or across a streambed are used to measure thermal profiles and allow for spatially and temporally resolved groundwater inputs to surface water bodies when groundwater temperatures are distinct from the surface water temperature (Schmidt et al., 2006). Advancements in pressure transducer technology to increase measurement frequency and decrease cost allow researchers to easily and affordably measure hydraulic head allowing for estimates of groundwater discharge to the surface (Kalbus et al., 2006). Hydrograph separation can also be used to estimate groundwater discharge to streams with high-frequency measurements of stream stage (e.g., Barlow and Leake, 2012). Similar to temperature sensors, the ease at which we can deploy multiple conductivity sensors and the rate at which they can collect data also allow for the determination of groundwater-surface water interaction when conservative tracers (e.g., Br) are injected into the system (Kuntz et al., 2011).

4.1.2. Environmental signatures

The environmental signature of water chemistries, which can now be collected with high frequency due to advancements in optical sensor

technology, can be used to track material sources and flow paths allowing us to discern distinct groundwater contributions to surface water using, for example, algal pigments, nitrate, orthophosphate, dissolved oxygen, and suspended sediment (Abbott et al., 2016; Burns et al., 2019; Miller et al., 2016; Pellerin et al., 2016). Although sizeable advancements have been made in sensing dissolved materials, current sensor technology is unable to determine particulate nutrient concentrations (Pellerin et al., 2016). High frequency water quality data can be used in conjunction with discharge data to identify and quantify groundwater contributions of key resources controlling ABs. Environmental sensors that are collocated at gage stations are especially useful as they may be used together to identify groundwater source and relative contributions of key resources which contribute to ABs. For example, concentration-discharge relationships based on high-frequency sensor data have shown chemostatic nitrate behavior in many agricultural and urban watersheds and suggest that legacy storage of nitrogen in groundwater can be sufficiently large enough that conservation practices will take a long time to see results (Bieroza et al., 2018; Thompson et al., 2011). Simultaneous comparison of dynamics of environmental tracers such as nitrate, temperature, dissolved oxygen, specific conductivity, with respect to the hydrograph can be used to quantify groundwater contributions of water quality and quantity and track algal density response.

4.1.3. Stable isotopes

Advances in our ability to measure stable isotopes (e.g., laser spectroscopy) are now enabling source tracking of water and identification of processes controlling biogeochemical conditions. For example, water isotopes can be used to differentiate source waters using techniques such as end-member mixing analysis (Carroll et al., 2018; Klaus and McDonnell, 2013), while the collection of high frequency stream water isotope data are now able to reveal travel time distribution of water. Recent developments have led to time-variant travel time distribution theory, recognizing the non-stationary nature of precipitation events and water storage (Botter, 2012; Harman, 2015; Rinaldo et al., 2015; van der Velde et al., 2012). This allows for the quantification of young water fractions to characterize catchment travel time as a way of bypassing the bias from spatial heterogeneity and temporal non-stationary (Jasechko et al., 2016; Kirchner, 2016). Specifically, linking transit time distributions (McGuire et al., 2005; McGuire and McDonnell, 2006) and storage ages (Botter, 2012; Harman, 2015; Rinaldo et al., 2015; van der Velde et al., 2012) with biogeochemical models (e.g., Bio-RT-FluxPIHM; Bao et al., 2017) are the leaps that need to be made to test the hypotheses presented here, such as the influence of aquifer redox conditions (H1) and rock-water interactions (H2) on AB dynamics.

Like water isotopes, the ease at which nitrogen isotopes (¹⁵N) can be measured has also dramatically increased, advancing its use as a tracer of water and nutrient sources and biogeochemical processes that affect nitrogen species (Sebestyen et al., 2014). When paired with techniques of examining elemental stoichiometry (e.g., N, P, OC; Stutter et al., 2018) and elemental concentrations, it is possible to deduce both the controls on aquatic biogeochemical condition that can influence AB dynamics and the sources of water, especially groundwater contributions to surface water. For example, databases such as US Geological Survey (USGS) National Water Information System (NWIS; <https://waterdata.usgs.gov/nwis>) contains groundwater chemistry from sites across the US, which when paired with estimates of groundwater discharge to streams can be used to evaluate fluxes of solutes from aquifers to streams.

4.1.4. Aquifer micro-and-macro biology

Knowledge of aquifer biology will be necessary to develop a mechanistic understanding of the relationship between groundwater discharge and algal growth because of the significant geochemical-microbial couplings that impact groundwater chemistry. Such an

understanding is essential to predicting feedbacks between algal, microbial, and geochemical conditions. Aquifer microbiology can be assessed indirectly using groundwater geochemistry. For example, dissolved hydrogen concentration can be used as an indicator of microbial processes in aquifers (Chapelle et al., 1995; Lovley and Goodwin, 1988). Different groups of microorganisms have different affinities for the hydrogen produced during organic matter degradation thus the steady state concentration of hydrogen in groundwater may depend on which microbial groups are dominant. Groundwater microbial processes can also be evaluated using the framework approach described by McMahon and Chapelle (2008), which uses concentrations of routinely monitored water quality parameters together with a model of thermodynamic hierarchy to predict preferential electron acceptor consumption.

Alternatively, microbial populations can be directly analyzed using cultivation and molecular analyses to assess presence/absence as well as biodiversity metrics, however, many of the microorganisms in environmental samples are difficult to cultivate. Thus, molecular analyses have greater potential for quantitatively evaluating microbial community composition. Quantitative analysis of the presence, abundance, biodiversity and functional role of macro-and-micro fauna in aquifers is a relatively unexplored research direction (Zeglin, 2015). The use of invertebrates as biomonitors of groundwater biogeochemical conditions is an approach with great potential as indicators of the susceptibility for algal blooms (Malard et al., 1996). This analysis is currently challenging because methods to sample these systems (Dole-Olivier et al., 2014), and methods to analyze these systems with metagenomics and metabolomics remain costly. However, powerful new molecular tools are now available to evaluate micro and macro community composition and identify functional genes and gene expression. Those techniques can be used to shed light on the vast metabolic and phylogenetic diversity that can exist in aquifer microbiomes (Anantharaman et al., 2016; Castelle et al., 2013) as well as identify keystone taxa that may eventually be used to predict impacts of groundwater discharge, as well as groundwater microbial community composition on algal growth.

4.2. Modeling methods

Model development in hydrologic flow and reactive transport relevant to ABs has advanced along separate lines. Hydrologic flow models focus on solving for storage and fluxes of water in various components of the terrestrial hydrologic cycle, ranging from separate groundwater and surface water models, to fully-integrated surface/subsurface/atmospheric models (e.g., Fatichi et al., 2016). Reactive transport models (RTMs) have centered on transport and multi-component biogeochemical reactions typically in “closed” groundwater systems without much interaction with “open” watersheds directly receiving precipitation and sunlight (Li Li et al., 2017; Steefel et al., 2015). Given the feedbacks between physical flow, transport and reaction processes that can all shape the conditions for ABs, there is a need to integrate these separate lines of development to not only forecast, assess, and manage AB conditions, but to gain fundamental understanding of reactive transport in both the surface and subsurface systems.

4.2.1. Hydrologic flow models

The hydrology community has developed and utilized models for more than five decades (e.g., Abbott et al., 1986; Bergström, 1976; Beven, 1989; Brunner and Simmons, 2011; Fatichi et al., 2016; Freeze and Harlan, 1969; James, 1972; Jarboe and Haan, 1974; Kumar et al., 2009; McDonnell et al., 2007; Qu and Duffy, 2007; Quinn et al., 1991; Simmons et al., 2020; VanderKwaak and Loague, 2001). Recent advances in computational ability has allowed for these models to develop towards a simultaneous solution of the governing equations for surface and subsurface flow to directly quantify GWSWI. With the integration of surface energy balance, the recent introduction of land surface

processes into hydrological models marks a new advance toward more accurate representation of evapotranspiration (Davison et al., 2018; Maxwell and Miller, 2005; Shi et al., 2013). The Soil and Water Assessment Tool (SWAT) model, with its coupling with the groundwater model MODFLOW (Bailey et al., 2017; Ochoa et al., 2020), can simulate groundwater recharge and the quality and quantity of surface water and groundwater. While many of these models can simulate surface and groundwater interactions, they do not explicitly solve the multi-component reactive transport equations that prescribe solute transport and biogeochemical reactions that transform nutrients in water.

4.2.2. Reactive Transport Models (RTMs)

Multi-component RTMs originated in the 1980s and have been extensively used in the subsurface geochemistry community (Chapman et al., 1982; Chapman, 1982). RTMs explicitly solve flow, transport, and multi-component reaction equations within a biogeochemical thermodynamic and kinetic framework (Steefel et al., 2015), therefore enabling explicit tracing of spatial and temporal evolution of geochemical species in water and solid phases. Built upon the theoretical framework for reaction thermodynamics and kinetics (Lichtner, 1985, 1988), RTMs have since been used as an integration and interpretation tool across diverse environments for many processes, including tracer transport, mineral dissolution and precipitation, ion exchange, and microbial kinetics (e.g., Jin et al., 2013; Meile and Scheibe, 2019; Seigneur et al., 2019). These RTMs have been used in “closed” groundwater systems without integration into the surface hydrology dynamics.

Only recently have RTMs been introduced to integrate the transient hydrological conditions in open watersheds (Bao et al., 2017; Singh and Frevert, 2010). In particular, the recently developed BioRT-Flux-PIHM (hereafter BioRT) integrates processes of land surface interactions, surface hydrology, and multi-component reactive transport (Wen et al., 2020; Zhi et al., 2019, 2020). The model enables the shallow soil lateral flow and deep-water exchange with streams, transport of solutes (including nutrients, carbon, cations and anions), and biogeochemical reactions that leach solutes. The model can quantify groundwater's contribution to surface water bodies, and its role in ABs. As an example, BioRT has been used to simulate processes relevant to nitrate, including the leaching of nitrate in soils and biogeochemical processes such as denitrification (Zhi and Li, 2020). The integration of nitrate data from more than 200 sites in US and the BioRT model has led to the Shallow and Deep Hypothesis, which states that the nitrate concentration contrasts in shallow soil water and groundwater shape the export patterns (specifically concentration-discharge relationship) of nitrate.

Models have also been developed specifically for coastal regions. For example, the model MOHID, a process-based hydrodynamics model for coastal regions (de Pablo et al., 2019), has been coupled with ecological models to assess the influence of light and nutrients on phytoplankton production in the Tagus estuary (Lisbon, Portugal) (Mateus and Neves, 2008). More recently, MOHID has also been augmented with capabilities of simulating sediment transport processes and nutrient and ecological processes (Franz et al., 2014; Franz et al., 2017).

5. Directions for improving the quantification of groundwater's control over ABs

The recent advances made in measurement and modeling of environmental systems, as described above, provides opportunities for other advances towards improving our understanding and quantifying groundwater's control over ABs. Here we briefly discuss opportunities in measurement and analysis, and modeling that can readily achieve significant advances towards these goals. These include the development of coupled algal/food-web/nutrient/flow models, the use and integration of machine learning analyses methods with these models, and the use and integration of DNA and remotely-sensed data in analyses and model application.

5.1. Coupled algal/food-web/nutrient/flow models

Poorly resolved mechanistic understanding and process representation of the coupled food-web and hydrobiogeochemical conditions in watersheds currently limits a predictive understanding of food-web structures and re-establishment after climate and hydrological perturbations (Bajracharya et al., 2014). Although recent modeling developments can simulate GWSWI and reactive transport, the microbe-mediated reactions captured by these models are based on dynamics relevant to bacteria. Work is needed to advance a coupled algal/food-web/nutrient/flow model that can simulate responses to and feedbacks on nutrient-algal conditions in a watershed and where watersheds meet the ocean-terrestrial interface. Limiting development of this numerical capability is poor conceptual representation and limits on our understanding of drivers and controls on ABs. Advancing conceptual models of our systems that include and acknowledge the complexity of hydrological and food-web conditions as important linked systems that control ABs will be the first step towards advancing numerical representation.

5.2. Machine learning

Machine learning approaches have been used extensively in recent years in earth and environmental sciences (Reichstein et al., 2019; Shen, 2018). They have proven to be an effective method of gaining insight into complex environmental systems, and is complementary to mechanistic modeling (Tahmasebi et al., 2020). Often based on statistical and/or analytical methods, they are often less computationally demanding, enabling pattern recognitions and identification of influential factors. Machine learning approaches can be used to offer insights on controls of groundwater over ABs, which can be further used to decide key processes to be included in the mechanism-based modeling approaches, enabling efficient model development. New machine learning models can also help to reveal important interactions between microbial populations, nutrients and AB growth and decline, and provide great potential in places where biological-chemical-physical data are all available (Newcomer et al., 2019). Indicators of groundwater's role in ABs could also be detected, providing insight into whether groundwater's contributions need to be considered at all. Overall, machine learning techniques can improve our ability to efficiently and effectively quantify groundwater's contribution to ABs.

5.3. DNA data

Sampling methods continue to evolve, and new methods have recently emerged allowing for use of novel genomic datasets such as environmental DNA (eDNA). eDNA is a technique used to indicate total biodiversity of a landscape by cataloging microbes to mammals and plants using abundance, genetic, and functional biodiversity (Meyer et al., 2019). Community science initiatives, such as the California eDNA program (<https://ucedna.com/>), enables scalable baseline biodiversity data collection for freshwater systems in public platforms to build biodiversity inventories at state-wide scales. Methods such as eDNA provide promising solutions to two difficult problems in freshwater science: 1) measuring the presence and abundance of taxa in streams, and 2) measuring the true absence of taxa in streams. Building an inventory for a specific stream allows for the detection of taxa and the construction of the local food-web and organism community even if not directly visible. By creating inventories and quantifying the biodiversity and function of aquatic and aquifer taxa, this method can help to reveal the role of total biodiversity across aquatic-aquifer systems on controls of ABs.

5.4. Remotely sensed data

Advances in satellite and unmanned aerial vehicle (UAV) technology provide unprecedented accessibility to environmental data across large

spatial areas (Chen and Wang, 2018). Over a dozen satellites currently in orbit are collecting data directly relevant to hydrologic conditions, and can therefore be relevant to the development of ABs, and several other satellite missions are scheduled for launch in the near future (Chen and Wang, 2018; McCabe et al., 2017). UAV applications also collect parameters of interest to the development of ABs, including surface temperature, geomorphology, and vegetation types (e.g., Cook, 2017; DeBell et al., 2015; Lottes et al., 2017). These datasets can help detect the presence of ABs, and recent research has begun integrating remotely sensed data into calibration of mechanistic models (Chen and Wang, 2018). Further advances in the integration of remotely sensed data into model development will improve the representativeness and predictions of these models, and thus improve our ability to evaluate groundwater's control over ABs.

6. Conclusions

Watersheds sustain life on Earth by supplying water, nutrients, and supporting biodiversity. These essential resources are increasingly impacted by growth of ABs, harmful and otherwise, driving research into factors that affect the frequency, duration, and magnitude of blooms. Although much has been learned so far, our review sheds light on the often overlooked role of groundwater as a significant knowledge gap in understanding controls of AB development in inland aquatic habitats.

Nutrient availability and stoichiometry, together with environmental stability, are key factors in bloom development and taxonomic dominance. But inputs of water and solutes from the surface alone do not decide these factors for many inland watersheds as well as coastal waters. Under many circumstances, groundwater discharge makes significant contributions.

Groundwater generally has a significantly longer residence time than surface water, leading to differences in the physical and geochemical properties and processes. The long residence time of groundwater in the subsurface provides more opportunities for mineral weathering and microbial reactions to impact nutrient availability. Groundwater discharge can supply nutrients and affect nutrient ratios in surface waters, including nutrients that affect algal growth rates and taxonomic dominance such as P, N, Fe, and Si. Groundwater can also promote algal growth in surface waters by helping stabilize biogeochemical conditions.

The impact of groundwater discharge is likely spatially and temporally heterogeneous, reflecting the complexity of subsurface environments and groundwater-surface water interactions. We hypothesize that factors that decide groundwater's contribution to AB development include the types of microbial reactions that occur along the groundwater flow paths, the extent of water-rock interaction, and the proportion of groundwater discharge in streamflow. Numerous tools are available to help test these hypotheses, including tools that assess groundwater composition and microbiology, tools that quantify contributions to streamflow from groundwater discharge, and tools that simulate fluid fluxes and biogeochemical reactions.

Testing these hypotheses will advance our understanding of the roles of groundwater discharge on algal growth and will improve our ability to predict how changing climate and water resource management will influence bloom frequency and toxicity. Therefore, we can use this understanding to refine management practices and better prepare for future uncertainties. Groundwater contributions to surface water is not the only control on AB development in inland aquatic habitats, but our review indicates that it is an underappreciated factor that deserves more attention.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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