

## Integrating periphyton and surface water–groundwater methods to understand lake ecosystem processes

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### Abstract

Groundwater–surface water (GW–SW) interactions represent an important, but less visible, linkage in lake ecosystems. Periphyton is most abundant at the GW–SW interface and can rapidly assimilate nutrients from the water column. Despite the importance of periphyton in regulating whole-lake metabolism, they are less well studied or monitored in comparison with planktonic taxa and pelagic systems. This is in stark contrast to studies of flowing waters and wetlands, where variability in GW–SW connectivity and periphyton productivity is more often incorporated into study designs. To bridge the gap between groundwater's influence on lake benthic communities, this synthesis aims to prime researchers with information necessary to incorporate groundwater and periphyton sampling into lake studies and equip investigators with tools that will facilitate cross-disciplinary collaboration. Specifically, we (1) propose how to overcome barriers associated with studying littoral ecological-hydrological dynamics; (2) summarize field, laboratory, and modeling techniques for assessing spatio-temporal periphyton patterns and benthic hydrological fluxes; and (3) identify paths for hydrological techniques to be incorporated into ecological studies, deepening our understanding of whole-lake ecosystem function. We argue that coupling hydrological and periphyton measurements can yield dualistic insights into lake ecosystem functioning: how benthic periphyton modulate constituents within groundwater, and conversely, the extent to which constituents in groundwater modulate the productivity of periphyton assemblages. We assert that priming ecologists and hydrologists alike with a shared understanding of how each discipline studies the nearshore zone presents a tangible path forward for both integrating these disciplines and further contextualizing lake processes within the limnological landscape.

Groundwater–surface water (GW–SW) interactions represent an important cross-ecosystem linkage that is hidden in plain sight. Since the late 19<sup>th</sup> century, scientists have highlighted how lakes can be used for studying interconnected physical, chemical, and biological processes (Forbes 1926; Lindeman 1942). Despite these connections, there is a disproportionate focus on the pelagic zone relative

to the littoral (Vadeboncoeur et al. 2002). Periphyton, or substrate-attached microbial communities, in the benthic and littoral zones of lakes respond to surrounding conditions including water and solute exchange through the GW–SW interface. Periphyton thereby function as indicators of subsurface connectivity and integrators of subsurface solutes into the lacustrine food web. However, because periphyton measurements are rarely coupled with hydrological measurements, our understanding of how they mediate interactions on larger scales, including the whole lake or watershed level, is limited.

Because periphyton are most abundant at the GW–SW interface, they can be early indicators of eutrophication of the water column, rapidly assimilating nutrients before they reach the pelagic zone (Kann and Falter 1989; Gettel et al. 2013). In

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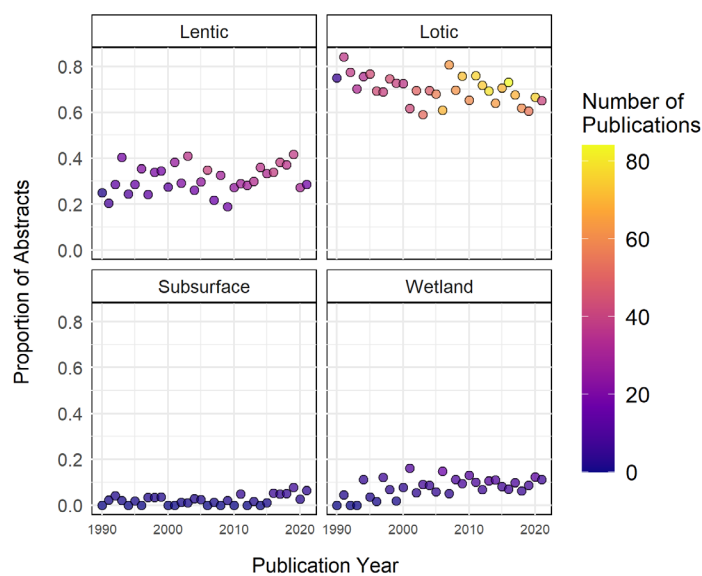
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both monitoring work and paleolimnological investigations, periphyton are indicators of environmental change, chemical fluxes, and groundwater influence in lakes (Battarbee et al. 2012; Schneider et al. 2012; DeNicola and Kelly 2014). Periphyton are as, if not more, productive than planktonic algae and macrophytes which are generally considered the predominant producers in most lakes (Vadeboncoeur et al. 2002; Gaiser et al. 2011), particularly in oligotrophic and mesotrophic systems.

As a main resource for the aquatic food web, higher trophic levels rely on periphyton as a source of essential macronutrients as well as habitat for population and community processes (Hecky and Hesslein 1995; Trexler et al. 2015). Primary and secondary consumers such as benthic invertebrates, fish, and turtles feed on periphyton, creating an energetic link between periphyton and the environment surrounding the lake (Chessman 1986; Jin et al. 2003). Periphyton can also compete with other nearshore primary producers, such as macrophytes, for incoming nutrients from sediment, groundwater influxes, and surface water inflows (Périllon and Hilt 2019). While periphyton may take up nutrients more slowly than planktonic counterparts, they retain nutrients more efficiently, immobilizing nutrients before they are circulated into the water column (Vadeboncoeur and Steinman 2002; Gaiser et al. 2006). In response to subsurface inputs, periphyton contribute significantly to lake biomass production and energy flow by moderating the exchange of nutrients between the open water and the littoral zones.

Despite the importance of groundwater in regulating periphyton dynamics, GW–SW connectivity is a less well-studied aspect of lake ecology and hydrology relative to surface and midlake processes (Vanek 1987; Healy et al. 2007; Rosenberry and Winter 2009). Even in studies examining periphyton communities, groundwater has remained historically less represented in the literature relative to lotic and lentic environments (Figure 1). Likewise, in comparison with lotic systems, lentic periphyton is less represented in the literature, implying that our overall understanding of periphyton dynamics has largely been based in rivers and streams, although significant contributions have also been made in wetlands and coastal areas (Valett et al. 1997; Boulton et al. 2010; Gaiser et al. 2011; Krause et al. 2011; Lecher and Mackey 2018; Taniguchi et al. 2019). It is understandable that the subsurface has been less represented in the lake-focused limnological literature: groundwater can be “out of sight, out of mind.” It is more difficult than surface water to measure, it has spatially and temporally complex flow dynamics, and groundwater flow and solute contributions are often assumed to be small enough to ignore, though they can account for significant portions of nutrient budgets (Rosenberry et al. 2014; Lewandowski et al. 2015).

Our methods of monitoring groundwater discharge to streams and lakes have advanced in recent decades leading to greater understanding of these systems. Rather than siloing groundwater from surface water, researchers and managers



**Figure 1.** Time series of proportion for lentic, lotic, subsurface, and wetland systems papers referencing “periphyton,” “attached algae,” or “benthic algae” in primary, peer-reviewed literature ( $n = 2,482$  abstracts; 49% of all total studies referencing any of our Web of Science search terms). Since 01 January 1990 through 27 July 2021, lotic systems (i.e., rivers and streams) have most frequently incorporated periphyton into their sampling schemes in comparison to studies in lentic, subsurface, and wetland systems. While periphyton literature has consistently represented lentic systems, wetland periphyton representation increased in the early 1990s then leveled off, maintaining a consistently low presence. Subsurface systems are marginally prevalent throughout the entire time series, although literature from 2014 to 2020 suggests a gradual increase in subsurface systems. While these data broadly suggest groundwater–periphyton linkages as a clear and distinct knowledge gap, they also suggest a surface water specific understanding of benthic primary productivity. Furthermore, the discrepancy between systems reflects that the periphyton literature has foundations in systems with shorter hydraulic residence times. In contrast, lentic, subsurface, and wetland environments tend to have longer hydraulic residence times, where solutes may concentrate differently thereby requiring biological communities to develop system-specific adaptations. By addressing periphyton dynamics in lakes and especially in relation to groundwater, the literature can build on its established foundations for more holistic synthesis across systems. Methods detailing how the quantitative evidence synthesis (Meyer et al. 2019) was performed can be found in the supplemental information.

have begun to view water as one resource, acknowledging water’s flow within a mixed groundwater and surface water system (Winter et al. 1998). With this, methods to measure and conceptualize groundwater movement including seepage meters, temperature peepers, three-dimensional (3D) models, et al have greatly improved (Rosenberry and LaBaugh 2008 and citations therein). These newer sampling and modeling methods for groundwater study have created opportunities for ecologists and hydrologists alike to more robustly incorporate groundwater into sampling designs, and therefore bridge the gap between littoral, and even pelagic, productivity and subsurface processes.

Pairing hydrological techniques with established and emerging periphyton methods will advance our understanding of

littoral ecology and responses to ongoing environmental change, such as the increased occurrence of filamentous algal blooms in clear-water lakes (Vadeboncoeur et al. 2021). In this review, we outline common field methodologies and modeling techniques in hydrology and ecology, as these methods are sparse in limnological training programs. Rather than viewing heterogeneity in benthic structure and function as a hurdle, we argue that this “patchiness” can be used to provide valuable insight into hot spots and hot moments of biogeochemical processing (McClain et al. 2003; Lambert et al. 2008; Spitale et al. 2014). We aim to offer a concrete path forward for integrating hydrological and ecological processes in nearshore zones of lakes. The overarching goal of this synthesis is to prime researchers with information necessary to incorporate groundwater into lake study and equip investigators with tools and knowledge that will facilitate cross-disciplinary collaboration. This overarching goal can be further divided into three components:

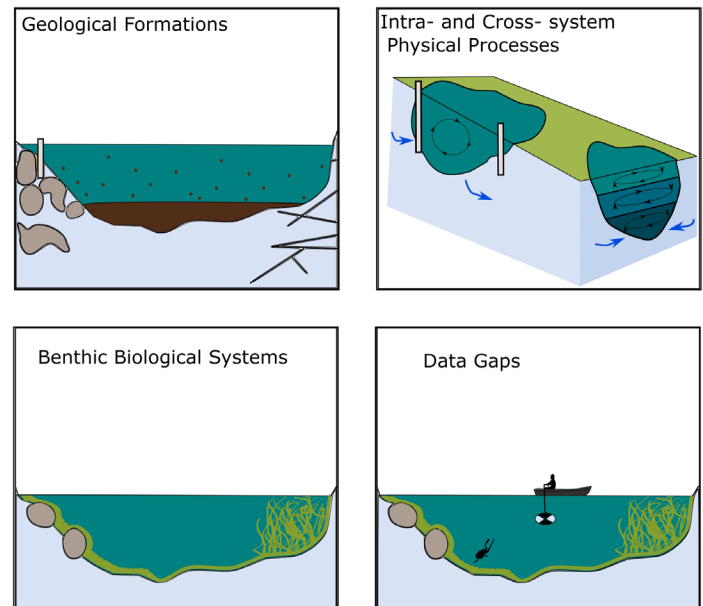
1. Propose solutions for overcoming barriers associated with studying littoral ecological–hydrological dynamics.
2. Summarize field and modeling techniques for assessing spatiotemporal periphyton patterns and hydrological fluxes.
3. Identify ways that hydrological techniques can be incorporated into ecological studies to deepen our understanding of whole-lake ecosystem function.

### Overcoming barriers to benthic and hyporheic zone study

When integrating groundwater and benthic ecology techniques for holistic study, it is important to acknowledge the spatial and temporal variation of groundwater inputs and biological processes throughout a lake (Lodge et al. 1989; Rosenberry et al. 2014). Although there are several causes of this heterogeneity, four crucial factors make benthic and hyporheic zones a complex system to study: (1) underlying geology, (2) intra- and cross-system physical processes, (3) biological benthic communities and processes, and (4) data gaps (Figure 2). Together, these barriers are among the primary reasons that the subsurface may be seen as too complex to accurately account. Although incorporating the subsurface into lake studies is admittedly challenging, understanding the challenges allows future research to more accurately incorporate new tools and approaches for studying the subsurface. Below, we briefly detail each of these four factors to facilitate deeper understanding and appreciation of the similar barriers to both hydrological and periphyton study.

#### Underlying geology

Underlying geology influences both groundwater flow and periphyton dynamics. Periphyton composition is directly related to substrate type, as periphytic species and communities are often limited by their motility and attachment



**Figure 2.** Primary barriers to studying the benthic zone include (a) the heterogeneity of geological formations and their properties; (b) intra- and cross-system physical processes, (c) the active role of benthic biological systems, and (d) data gaps. Each panel depicts a characteristic example of how each barrier may be encountered in a system. Geological formations (a) can include disparate particle sizes, ranging from porous gravel with high hydraulic conductivities to impermeable bedrock layers with unknown orientations. Spatial layouts and physical geological properties can direct groundwater flow and influence solute concentrations, which can be consequential for receiving periphyton communities. Intra- and cross-system physical processes (b) can allow for certain systems to act as sources or sinks of necessary solutes. Mixing patterns, for example, may influence solute residence time within a lake, whereas groundwater flow fields and a system’s position within the limnological landscape may influence cross-system transport. Benthic biological systems (c) can likewise complicate periphyton studies, as ecological processes such as competition, facilitation, and grazing may drive community patterns in unexpected ways. Lastly, even when data may be available, data gaps (d) resulting from the spatial or temporal resolution or methodological constraints of a given sampling protocol may render data less useful for asking questions pertaining to whole-lake benthic processes.

techniques, bounding them to niche substrates on rock, sand, mud, and others (Lowe 1996; Vadeboncoeur and Steinman 2002). With regard to hydrology, the local recharge, hydraulic properties of the sediments, hydraulic gradients, and degree of urbanization can influence the timing, location, and rate of solute influx via groundwater. The porosity and hydraulic conductivity of the substrate surrounding a lake will determine its capacity for groundwater flow. The increased flow in substrates like sand and carbonate rock allows for greater hydrological and ion fluxes between the lake and groundwater, while lakes situated on non-porous bedrock or dense organic substrates may have little or no groundwater exchange. In many lakes, substrate type is heterogeneously distributed. For example, lakes within watersheds with substantial near-surface horizontal flow will have greater substrate

porosity and flow in their littoral zones. More broadly, sediment pore size and hydraulic connectivity, which may be altered through urbanization (Bhaskar et al. 2015; Shannon et al. 2020), also impact the degree to which water and solutes can move from groundwater into surface waters following rain or storm events (Robinson et al. 2017).

Sediments and deeper geologic layers also can influence the chemistry of groundwater delivered to lakes. For example, areas with carbonate rock often have more alkaline groundwater, while areas with metamorphic rock tend to have more acidic groundwater inputs (WDNR 2015). In Karstic ecosystems, where groundwater flow is especially prevalent, limestone and marl substrates rapidly adsorb phosphates from groundwater, reducing the amount of total phosphorus which is ultimately delivered to the lake via groundwater.

#### **Intra-lake and cross-lake landscape processes**

The location, magnitude, and direction of GW–SW exchange within a lake is largely determined by the lake's position in the landscape (Webster et al. 2005) and terrain type (Winter et al. 1998). Intra-lake hydrodynamics complicate the direction and movement of hyporheic zone solute gradients. In flow-through systems, differences in groundwater and surface water chemistry create intra-lake nutrient and ion gradients (Hagerthey and Kerfoot 1998), leading to spatial variability in periphyton structure (Hagerthey and Kerfoot 2005) and function (Hunt et al. 2006). The general finding of these studies was that areas of groundwater influx are associated with increased nutrient loading, periphyton production, and periphyton diversity. In lakes, wave action, seiches, currents, convective overturn, and seasonal turnover events also promote internal mixing and solute transport (Conant et al. 2019). The same processes can cause surface water to enter the subsurface (Heiss et al. 2015) and even cause near-shore surface water to circulate through sediments at a deeper depth (Valett and Sheibley 2009). Seiches cause lake-level fluctuations and temporary reversals in local hydraulic gradients that drive water into and out of nearshore and lakebed sediments (Taniguchi and Fukuo 1996).

At larger spatial scales, lakes within a regional landscape experience differences in groundwater dynamics and influence based on both local and watershed-level factors (Webster et al. 2005; Johnson and Host 2010). Locally, terrestrial community composition plays a role in the groundwater carbon and nutrient content (Murphy et al. 2015; Ward et al. 2017). At the landscape level, the role of groundwater hydrology has long been recognized as a driver of heterogeneity across lakes (Juday and Birge 1933). Lake morphometry, substrate composition, and light attenuation (Vadeboncoeur and Steinman 2002) can likewise influence periphyton production (Lowe 1996; Vadeboncoeur and Steinman 2002). Further insights may be taken from analogous work on periphyton

landscape dynamics done in wetland ecosystems (Gaiser et al. 2011).

#### **Benthic biological systems**

Littoral biota play an active role in GW–SW exchange processes. Water and solutes passing through the benthos may be altered by the organisms and biogeochemical processes of the littoral zone, complicating chemical mass balance estimates between surface and groundwater systems. Over the course of a growing season, periphyton mats themselves play a large role in these dynamics due to their position at the boundary between the benthos and the water column (Bloesch 2009). The development of these mats on sediments can lead to colmatation, thereby altering the hydraulic and thermal properties of sediments, mixing patterns, and the movement of nutrients (Brunke 1999; Naranjo et al. 2015). Periphyton can act as a filter between surface and groundwaters, assimilating groundwater-sourced nutrients before they can reach the lake (Carlton and Wetzel 1988; Hansson 1990). However, periphyton likely compete for groundwater nutrients with rooted macrophytes which actively uptake solutes from porewater (Bristow and Whitcombe 1971; Granéli and Solander 1988). Aside from competition, periphyton successional patterns can be complex and rely upon disparate properties such as mat thickness and species-specific tolerance to resource limitation (Johnson et al. 1997), disturbance (McCormick and Stevenson 1998), recruitment (Lowe and Pan 1996), and facilitation with heterotrophic assemblages and successional patterns (Jackson et al. 2001), all of which can be directly or indirectly influenced by groundwater inputs. As a result of this complexity of environmental factors, littoral communities often display patchiness in their composition.

#### **Data gaps**

A lack of available information on benthic and edge-zone biogeological systems has been a barrier to the advancement of understanding lakes. Data repositories for biological and geological processes are often isolated entities, making syntheses and meta-analyses of these cross-discipline dynamics less accessible (Waide et al. 2017). Even in instances when data may be considered more available, data at a spatial and temporal resolution necessary to draw robust insights coupling groundwater with benthic processes are not common. In instances where sediment profile data are available (e.g., USDA Web Soil Survey; USDA 2020), the data may be too coarse in space or depth to investigate groundwater in a particular system. In terms of biological data gaps, periphyton community abundance or productivity data often exists as single snapshots that do not explain the spatio-temporal dynamics of periphyton succession (Atkins et al. 2021). Periphyton's heterogeneity can sometimes limit monitoring efforts, as its patchy distribution and uneven community composition can make routine sampling at a given point less representative of the whole system. The extent to which these data gaps create

information barriers depends on the specific research question. Complete knowledge of any system is of course unattainable, but emerging technologies and creatively combined approaches to coupling groundwater and benthic biological processes can help overcome these hurdles and close some of our knowledge gaps.

### **Measuring periphyton and groundwater in the field**

To overcome system complexity, the best-fit field technique depends on the question being asked. Regarding GW–SW flux measurement techniques, Kalbus et al. (2006) provide a thorough review of sampling methods with recommendations for best overcoming issues of heterogeneity and scale, and Cremeans et al. (2020) compare common field methods. We refrain from reiterating the findings of those works at length, and instead have provided a table of useful field methods and their strengths and drawbacks, with citations to relevant work for more in-depth understanding (Table 1).

With respect to periphyton methodologies and trade-offs in field sampling styles, others have offered insight into the most used sampling methods. The most straightforward methods are sampling and assessing natural substrates as used in Bergey and Getty (2006), Biggs and Kilroy (2000), Sawyers (2012), and Larson and Collyard (2019). Nutrient-diffusing substrates and devices are often used to conduct controlled manipulations of periphyton responses to nutrient or chemical influx as used in Bulthuis et al. (1992), Flothmann and Werner (1992), Worm et al. (2000), Douglas et al. (2016), Pringle and Bowers (1984), Fairchild and Lowe (1984), Pringle and Triska (2006), Tank et al. (2006), and Matlock et al. (1998). Typical designs allow a nutrient-rich agar within a container to permeate over time through the container's semi-porous surface, on the outside surface of which periphyton may grow. Similar methods could also provide a methodological framework for testing the effects of groundwater contaminants including nutrients and water-soluble toxins on periphyton biomass, community, and other metrics.

These works detail the strengths and drawbacks of various fundamental periphyton sampling and experimental techniques; to complement the context of these papers, we discuss the rich and rapidly expanding suite of observational tools capable of addressing innovative, interdisciplinary questions related to periphyton productivity. These technologies and methodologies can refine spatial resolution and temporal frequency of periphyton sample collection and processing at unprecedented scales. We focus on whole community analysis, rather than methods pertinent to specific types of periphyton such as cyanotoxin analyses. Below, we briefly review some well-established periphyton methods and also showcase these emerging methods at the forefront of periphyton research (Table 2).

### **Quantifying periphyton biomass and production**

Regardless of whether periphyton are collected from natural or artificial substrates, there are a suite of tools for assessing algal function. We briefly discuss those tools here and also provide a comprehensive table of their applications, strengths, weaknesses, and relevant authorities in Table 2.

Ash-free dry mass (AFDM), sometimes called loss-on-ignition or ash-free dry weight, is one of the most common biomass metrics that quantifies the portion of organic (carbonate) and nonorganic material in a sample. Specific methods to calculate AFDM vary but the concept is based on finding the difference in mass between dried algae and “ashed” algae (Biggs and Kilroy 2000). Alongside AFDM, many investigators also quantify chlorophyll *a* (Chl *a*). The pigment Chl *a* is an essential component of photosynthesis in all phototrophs, including cyanobacteria, making it a widely used analogue for measuring algal biomass or photosynthetic capacity. Periphyton must first be separated from other photosynthetic organisms such as macrophytes. Chl *a* is commonly quantified via spectrophotometry, fluorometry, and high-performance liquid chromatography (HPLC) (Biggs and Kilroy 2000). Though Chl *a* analysis is one of the most common ways to characterize periphyton biomass, pigment levels can vary between taxa and in response to environmental conditions (Baulch et al. 2009). Pigment analyses more broadly can be used to characterize periphyton assemblages and are described below.

The traditional method for measuring benthic production is accomplished by measuring flux of O<sub>2</sub> or CO<sub>2</sub> gas exchange or consumption of <sup>14</sup>C. Experimental chambers must be deployed to the substrate, or the substrate must be carefully removed and brought to the experimental chambers. Isolation from the surrounding water column provides an experimental control, but can also lead to nonrepresentative dynamics of benthic production, metabolism, or water mixing (Glud et al. 2001; Berg et al. 2003). Nonetheless, benthic metabolism estimates from in situ chambers can yield important insights into the extent to which the benthos contributes to whole-lake metabolism (Sadro et al. 2011) and the governing controls of benthic production across gradients of nutrient and light availability (Godwin et al. 2014). While this method has its drawbacks (Table 2), the design could be coupled with hydrological flux measurements to provide an understanding of GW–SW exchange as it is moderated by periphyton productivity.

Aquatic eddy-covariance (AEC) devices deployed just above the benthos simultaneously record fluxes in O<sub>2</sub> via microelectrode, and vertical water velocity via acoustic Doppler velocimeter, to produce information of benthic metabolism or production at fine temporal scales without disturbing the benthic surface. Because the sensors do not interfere with natural benthic processes, AEC devices have potential application to studies involving GW–SW exchange and by extension periphyton processes (Rovelli et al. 2017). Berg et al. (2003) note that other devices aside from O<sub>2</sub> microelectrodes, such as sensors

**Table 1.** Common quantitative groundwater methods. Relative method costs are based on a per sample cost and times are grouped from the lowest costs (\$) to highest costs (\$\$\$) and from the least time (T) to the most time (TTT). We recognize that technological and methodological improvements may vastly influence the time-intensiveness and funds required to process a sample, and so these relative estimates are based on the typical prices and times expected in 2021.

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**Groundwater methods**


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Method (relative cost, relative time)	Purpose	Strengths	Weaknesses	Literature examples
Piezometers (\$, TTT)	Tool used to measure groundwater hydraulic gradients using pressure sensors located along the water table.	Allows for effective understanding of watershed groundwater horizontal and vertical flow; can be used to sample groundwater nutrient concentrations, although this does not necessarily reflect concentrations entering the lake system.	Indirect measure of groundwater flow based on pressure gradients and hydrological connectivity. Many point measurements are needed to accurately represent heterogeneous systems. Useful around a lake, not in it.	Naranjo et al. (2019), Meinikmann et al. (2015), Rosenberry and LaBaugh (2008)
Chemical tracers (\$\$, TT)	Identifies seepage locations and groundwater contributions through use of a geochemical tracer (e.g., calcium and chloride).	Can be used to estimate total percent groundwater input and spatial variation of groundwater inflows within a lake.	Must first quantify diffusive flux rate of the tracer(s) from benthic sediments and extensively sample for the tracer at various depths.	Genereux et al. (1993), Gates et al. (2008), Shaw et al. (2013)
Bioindicators (\$\$, TTT)	Use of indicator species or communities to assess location and magnitude of groundwater inputs.	Straightforward to implement.	Confounding variables can affect presence/absence of specific communities and yield inaccurate results.	Loeb and Hackley (1988), Lodge et al. (1989), Lafont et al. (1992), Malard et al. (1996), Sebestyen and Schneider (2004)
Stable isotopes (\$ \$\$, TT)	Uses differences in isotopic ratios between groundwater and surface water to infer groundwater contributions to the water budget.	Ability to quantify spatial heterogeneity more easily than using large piezometer networks.	Requires verification using other independent measurements of groundwater flow (such as piezometer point measurements) to increase confidence.	Krabbenhoft et al. (1990), Gates et al. (2008), Cook et al. (2008), Cook (2013), Genereux et al. (1993), Schmidt et al. (2010), Shaw et al. (2013), Kendall et al. (2010), Kendall et al. (2015)
Temperature profilers (\$\$, TT)	Tools such as temperature probes are used to estimate both vertical and horizontal flow in recharge and discharge conditions at variable temporal and spatial scales. Fiber optic temperature sensing can also be incorporated to measure quick upward seepage.	Fast, efficient, and can be used to map spatiotemporal changes and rates of change. Especially useful for detecting groundwater recharge in deeper water, unlike other terrestrially established methods. Can be powerful and reliable when paired with seepage meter measurements.	Is most informative when paired with head gradient data using numerical modeling. Tends to underestimate groundwater fluxes by an order of magnitude relative to other techniques.	Naranjo and Turcotte (2015), Anderson (2005), Schmidt et al. (2007), Westhoff et al. (2011), Lu et al. (2017), Cremeans et al. (2020), Rosenberry and LaBaugh (2008), Sebok et al. (2013), Rau et al. (2014)

(Continues)

**Table 1.** Continued

<b>Groundwater methods</b>				
<b>Method (relative cost, relative time)</b>	<b>Purpose</b>	<b>Strengths</b>	<b>Weaknesses</b>	<b>Literature examples</b>
Watershed and lake water budgets (\$\$, TT)	Uses measured water inputs and outputs for the lake/watershed and infers groundwater contributions as the residual.	Relatively straightforward to implement, but can require large effort to quantify all inputs depending on the size or complexity of the system.	Indirect measurement that is susceptible to error if other inputs/outputs are not measured accurately.	Zhou et al. (2013), Rosenberry et al. (2014)
Seepage meters (\$, TTT)	Involves sealing off a specific area of GW-SW interface using an open barrel or large diameter tube and measuring volume changes in the enclosed system to infer groundwater efflux volume.	Direct measurement of exchange. Sometimes requires correction factors that compensate for resistance to flow in tubing or pressure applied to the collection bag.	Tends to under-estimate flux relative to piezometer methods or point-velocity probes, although this can generally be accounted for by using a correction factor.	Lee (1977), Cremeans et al. (2020), Rosenberry and LaBaugh (2008); see Rosenberry et al. (2020) for an extensive review.
Point-velocity probes (SS, TT)	An adaptation of the point-velocity probe. Flow through a borehole between the aquifer and surface water is measured. May also be done for stream beds.	Direct measurement of exchange, and perhaps one of the most accurate measurement techniques, alongside piezometers.	Requires a borehole to the aquifer, making it expensive, difficult, or even impossible in some protected areas where drilling is prohibited.	Cremeans et al. (2020)

measuring carbon dioxide and methane, could easily be substituted to understand other flux dynamics at the benthic interface (Berg et al. 2003; Berg and Huettel 2008; Rovelli et al. 2017).

### ***Periphyton community composition analysis***

Aside from assessing periphyton productivity, algal community composition can also be useful for identifying taxon-specific changes in periphyton community structure and function. While some techniques can be laborious and require system-specific knowledge, rapidly developing technologies like flow cytometry can enable expedient, reliable community composition estimates. Regardless of the specific methodology, these techniques can be used to compare periphyton communities' richness, evenness, or taxonomic and functional dissimilarity to communities at various spatial locations or points in time. These data can also be useful for inferring periphyton responses to various disturbances, such as wastewater inputs (Rosenberger et al. 2008) and changing terrestrial plant communities (Moran et al. 2013). Here, we detail each of these methods as well as the associated benefits,

assumptions, and tradeoffs; a summary of these methods is available in Table 2.

### **Light microscopy**

Algal cell identification and enumeration via light microscopy is considered the gold standard for estimating community composition for algal communities. An ideal enumeration should approximately reflect both the in situ and sampled periphyton community, and so the total number of cells counted for a given sample is important to consider. Once enumeration is complete, biovolume can be calculated by summing the average volume of each cell type. This calculation is done by either averaging micrometer-measured cell volumes collected in the sample or by using published values (Wetzel and Likens 1991; see Hillebrand et al. 1999 for genus-specific equations).

### **Flow cytometry**

Flow cytometry is an emerging method for direct, reliable analysis of algal cells. Flow cytometry uses laser analysis or photometry to identify the physical and chemical characteristics of cells in an algal sample, generating information on

**Table 2.** Common quantitative periphyton methods. Relative method costs are based on a per sample cost and times are grouped from the lowest costs (\$) to highest costs (\$\$\$) and from the least time (T) to the most time (TTT). We recognize that technological and methodological improvements may vastly influence the time-intensiveness and funds required to process a sample, and so these relative estimates are based on the typical prices and times expected in 2021.

Method (relative cost, relative time)	Purpose	Strengths	Weaknesses	Literature examples
Rapid assessments (\$, T)	Provides basic information (percent cover, mat thickness) on the amount and spatial distribution of periphyton.	Fast to conduct.	May need to do surveys regularly and/or pair with another metric to answer specific questions about the community.	Plafkin et al. (1989), Barbour et al. (1999), Winger et al. (2005)
Ash-free dry mass (\$\$, TT)	Provides analysis of the mass/ratio of consumable carbons and other constituents of periphyton.	Useful for analyses of system energetics, carbon stocks, trophic balances.	Drawbacks include an inability to distinguish live from dead tissue and the need to remove invertebrates embedded within the algal mat.	APHA (1998), Steinman and Lamberti (1996)
Chl $\alpha$ (\$\$, TT)	Useful for quantifying the abundance of periphyton in the sample via spectrophotometry, fluorometry, and high performance liquid chromatography.	Direct correlation with production, photosynthesis rates, and metabolism.	Drawbacks include community oversimplification, variation in response to varying light conditions, and species compositions which can confound the Chl $\alpha$ : biomass relationship.	Sartory (1985), Harris and Graham (2015), Garrido and Zapata (2007)
Light microscopy (\$\$, TT)	Algal cell identification and/or enumeration	Is the accepted standard for snapshots of community composition.	Taxonomic identification requires expertise and enumeration can be time consuming.	Lauridsen et al. (2011), Wetzel and Likens (1991)
Pigment taxonomy (\$\$, TT)	Useful in quantifying relative composition of major algal taxonomic groups.	More detail than bulk chlorophyll analyses; can give investigator insight into assemblage shifts through time; highly sensitive to low pigment concentrations.	Pigment standards can be costly; resolution of assemblage taxonomy is coarse.	Leavitt and Hodgson (2001), Steinman et al. (2017)
eDNA metabarcoding (\$\$\$, TTT)	Powerful technique for fast and precise assemblage classification.	Offers reliable taxonomic data when visual identification may lead to misclassification.	Care must be taken when designing metabarcoding studies to ensure that the methodology captures the community of interest; phototrophic eukaryote libraries are still developing.	Groendahl et al. (2017)

(Continues)



**Table 2.** Continued

Method (relative cost, relative time)	Purpose	Strengths	Weaknesses	Literature examples
Biovolume estimates (\$\$, TTT)	Inferring carbon stocks of total algal community and specific taxa.	Detailed assessment of periphyton composition; Estimates of biomass may be drawn using cited averages for species mass or empirical estimates of cell length/width; more accurate estimate of algal C stocks than pigment assessments.	Extremely time intensive, both in processing samples and time needed to learn methodology; this level of detail is often unnecessary to answer relevant questions.	Gotelli and Colwell (2001), Uglund et al. (2003), Hillebrand et al. (1999)
Flow cytometry (\$\$\$, TT)	Can provide information on biovolume, pigmentation, cell density, taxonomy, and cell size and density.	Fast to use and provides large amounts of detailed, precise information.	Instrumentation is expensive, methodologies for periphyton are still emerging.	McCall et al. (2017), Sgier et al. (2018), Graham et al. (2018)
Benthic metabolism and production assessments (\$\$, TTT)	Used as a proxy for growth rates but measures carbon assimilation.	Can be measured as anything from ecosystem rates, which includes the whole periphyton mat and associated fauna, or down to species-specific rates.	Can be difficult to measure if algal biomass is low and the water is near saturation.	Sadro et al. (2011), Godwin et al. (2014)
Nutrient-diffusing substrates (NDS) (\$\$, TTT)	Allow for in situ controlled manipulation studies of periphyton responses to nutrients or other chemicals.	Provides a standardized substrate and ion delivery, enabling quantitative analysis of periphyton nutrient limitation or pollutant response.	Substrate type may influence the community which attaches to it. Diffusive NDS methods may release ions too rapidly and without consistent release rates over the course of deployment.	Fairchild and Lowe (1984), Capps et al. (2011), Costello et al. (2016), Douglas et al. (2016)
In situ pulse amplitude fluorometers (e.g., BenthosTorch) (\$\$, T)	Useful for rapid assessments and approximate community composition (as % green algae, diatoms, cyanobacteria).	Fast, relatively inexpensive; high sample size without need for laboratory analyses.	May overestimate algal standing stocks in some cases, while underestimating biomass on thicker periphyton mats.	Kaylor et al. (2018), Echenique-Subiabre et al. (2016), Kahlert and McKie (2014)
Remote sensing (\$\$, TT)	Provides information about the spatial extent of periphyton blooms. In some cases, can provide taxonomic information.	Can cover much larger spatial scales than most other techniques.	Techniques are still in development for periphyton deep below the water's surface and each site may require local calibration.	Richardson (1996), Gann et al. (2015), Ward et al. (2016)
Fatty acid profiles (\$\$, TT)	Characterizes periphyton nutritional quality and community composition.	Can increase understanding of the entire food web.	Fatty acid content can vary with environmental conditions.	Kelly and Scheibling (2012), Taipale et al. (2013), Galloway and Winder (2015), Galloway et al. (2015)

particle size, particle density, biovolume, pigments, and rough taxonomy at one time (Sgier et al. 2018). While the initial calibration and machine training can be time intensive, once mastered, the procedure can lead to fast results. In preparation for a project, the optimal flow parameters must be identified and a reference data set must be created. Samples should be run soon after collection (McCall et al. 2017) or fixed to be run after longer periods of time (Marie et al. 2014), thus ensuring that cells remain intact. Flow cytometry is more commonly done for phytoplankton analysis due to the relative ease of processing floating single cells; in periphyton samples, extra steps may be needed to homogenize filamentous samples and filter impurities from the sample (McCall et al. 2017). The flow cytometer processes samples in a few minutes and statistical software allows data to easily be plotted and separated into clusters of taxa. Some flow cytometry tools, such as the FlowCam (Yokogawa Fluid Imaging Technologies), specialize in algae identification and use imaging libraries to streamline the taxonomic grouping and identification process (Graham et al. 2018).

The rapid speed of periphyton analysis made possible by flow cytometry makes the technique well suited for keeping pace with high-resolution sampling regimens while retaining taxon-level specificity. For researchers looking to understand fine-scale changes in temporal or spatial processes, flow cytometry may provide the means for processing large numbers of periphyton samples.

### Pigment analysis

Leveraging taxon-specific signatures, periphyton samples collected in the field may be analyzed for community composition without microscopy through extracted pigment analysis via fluorometry, spectrophotometer, or chromatograph. This technique can be used as a complement to more conventional Chl *a* analyses, described above, which allows for the estimation of total algal biomass, but pigment analysis further quantifies the relative proportions of major taxonomic groups (Schlüter et al. 2006; Lauridsen et al. 2011; Tamm et al. 2015). Since algal taxonomic groups differ in their major pigment production (e.g., Chl *b* is only produced by Chlorophyceae, diatoxanthin is only produced by Bacillariophyceae), specific algal pigments and linear, simultaneous linear, or Bayesian approaches can be used to reconstruct the taxa assemblage of the periphyton sample (Browne 2010; Louda 2015). While techniques for classifying algal community composition are increasingly common in paleolimnological (Leavitt and Hodgson 2001; McGowan et al. 2012), marine (Letelier et al. 1993; Schlüter et al. 2000), and to a lesser extent contemporary stream studies (Steinman et al. 2017), at present they have not been widely applied in lentic studies (but see Hogan et al. 2014; Oleksy et al. 2021).

Where taxon-specific pigment analysis may be challenging, in situ pulse amplitude fluorometers (ISPAMFs) are an appealing option for rapid periphyton assessments (Whorley and

Francoeur 2013). ISPAMFs are used as a proxy for chlorophyll concentrations (Kromkamp and Forster 2003). The most widely used ISPAMF is the BenthosTorch (bbe Moldaenke GmbH) which was developed to measure periphyton biomass as Chl *a*, in addition to the spectral signatures of diatoms, green algae, and cyanobacteria pigment complexes to estimate the relative contribution of each group to total algal biomass (Beutler et al. 2002).

ISPAMFs are criticized for not always being directly comparable with traditional algal biomass and community composition measurement methods (e.g., fluorometry, taxonomic classification). Studies comparing the BenthosTorch to cell counts and fluorometric and spectrophotometric quantification of algal pigments have shown poor to moderate agreement (Harris and Graham 2015; Echenique-Subiabre et al. 2016; Kaylor et al. 2018). Despite their limitations, ISPAMFs show promise in rapid bioassessments and characteristics of algal biomass distribution within ecosystems (Kamjunke et al. 2015; Peipoch et al. 2016) and in laboratory experiments (Kotalik et al. 2019; Oleksy et al. 2021) because the biofilms are not destroyed in the process of sampling. Including pigment analyses in biomass assessments can increase the resolution at which investigations can understand how environmental drivers alter not just total algal abundance, but responses of different algal taxonomic groups in a more time- and cost-effective manner than traditional microscopic assessments (Thomas et al. 2013; Lawrence et al. 2015).

### Remote sensing

Beyond chemical and molecular techniques, recent advances in aerial and satellite photometry, as well as in image processing capabilities, have opened the door for remote sensing techniques which can deliver high resolution taxonomic and spatial information about periphyton. Aerial or satellite hyperspectral imaging can be used to detect unique fluorescent signatures of algal pigments or algal byproducts produced by specific taxon groups or communities, allowing a community assemblage to be determined for each pixel (Richardson 1996; Gann et al. 2015). These techniques in tandem with spatial models can inform periphyton biomass, composition, and growth rates at much larger spatial scales than would be manageable with traditional in situ field techniques (Defriez and Reuman 2017). At such large spatial scales and with high-resolution data, heterogeneity becomes an area of study focused on the synchrony of community dynamics as they relate to temporally or spatially organized environmental variables (Defriez et al. 2016). While much of the aerial and satellite imaging work has focused on phytoplankton blooms (Xi et al. 2015; Defriez et al. 2016; Dierssen et al. 2020), important contributions have been made to assessing the distribution and composition of periphyton in lake benthos more than 2 m below the water surface (Richardson 1996), in wetland and epiphytic periphyton (Gann et al. 2015), and macrophyte-attached epiphytic communities (Ward et al. 2016).

### eDNA metabarcoding

Metabarcoding (or environmental DNA [eDNA] analysis) is quickly becoming a powerful technique for fast and precise algal identification, which offers reliable taxonomic data when visual identification may lead to misclassification. Metabarcoding uses next-generation sequencing to identify short unique gene sequences for multiple species within a single sample (Taberlet et al. 2012). This may be done for a specific algal sample or via eDNA by sampling the open water directly as an aggregate measure of all species within the water body. Specific taxonomic identification beyond the status of operational taxonomic units requires that the present species' genetic markers have been previously entered in an available database, which can be a major limitation for many periphyton species. In addition, care must be taken when designing metabarcoding studies to ensure that the methodology captures the community of interest, including active members of the algal assemblage, and that cross contamination via sampling tools is minimized (Kelly et al. 2021). 18S rDNA sequencing, for example, will only detect eukaryotic species and so will not detect cyanobacteria (Groendahl et al. 2017). However, cyanobacteria can still be detected using other primers (Wood et al. 2012). The use and wealth of knowledge this method provides continues to grow and it will likely become a dominant method for future algal taxonomy.

### Fatty acid profiles

When coupled with community composition or genetic information, fatty acid profiles have been useful to characterize algal communities in terms of community composition and nutritional quality (Kelly and Scheibling 2012; Taipale et al. 2013; Galloway et al. 2015; Galloway and Winder 2015). Phytoplankton communities have demonstrated consistent fatty acid signatures at coarser taxonomic levels (Galloway and Winder 2015; Strandberg et al. 2015), such that given a phytoplankton community, relative fatty acid compositions can be estimated (Hampton et al. 2015). Unlike genetic data, fatty acids can vary with respect to environmental conditions, such as available nutrients, light, and temperature (Hill et al. 2011; Flaim et al. 2012; Flaim et al. 2014). However, a recent synthesis across fatty acid studies, demonstrated that interspecific variation in multivariate fatty acid profiles tends to be greater than intraspecific variation, implying that varying environmental conditions are negligible for fatty acid profiles relative to taxonomic-specific patterns (Galloway and Winder 2015).

Fatty acids offer powerful information to infer algal nutritional quality, which can be used to infer available nutrition for the entire food web (Cashman et al. 2016; Guo et al. 2016; Winder et al. 2017). Diatoms, for example, are commonly associated with certain long-chain polyunsaturated fatty acids (PUFAs), such as eicosapentaenoic acid (EPA), whereas chlorophytes are more associated with short-chain PUFAs, such as  $\alpha$ -linolenic acid and linoleic acids (Taipale et al. 2013). In the context of a food web, the relative availability of long-

chain to short-chain fatty acids can be important for mediating grazing macroinvertebrate growth (Guo et al. 2016) or capacity for surviving cold temperatures (Nichols et al. 1993). As such, fatty acid data can be a powerful tool for periphyton researchers by offering information about the periphyton's community composition and the available nutrition to the food web.

### Modeling the benthos

Lake ecosystem dynamics are mostly influenced by external loadings of nutrients from inflowing streams. However, groundwater loads can still be an important factor for in-lake dynamics and cycling of nutrients (Lewandowski et al. 2020). Lakes can be generally characterized as groundwater-fed or seepage systems depending where the lake is located relative to the groundwater table of the surrounding catchment. The influence of groundwater discharges and loadings into a lake system depends on the lake's size and volume, retention time, internal ecosystem dynamics, and the relative importance of the groundwater discharge in the lake's mass balance. Notably, human modification of lake and reservoir hydrology can reverse the groundwater flow field (Gillefalk et al. 2019), which may modify ecological dynamics in nearshore habitats.

In order to quantify GW-SW interactions, an understanding of spatiotemporal variation in ecological, biogeochemical, and physical processes is key. The hyporheic zone is defined as a 3D space beneath and adjacent to surface water bodies where GW-SW interactions occur (Conant et al. 2019). This zone, sometimes referred to as the ecohydrological interface (Krause et al. 2017), includes subsurface materials that can influence the flow, biogeochemical, and ecological conditions of water passing between groundwater and surface water. In addition, it is an area of high reactivity that exerts much of the biogeochemical processing due to mixing dynamics of different waters and temperature effects.

Groundwater flow in the hyporheic zone can be perennial, intermittent, or ephemeral, which has implications for the subsurface flow processes and GW-SW exchange. Sources of recharge and discharge can alter the water balance and, therefore, quantity of water reaching the hyporheic zone. At the bottom of a lake, where bedload transport occurs, bed turnover and entrainment can take place as migrating sediment such as bedforms entrap surface water during saltation. The sediment can be released as the beds migrate or erode (Packman and Brooks 2001). When water traverses through the lakebed materials, mechanical dispersion and diffusion within the hyporheic zone can affect concentration gradients. In addition, the chemistry of groundwater entering the hyporheic zone depends on the source of recharge, sediment-aqueous reactions, the geochemical evolution of groundwater along its flow paths, and anthropogenic inputs to the groundwater system.

### Overview of periphyton modeling techniques

Approaches to periphyton modeling are varied and address a multitude of questions. Empirical models work by assessing observed trends in algal dynamics and linking those trends with other environmental conditions like nutrients, light, temperature, and hydrology to create predictions of likely future algal dynamics under specific conditions. Most of these statistical periphyton models, such as the Everglades Landscape Model (Naja et al. 2017), focus on biomass dynamics.

Statistical models apply regression-style approaches between periphyton biomass and individual predictor variables (ter Braak and Juggins 1993; Birks 2010; DeNicola and Kelly 2014), although more sophisticated models can rely on computationally intensive regression or Bayesian models (Auer and Canale 1982; Rodriguez 1987). The strength of these statistical models is their ability to establish trends, which is especially useful when algal successional dynamics and composition differ from site to site (Wood et al. 2012). Conversely, deterministic, process-based models use well-understood algal functional group dynamics like growth, nutrient uptake, and predation rates to construct a mathematical model of algal function or larger ecosystem interactions and behavior. The specificity of these models can make them useful for evaluating particular characteristics of periphyton communities, such as the vertical structure of the periphyton mat (Asaeda and Hong Son 2001).

Although statistical models can sometimes be limited when data are scarce, technological advances and increased data sharing infrastructures can allow for more data-intensive, statistical modeling frameworks. For example, structural equation models (SEMs) are a promising statistical method for studying periphyton dynamics. By simulating multiple cause-effect relationships at once, food webs and ecosystems can be modeled in a comprehensive manner (Grace 2006). Furthermore, SEMs provide a way to overcome some of the challenges of separating the influences of true environmental drivers from natural ecosystem heterogeneity, something traditional approaches struggle with (Hatami 2019). While SEMs can be influenced by ecological data not conforming to assumed underlying distribution, incorporating copulas and even distance-based approaches to SEM can offer flexible pathways for multivariate analyses of species composition, especially when data may have a high degree of over-dispersion or zero-inflation (Anderson et al. 2019).

In addition to statistical approaches, process-based growth models can be flexible for modeling diverse algal types and systems by employing growth kinetic equations (Schmidt et al. 2019). For example, the Monod equation uses ambient nutrient input rates and consumption rates to model bulk algal growth rates but assumes that the nutrient requirements for all algal species are equal. Examples of periphyton models utilizing the Monod equation include the Water Quality Analysis Simulation Program (WASP; Martin et al. 2006), CE-

QUAL-R1 (Environmental Laboratory 1995), Chesapeake Bay 3-D water quality model, CE-QUAL-ICM (Cercio and Cole 2006), and Hydrological Simulation Program Fortran, HSPF (Bicknell et al. 2005; Model list and citations from Schmidt et al. 2019).

As an alternative, the Droop equation accounts for algal and functional group variation in optimal nutrient uptake stoichiometry ratios (Droop 1974). This allows for more accurate biomass estimates as well as community composition change models. Models implementing the Droop approach include steady-state models (e.g., QUAL2K Chapra et al. 2008) and dynamic models (e.g., WASP; Martin et al. 2006; Cerucci et al. 2010; model list and citations from Schmidt et al. 2019). However, the benefit of this growth equation type is also its drawback: the specific nutrient uptake ratios and growth rates of different algae species are not widely available, and the work required to gain these equation coefficients is impractical for many researchers and managers.

For process-based modeling, it is important to specifically define the characteristics of periphyton biomass and their dynamics to set up periphyton-specific mathematical equations. The WASP model, in particular, formulates criteria that differentiate periphyton, defined as bottom algae, from phytoplankton (Martin et al. 2006). Specifically, (1) periphyton do not move via advection by the water currents, (2) periphyton light limitation is governed by how much light reaches the lake bottom, or the depth at which the periphyton is attached to a surface, and (3) there is a maximum density for periphyton attachment to surfaces (e.g., sediment, macrophytes). The U.S. EPA's AQUATOX is another widely used periphyton modeling software, which simulates entire aquatic ecosystems and allows the user to specify the unique aspects of a given lake's physical, chemical, and biological conditions for more accurate model outcomes. AQUATOX can provide risk assessments, ecosystem change effects, and analytical tools unique to the specified system, including functions to predict periphyton levels (Park et al. 2008; Khare et al. 2020). Another periphyton modeling tool, LakeWeb, requires only seven easily measured variables: lake area, mean depth, maximum depth, epilimnetic temperatures, total phosphorus, pH, and color (Håkanson and Boulion 2004). LakeWeb assumes that phosphorus is the limiting nutrient to periphyton growth and does not differentiate between phosphorus deriving from groundwater as opposed to pelagic phosphorus. These sorts of models provide predictions at the lake-wide scale rather than the site-specific scale, at a longer time step, and often require algae to be categorized into functional groups. Despite their limitations, these models can be useful to assess lake-wide biomass and production dynamics over time or for making predictions across several lakes.

### Process-based modeling of lakes

Process-based models are especially useful to managers because they are more universally applicable, less site-specific,

and do not require extensive prior data and trends to have been collected in order to operate the model. These models are capable of accounting for the mechanistic ecological nuance that statistical models cannot, and so may be better able to model scenarios that have not yet occurred. However, process-based models have drawbacks which are important to consider. Failing to account for a specific dynamic or interaction can significantly alter the model outcome, rendering it useless or misleading. Like probabilistic models, most deterministic algal models tend to be designed for lentic phytoplankton or lotic periphyton and may require precise and specific model parameters, which are not abundantly available in the periphyton literature.

In general, lake systems have a more profound density gradient over the vertical than the longitudinal axis, which allows these systems to be abstracted by vertical one-dimensional (1D) process-based models that solve the vertical heat transfer equation to account for the hydrodynamics of the system. A popular vertical 1D hydrodynamic and ecological lake model is the General Lake Model-Aquatic Ecodynamics Model Library (GLM-AED), which can be used to simulate lake temperature, nutrient dynamics, and light extinction (Hipsey et al. 2019). Vertical 1D lake models have successfully been applied to lakes across the world (Read et al. 2014; Yao et al. 2014; Hansen et al. 2017; Bucak et al. 2018; Ladwig et al. 2018).

These process-based models calculate vertical layers of varying density using a Lagrangian structure (time-dynamic thickness of each spatial grid cell). In GLM, each vertical grid cell has an amount of sediment associated with it based on user-provided lake bathymetry; the model simulates diagenetic reactions as well as heat transfer processes over the water-sediment interface. The model requires a time series of meteorological and stream inflow data as well as initial conditions of the variables of interest, such as a vertical water temperature profile if attempting to model thermal dynamics. Many lake models, including GLM, allow for submerged inflows to replicate the intrusion of groundwater aquifers into the lake system, and seepage outflows from the lake based on a constant seepage rate or calculated by Darcy's law (Hipsey et al. 2019). Here, a groundwater model can be run in parallel to the lake model, in which both models would interact over their boundary interfaces. Menció et al. (2017) have used groundwater data and GLM to understand the dynamics of coastal lagoons. To model nutrient flux pathways and ecological components, GLM is internally paired with AED in a two-way configuration, allowing feedback between the hydrodynamic and water quality model.

Currently, there is no specific AED periphyton module, so creativity is required to use the existing infrastructure to simulate periphyton. The closest thing to a periphyton calculation in AED is a microphytobenthos calculation that is part of the phytoplankton module. The calculation is based on a maximum rate of growth and respiration, a half-saturation

constant for light limitation, and a biomass maximum. The module enables the user to create multiple algal groups with different rates. Although this module was not intended for periphyton, one workaround is to set a microphytobenthos resuspension coefficient to 0, functionally keeping the algae in the sediment. Nonetheless, AED is an open-source and open-access resource, and its modularized structure allows the inclusion of custom models. Therefore, future studies could work on the implementation of periphyton dynamics inside the coupled GLM-AED modeling framework.

The 1D model assumption of a lake works well to model many pelagic processes but falls short when modeling the complexities of benthic and littoral zones. For instance, assuming horizontal homogeneity is problematic for answering questions related to the benthos because the water is interacting with small-scale heterogeneous boundary conditions related to inflow quality and quantity, underlying geology, and competitive interactions among lake organisms. Furthermore, vertical 1D models do not account for the differences between littoral and pelagic conditions (Roberts et al. 2019); littoral temperatures and nutrient levels are assumed the same as pelagic. As a result of benthic and littoral variability, 1D modeling can only be used to represent integrated dynamics occurring in the lake at a time. While these conditions may be useful for some investigators, in order to consider the localized influences that result in spatial heterogeneity, a 3D model is critical for representing various locations and scenarios around the lake.

A prominent and state-of-the-art 3D-coupled hydrodynamic-water quality model is Delft3D, which can be coupled to the water quality module D-Water Quality for water quality simulations (Deltares 2021a,b). Although the coupled Delft3D model has no specific simulation options for periphyton, the modeling framework provides multiple options to simulate functional phytoplankton groups, and advanced optimization functions to replicate ecosystem metabolism dynamics. For 3D flow simulations, Delft3D solves the Navier Stokes equations assuming an incompressible fluid under shallow water and Boussinesq assumptions. The lake domain is spatially discretized using a finite differences grid.

For vertical momentum and transport, two different vertical grid options are available: either the  $\sigma$ -coordinate system (Phillips 1957), or the Cartesian  $Z$  coordinate system. The former allows for a smooth representation of lake bathymetry using a fixed amount of vertical layers with flexible finer discretizations at specific depths. The latter,  $Z$  coordinate system, has horizontal lines that are parallel with horizontal density gradients and is preferred for lakes with a steep bathymetry (Stelling and van Kester 1994). A common lake-groundwater model coupling is the one-way approach, either simulating groundwater flow after surface water flow or the other way around. For instance, Sawyers (2012) used a one-way coupling approach to simulate saturated groundwater flow from steady-state morphology and surface water hydraulics computed via

DELFT3D. The D-Water Quality module calculates mass transport and reaction processes using the advection–diffusion equation with source terms that represent inflow and/or reaction terms. The coupled model is able to simulate a variety of water quality variables such as dissolved oxygen, nutrients, grazers, and bacteria. For phytoplankton simulations, Delft3D can apply the BLOOM model to optimize the algae species composition in an ecosystem to obtain an optimal maximum growth rate.

### Process-based modeling of groundwater dynamics

Complex exchanges between GW–SW within the hyporheic zone require an understanding of flow and reactive transport. As a primer, we present a quick summary of physics-based open-source models for modeling nutrient fate and transport in groundwater. Each of these models can be applied at various spatial (1D to 3D) and temporal (hour to year) scales. We focus on four existing open-source models that are popular and used in many disciplines: MODFLOW, MT3DMS, OPENFOAM, and PHREEQC. While there are many models that span across surface water, mixing, and groundwater that are important to the full characterization of nutrient transport (Sinshaw et al. 2019), we focus strictly on numerical physics-based models that solve a series of conservation principles described by partial differential equations along with constitutive equations.

MODFLOW, developed in 1988 by the U.S. Geological Survey (McDonald and Harbaugh 1988), uses the finite difference method in space and time to solve the groundwater flow equation, a combination of continuity equation and Darcy's law in 3Ds, to calculate changes in the level of groundwater. Using the Lake Package for MODFLOW the user can account for lake-groundwater interactions, including allowances for lake expansion, contraction, multiple inflow and outflow streams, and user-specified relationships for both steady-state and transient conditions (Council 1997).

The lake package provides two major functions. First, it formulates boundary conditions for the system of equations solved iteratively by MODFLOW. Second, it computes lake-wide budget information. These two systems are related through the lakebed hydraulic conductance, which controls the degree of lake–groundwater interaction. In addition, the package calculates lake stage as a transient response to evaporation, precipitation, streamflow, and groundwater flux. Furthermore, this package works with other packages, including recharge, well, river, drain, streamflow routing as well as evapotranspiration. Many graphical user interface versions of MODFLOW exist in the form of open source as well as proprietary software. There are also open-source sensitivity and calibration codes for parameter estimation in groundwater flow such as UCODE (Hill and Tiedeman 2005) and PEST (Doherty 2015) that can be used with MODFLOW.

MT3DMS is used to model transport of chemical constituents within the Eulerian framework (Zheng and Wang 1999).

Using the flow fields generated from MODFLOW, this model solves the advection–dispersion–diffusion equation using finite differences with various numerical solvers (Zheng and Wang 1999). The MT3D-USGS (Bedekar et al. 2016) version of MT3DMS supports simulation of transport using MODFLOW 6 with structured grids only. This model can handle unsaturated zone transport as well as transport within streams and lakes, including solute exchange with connected groundwater. Lastly, there is a chemical reaction package that includes the ability to simulate inter-species reactions and parent–daughter chain reactions.

For more complex equilibrium and kinetic reactions, MT3DMS can be connected to PHREEQC (Parkhurst and Appelo 2013), a highly flexible USGS geochemical code. It is capable of simulating a wide range of geochemical reactions such as mixing of water, precipitation and dissolution of minerals, surface complexation, ion exchange reactions and much more. PHREEQC itself is a stand-alone 1D reactive transport code that contains a thermodynamic database which can be altered for any equilibrium reaction as well as kinetic reactions given all parameters and equations. Therefore, periphyton dynamics, such as scouring, mortality, or decomposition (Asaeda and Hong Son 2001), can be described by kinetic equations and/or empirical equations within the free format input file. PHREEQC uses a sequential iterative operator splitting technique for the coupling between solute transport and chemical reactions.

In order to create a fully complete reactive transport code, these two codes are usually coupled with another open-source code called PHT3D (Prommer et al. 1999). PHT3D is prolifically used within the hydrogeology community to model projects ranging from remediation to carbon dioxide storage and sequestration. It is important to note that for reactive transport modeling the coupling technique, the partial differential equation discretization mechanism and the method in which the domain is considered are all problem dependent.

Finally, OPENFOAM is a C++ object-orientated library for solving computational continuum mechanics (Jasak 2009). Unlike the previously described software, the object-oriented method provides a toolbox of building blocks that can be combined by the user to construct new models and new user-defined building blocks. In terms of spatial meshing, OPENFOAM has the option of finite element or finite volume discretization. There is a post-processing tool in order to visualize the results as well as many other tools to assist the user in meshing. In terms of reactions, OPENFOAM has the capability to do simple kinetic and equilibrium reactions that are defined by the user. However, for more complicated geochemical reactions, it is combined with other third-party applications, such as CHEMKIN, that include thermodynamics and reaction data files.

### Coupled lake–groundwater models

To the best of our knowledge, most groundwater–lake coupling approaches focus heavily on the groundwater side,

describing lakes as simple prescribed boundary conditions that affect groundwater mass balances (Frick et al. 2019). Our envisioned groundwater–lake model would focus on in-lake ecosystem dynamics to better understand periphyton dynamics. We envision multiple paths forward to model the interactions between groundwater aquifers and lakes.

First, the groundwater inflow can be described as a steady boundary condition acting as a submerged inflow at a fixed elevation. Prescribed water masses and loadings would enter the lake, which can be approximated by a vertical 1D model. As in the 1D approximation, the water mass enters the lake, in a subsequent step, mixes with neighboring vertical layers, which can affect the lake's thermal stratification and result in vertical transport.

A more advanced approach similar to the first one could consist of running a groundwater model and a lake model simultaneously, whereas the lake model receives the boundary conditions at every time step from the groundwater model. In this one-way coupling approach, the groundwater discharge would depend on the aquifer's water table height as well as the height of the lake's water elevation.

Finally, we envision a coupled model approach, where the outflow of the lake can be used as a boundary condition for the groundwater model, which would be suitable for hydrologically open basins (e.g., drainage lakes; Rosen 2015). This complex approach would couple a 3D groundwater model to a 3D lake model that solves the momentum, transport, and reaction kinetics in  $x$ ,  $y$ , and  $z$  dimensions. In such models, the aquifers could directly discharge into the lake's littoral areas at dynamic depths influencing ecosystem dynamics and reactions. Reaction hotspots would highlight potential areas of interest between groundwater aquifers and the lake system. Such a coupled 3D groundwater-lake model would be an ideal candidate to investigate alternative scenarios that deal with littoral to pelagic ecosystem differences in lake ecosystems, and the contribution of groundwater inflows to near-shore metabolism dynamics.

A wide range of groundwater modeling tools including conceptual, statistical, physical, and mathematical models are used to represent physical, chemical, and biological systems not only within groundwater, but also across the continuum of groundwater systems embedded within surface water systems, the hydrological cycle, ecology, anthropogenic land use, and economic and social systems. Over time, models from the USGS have become more accessible with more graphical user interfaces and post-processors (<https://water.usgs.gov/software/lists/groundwater/>). Steefel et al. (2015) and Gamazo et al. (2016) performed an extensive review of numerical reactive transport codes relevant to environmental modeling. More recently, Arora et al. (2015), Li and Şengör (2020), Ng et al. (2020), and Rodríguez-Escapes et al. (2020) show case studies that have used reactive transport modeling in lakes and ponds.

Recent water quality modeling studies have intensively investigated nutrient cycling and oxygen dynamics in lake ecosystems using a variety of numerical modeling tools

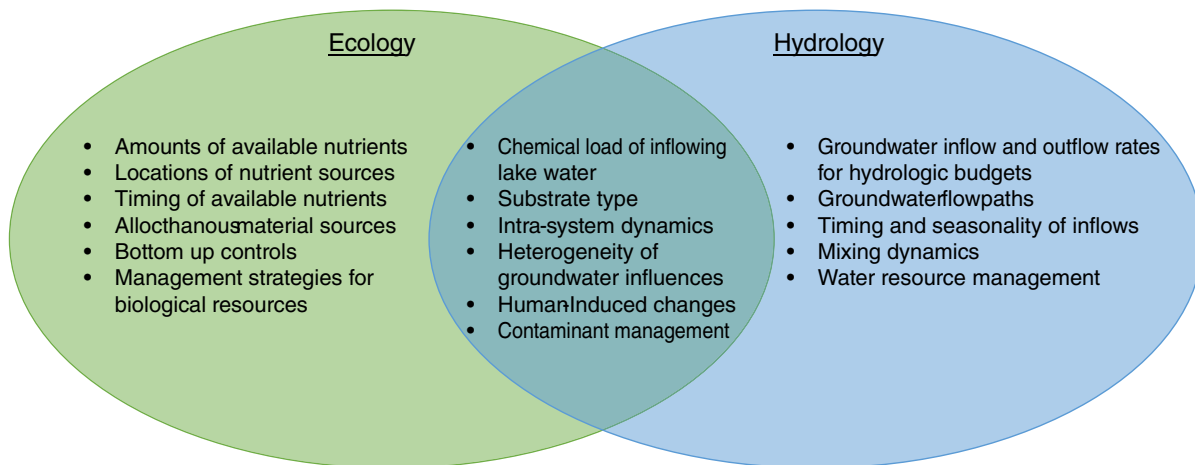
(Magee et al. 2019; Andersen et al. 2020; Bocaniov et al. 2020; Farrell et al. 2020; Mi et al. 2020; Ladwig et al. 2021). Periphyton incorporation in certain studies has been predominantly featured in streams, rivers, and hyporheic flow, by Xia et al. (2018), Liu et al. (2017), Boano et al. (2014), and many others. However, exploration into periphyton representation in reactive transport models in lakes has been limited (Hua et al. 2013; Ginder-Vogel et al. 2019). By taking into account the residence times of hydrostatic and hydrodynamic factors of hyporheic flow, reactive transport models have been used to characterize relationships between vertical hydraulic gradients in groundwater and surface water that create chemical gradients in the hyporheic zone (Ng et al. 2020; Wu et al. 2020; Broecker et al. 2021). Therefore if considering sediment microbiology and enhanced aqueous chemistry, a similar modeling path could be used to study nutrient fluxes into lakes from groundwater. Ultimately, it is up to the user to determine which and what model is best suited for their problem. Model selection can be a challenging task in itself; however, Maher and Mayer (2019) provide a conceptual model to get started on reactive transport modeling.

### ***Integrating hydrological and ecological studies: A path forward***

Coupling measurements of groundwater flow and periphyton responses can yield insight into the interrelated, cross-system processes and can help overcome the disciplines' shared issues with accessibility and heterogeneity (Figure 3). For example, the heterogeneous distribution of groundwater inputs to a lake can be reflected in the heterogeneity of periphyton biomass and community composition at the benthic interface (Hagerthey and Kerfoot 1998; Hagerthey and Kerfoot 2005). As such, linking these approaches has potential to offer dualistic insights: benthic periphyton modulates constituents within groundwater, and constituents in groundwater modulate the productivity of periphyton assemblages.

Groundwater–periphyton interactions additionally provide opportunities to use new sampling and analytical techniques in one field to provide insight into the other. Localized sampling processes that historically are limited by fine-scale heterogeneity can become more site-representative via the use of integrated techniques. At broader spatial scales, newer techniques and models which provide fine-resolution data give us the ability to either average out or embrace variability to develop deeper understanding of the relationships between hydrology and ecology. Coupling these efforts can enable intensive study within a system as well as extensive analysis of periphyton responses to subsurface flows across limnological landscapes. We present two questions below to illustrate an interdisciplinary approach on a small and larger scale, and provide further applied examples in Table 3. To further this strategy, we address the importance of preparing future generations for interdisciplinary work.

Studying groundwater in lakes can lead to a better understanding of...



**Figure 3.** Venn diagram delineating insights that ecologically and hydrologically focused studies can offer individually and when considered together.

**Table 3.** Many questions about the benthos can be answered by pairing ecological methods with hydrological methods. Here are commonly asked questions about the benthos and the groundwater and periphyton methods that can be paired to answer them. Each method is detailed in Table 1 or Table 2.

Question	Approach	Relevant periphyton methods	Relevant groundwater methods
How dependent is the lake's productivity on groundwater nutrient inputs?	Observe: Seasonal or cross-lake comparison of groundwater nutrient influx and periphyton/whole-lake productivity.	Biomass estimates (AFDM, Chl <i>a</i> ), benthic metabolism and production assessments, benthic and whole-lake modeling	Watershed and lake water budgets, seepage meters, point-velocity probes
How will the introduction or increase of a chemical to inflowing groundwater impact my lake's productivity and trophic dynamics?	Model: Define the periphyton response to intrusion with experimental exposure manipulations, then use lake-level models of chemical mass balance and periphyton response to estimate changes to primary productivity and composition.	Nutrient-diffusing substrates, benthic metabolism and production assessments, linear response models, structural equation models	Piezometers, seepage meters, point-velocity probes, pressure transducers, lake-level mass balance models
Could groundwater be contributing to benthic greening in my lake?	Assess spatial extent and chemical composition of groundwater discharge; correlate to production and composition of benthic periphyton.	Rapid assessments, AFDM, Chl <i>a</i> , pigment taxonomy, eDNA metabarcoding, biovolume estimates, benthic metabolism and production assessments, in situ pulse amplitude fluorometers, nutrient-diffusing substrates, modeling	Piezometers, water isotopes ( <sup>18</sup> O and dD), temperature profilers, watershed and lake water budgets, seepage meters, point-velocity probes

**Zeroing in: How responsive are littoral periphyton assemblages to groundwater influxes?**

Within a single lake, integrating groundwater and periphyton assessments can better explain how groundwater influx modulates periphyton community dynamics for both basic

and applied questions. In many cases, in situ data capable of addressing such questions will be limited. Study designs should be outcome-based and the locations of research sites should be strategically chosen. Paired observations of both groundwater and periphyton biomass, at one or multiple



locations allow for correlative analysis. Experimental manipulations, such as those using nutrient-diffusing substrates, can simulate the response of periphyton growth under specific groundwater nutrient scenarios.

Groundwater flow and transport models targeted at understanding where and when groundwater enters a lake can inform critical locations and timepoints for expected periphyton responses. These model outputs could be used to inform areas and timings for paired periphyton scrapings, eDNA analyses, fatty acid profiles, or fluorometry data to explain patterns in periphyton productivity, community assemblage, and even succession. In an applied case, monitoring efforts could use this information to tailor sampling regimes around locations and timepoints when groundwater water influx is most likely, thereby enabling managers to make best use of limited resources.

#### **Scaling up: How does biological mediation of groundwater–surface water interactions matter to whole-lake and landscape ecosystem function?**

In instances where groundwater may connect multiple aquatic systems across a landscape, integrating groundwater and periphyton research can upscale local insights for within and cross basin synthesis. Within a common hydrological landscape, groundwater modeling can demonstrate how lakes are coupled via subsurface systems, thereby informing how solutes may be transferred between systems. Biological processes, such as periphyton production, present a mechanism for retaining key solutes, such as nitrogen, phosphorus, and silica, within a system. These antagonistic processes suggest a mirrored framework: periphyton can be a sink for solutes from groundwater; groundwater can be a source from allochthonous nutrient inputs leading to increased periphyton production. When studying periphyton and groundwater at larger scales and across systems, this framework can be used to compare systems' productivity relative to hydraulic residence time, ecological processes, and even position within the landscape.

Beyond basic research questions, upscaling periphyton studies also presents clear applied managerial implications. Managers interested in how subsurface connections between lakes alter potential for surface water eutrophication could couple groundwater and periphyton models to predict which systems may be most vulnerable and then allocate resources accordingly. Simultaneously, upscaling periphyton and groundwater studies could also apprise potential threats to water quality, which could then inform future threats to drinking water security, especially in instances where local agencies may rely on accessible surface water or groundwater storage. This same information could also be helpful for those developing drinking water policies, where synthesis targeted at identifying commonalities among vulnerable systems could help generalize policies for protecting certain types of systems.

#### **Developing a workforce**

By incorporating hydrological field measurements into ecological studies, we are poised to deepen our understanding of both inter- and intra-system dynamics and the underlying mechanisms driving patterns in periphyton structure and function. Ultimately, the best technique for further integrating groundwater and periphyton dynamics will depend on the particular research question at hand. Technological and methodological advances have created opportunities to investigate lake–groundwater linkages in new ways, but incorporating these methods will likely bring growing pains. Taking full advantage of groundwater modeling will likely necessitate advanced computational training, skills that vary greatly between institutions (Strasser and Hampton 2012; Barone et al. 2017; Hampton et al. 2017; Feng et al. 2020). Furthermore, where training may be available, discipline-specific mindsets or even data-formatting practices could further silo hydrological and ecological understanding, as has been observed with remote sensing, modeling, and in situ measurements of lake ice phenology (Sharma et al. 2020). Therefore, we recognize that further integrating hydrological and ecological frameworks requires not only creating cross-system understanding but also a savvy workforce.

#### **Conclusions**

Periphyton are important regulators and indicators of lake ecosystem function (Vadeboncoeur et al. 2002; Vadeboncoeur and Steinman 2002). Research in the last few decades has demonstrated that nearshore habitat and their associated periphyton production are ecological hotspots, but the field of limnology largely has not incorporated and operationalized this newfound understanding in our study designs and monitoring programs (Vander Zanden and Vadeboncoeur 2020). We recognize that this may be, in part, due to the assumption that littoral processes are too heterogeneous to be fully captured by conventional field studies. Here, we summarize methodological approaches in studying periphyton and the GW–SW connections and fluxes that influence their abundance and distribution.

Underpinning this whole framework, interdisciplinary collaboration between ecologists, limnologists, and hydrologists is critical for deepening our understanding of the magnitude, variability, and controls on periphyton biomass and productivity in lakes. Overall, combining ecological, limnological, and hydrological perspectives on nearshore periphyton productivity offers a synoptic view of littoral, benthic processes that has potential to benefit basic and applied research questions. These techniques may inform monitoring efforts with potential hot spots and hot moments for synergisms between periphyton and groundwater, further enabling agencies to tailor resources around critical locations and moments. Nevertheless, priming ecologists and hydrologists alike with shared understanding of how each discipline studies the nearshore

benthic zone presents a tangible path forward for both combining these disciplines and further contextualizing lake processes within the limnological landscape.

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National Science Foundation ABI development grant (#DBI 1759865). T.P.S. was supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-1610348. NTF was supported by the California State Water Resources Control Board, Lahontan Regional Water Quality Control Board, Contract No. 18-048-160.

### Acknowledgments

The authors wish to thank the Global Lake Ecological Observatory Network ([www.gleon.org](http://www.gleon.org)) for providing a forum for our initial collaboration. We would like to thank Kellie Merrell, Evelyn Gaiser, Paul Kemp, and two anonymous reviewers for their help in improving this manuscript. K.S.A. was supported by the David and Dana Loury Foundation and the Boyd Foundation. I.A.O. was supported by the National Science Foundation awards DEB-1754363 and DEB-1754561. R.L. was funded through a

*Submitted 30 March 2021*

*Revised 20 October 2021*

*Accepted 09 November 2021*

*Associate editor: Isaac Santos*