Title
The Drivers of Periphyton Blooms in Oligotrophic Lakes

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The Drivers of Periphyton Blooms in Oligotrophic Lakes

By

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Abstract

Around the world, oligotrophic lakes are changing. Once pristine shores are increasingly covered in dense mats of periphyton, known as filamentous algae blooms (FABs). Periphyton blooms occur in lakes' infrequently monitored littoral zones and thus are likely underreported and poorly understood. While some blooms have known causes, such as increased groundwater nutrient levels or an influx of invasive species, many FABs occur for unknown reasons. This dissertation examines the drivers contributing to periphytic FABs. In three chapters, Lake Tahoe, California-Nevada, USA, is selected as a case study because, unlike many lakes, Tahoe has a long history of periphyton monitoring.

Overall, eulittoral, splash zone, periphyton at Lake Tahoe did not show a biomass increase from 1982 through 2019. Periphyton was measured consistently at 0.5 meters depth at multiple locations. Thus, as lake level changed over a range of 2.5 meters, monitoring recorded the biomass of either the diatom and green algae dominated community that inhabited the near-surface substrate, or the cyanobacteria dominated community that thrived at greater depths. Trend analysis showed that the stalked diatom and green algae communities did not show a statistically significant change in biomass over time. However, the cyanobacteria measurements showed a significant decline in biomass over time.

The effects of temperature, lake surface elevation, bed-shear stress, mid-lake nutrients, days since the measured substrate was last exposed to air, and photosynthetically active radiation on periphyton biomass were evaluated using Bayesian modeling. The monitored and derived drivers of algae explained 32% of the variability in Lake Tahoe periphyton biomass. Temperature, nitrate, days since last exposed, and photosynthetically active radiation had significant correlations with periphyton biomass. The model could be improved by adding additional relevant data, such as more localized nutrient information.

Looking toward the future, climate change model results were analyzed to project periphyton community and biomass shifts over time in Lake Tahoe. Local climate change conditions will affect many of the drivers of periphyton, including warmer lake temperatures, more nutrient inflows, and greater variability in lake levels. Combining the many changes, two potential outcomes are offered. In one scenario, diatoms continue to dominate the euphotic zone of periphyton, but biomass increases. In the other scenario, an increase in nutrients and temperature shifts the lake towards a green algae dominated euphotic zone. In both scenarios, cyanobacteria are likely to remain the dominant periphyton in the sublittoral zone. These findings suggest that in addition to periphyton drivers, periphyton biomass and community composition should be continually monitored to understand potential change.

Despite the need for more ecohydrological information, few studies analyze groundwater and periphyton. Even fewer programs consistently monitor groundwater and periphyton together. Barriers to studying this transition zone area are created by underlying geology, intra-lake and cross-lake landscape processes, benthic biological systems, and data gaps. Trusted and new periphyton and groundwater monitoring methods are reviewed, and recommendations are proposed for integrating these methods. Using these combined methods and the combined knowledge of interdisciplinary experties, we can further hydrology and ecology.

The chapters of this dissertation provide rationale and methodologies for increased understanding of FABs. Ideas for further future research are provided in the conclusion section.

This dissertation has been formatted so that the chapters standalone as individual manuscripts. Each chapter has its abstract and references within the chapter.

Dedication

This work is dedicated to Anna K. Waarbroek, whom I loved with all my heart.

She *never* gave up.

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1. Introduction

1.1. Periphyton in Oligotrophic Lakes

Periphyton is organisms and detritus that are attached to substrate in aquatic systems. In this dissertation, I use the word 'periphyton' to refer to benthic algae and cyanobacteria and do not distinguish the heterotrophic microbes that live within periphyton matrices. Periphyton communities are found attached to nearly all submerged substrates, including rock, sand, and macrophytes. At low biomass, periphyton is not visible without a microscope and at larger biomass, they can form long filamentous strands that rise toward the water's surface or entwine, creating thick mats.

Periphyton serve as indicators of ecosystem function in the littoral zone. Changes in periphyton productivity can be used to measure areas of environmental stress, where anthropogenic influences cause lake ecosystems to deviate from their normal range of variation (Denicola et al., 2003; Vadeboncoeur et al., 2008). Periphyton is used as an indicator because it is easily visible from the shoreline, reacts rapidly to changing conditions, and plays a critical role in many lake processes, including nutrient cycling, energy flow, and food web interactions (Denicola and Kelly, 2013; Vadeboncoeur and Steinman, 2002). Periphyton and phytoplankton are the food web base in freshwater lake systems (Hecky et al., 1995; Yoshii, 1999). As a result of their significance to the interpretation of lake-ecosystem health, it is important to monitor and understand the factors driving periphyton biomass levels.

Around the world, periphyton blooms are increasing in many oligotrophic lakes (Vadeboncoeur et al., 2021). This change in the base of lacustrine food webs is of concern as it may foreshadow a larger shift away from oligotrophic lake ecosystems as they are today. Periphyton blooms are occurring in oligotrophic systems where they were not observed before.

These blooms are outside the classic paradigm of algal blooms occurring in eutrophic systems. While some of these blooms have known causalities, such as groundwater nutrient influxes (Timoshkin et al., 2018; Naranjo et al., 2019), many of their causes are still unknown.

Periphyton research lags behind research on phytoplankton and other lake biota, and many processes involving periphyton are poorly understood. While the effects of light, temperature, nutrients, grazing, groundwater, and wind-wave fetch on periphyton have been studied individually (Cattaneo, 1990; Hagerthey and Kerfoot, 2005; Kilroy and Bothwell, 2014), singularly-focused studies are rarely able to explain patterns in periphyton biomass thoroughly (Hillebrand and Kahlert., 2001). Further, climate change has likely affected and will continue to affect many of periphyton's biostimulatory conditions, adding further uncertainty to the future of periphyton blooms. Thus, there is a broad consensus of the need for additional periphyton studies to understand lake ecosystem function better. Specifically, new research methods, long-term monitoring studies, and periphyton modeling tools are required to help the scientific community better understand the causes of and management of periphyton blooms (Rounds, 2001; Vadeboncoeur et al., 2008; Vadeboncoeur and Steinman, 2002).

1.2. Objectives and Outline

This dissertation investigates the complex relationships between periphyton and the conditions that influence its growth and biomass accumulation. Periphyton growth tends to be highly spatially heterogeneous from a microscopic to a lakewide scale and temporally heterogeneous from a diel to an annual and even a multi-year timeframe. Periphyton research must make up for this complexity by using robust sample designs or large datasets. In three chapters to follow, periphyton at Lake Tahoe, USA, is the focus of study because its long history of lake and periphyton observation enables researchers to overcome some aspects of temporal and spatial heterogeneity to illuminate trends. These studies can be a jumping-off point for those seeking to understand periphyton in Lake Tahoe and other oligotrophic lakes, including managers and scientists. Further, this work may interest those who wish to bring periphyton study to another lake and wish to learn from these methodologies. The fourth chapter is a resource to help those beginning periphyton and groundwater research integrate the ecological and hydrological methodologies required for benthic understanding.

This dissertation addresses multiple conditions that affect periphyton biomass, including temperature, light, nutrients, groundwater, lake level, and bed shear stress (Figure 1). Temperature is considered because it influences periphyton metabolic rates (Scharfenberger et al., 2018) and plays a role in speciation. Incoming light is the driver of photosynthesis and productivity (Vadeboncoeur et al., 2014). Nutrients, including nitrogen and phosphorus, are essential to constructing algae’s amino acids, DNA, RNA, ATP, and other building blocks of life (Wetzel, 2001). Groundwater influxes are addressed because, in Lake Tahoe, periphyton is reliant on these flows for nutrient supply (Naranjo et al., 2019; Hecky and Hesslein, 1995; Loeb, 1987). Lake level changes affect many aspects of periphyton dynamics, including the availability of radiation and groundwater (Krabbenhoft et al., 1990). Finally, bed shear stress, the friction of water’s flow on the lake’s boundaries, can cause periphyton to slough off the substrate (Cattaneo, 1990) and can affect nutrient uptake, thereby reducing the biomass that is measured.

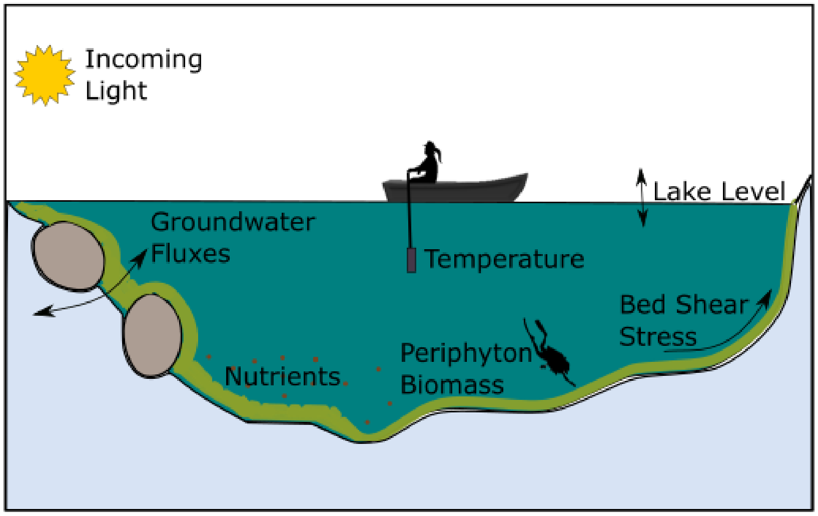

Fig 1.1. Schematic of the conditions investigated in this dissertation.

Chapter 2 analyzes a unique long-term periphyton monitoring dataset that measured biomass at 0.5 m depth spanning 1982 to 2019. This chapter assesses the spatial and temporal trends and variability of periphyton within the context of changing lake levels and explores the influence of lakeshore development on periphyton biomass. Periphyton communities observed by this monitoring scheme are analyzed to determine their contribution to the overall biomass of Lake Tahoe periphyton. The chapter addresses the limitations of the dataset created by the sampling scheme and emphasizes the importance of monitoring periphyton before major disturbances impact a lake and before changes in biomass are noticed. Though others collected the majority of the data from this 38-year data set, I performed the statistical analyses and interpretation of the long-term trends.

Chapter 3 attempts to understand to what degree physical, chemical, and biological factors play roles in determining Lake Tahoe periphyton dynamics. The long-term periphyton dataset was paired with meteorological, chemical, and physical information using Bayesian modeling techniques. These lake measurements accounted for 32% of the variability encountered. From this, we learn that nitrate, photosynthetically active radiation, days that the substrate has been submerged, and temperature were significantly correlated with periphyton biomass. The model could be improved by including information data on finer spatial and temporal scales—matching of the scales of the explanatory variable patterns.

Chapter 4 is a case study evaluating possible outcomes of Lake Tahoe periphyton under climate change conditions. While similar studies have been conducted on phytoplankton and generally studies have discussed climate change’s impact on periphyton conditions, this is the first known case study to use modeling to outline the effects of climate change on periphyton at a particular location. Using projections from lake models run under forecasted climate scenarios, a trend analysis showed which biostimulatory conditions were likely to change. The effects of these conditions individually and together were considered to inform future management decisions and our understanding of how periphyton growth is controlled. Here the downscaled climate projections were provided by Goloka Sahoo and Sean Trommer, and Sean Trommer provided the future lake hydrology and nutrient inputs. I used those results to explore the impacts of a range of future changes on periphyton through the end of the century.

Chapter 5 asserts that many lake monitoring programs neglect the littoral zone altogether or focus on either periphyton or hydrological measurements, but rarely both. However, groundwater nutrient influxes control periphyton in many lakes, and periphyton can function as indicators of subsurface connectivity. Thus, periphyton integrates subsurface nutrients into the lacustrine food web, and, ultimately, much could be learned if groundwater and periphyton were monitored together. This chapter discusses how to overcome the barriers associated with studying littoral ecological-hydrological dynamics; summarizes empirical and modeling techniques for assessing spatiotemporal periphyton patterns and hydrological fluxes, and identifies new ways that hydrological techniques can be incorporated into ecological studies to deepen understanding of whole lake ecosystem function. Current benthic monitoring practices need to be modified to increase understanding of the structure and function of lake littoral zones. This chapter provides guidance—currently lacking in the literature—for future littoral lake monitoring and research. This paper was produced by co-authors Karen Atkins, Bella Oleksy, Thomas Shannon, Michael Meyer, Devi Gurung, and Robert Ladwig through GLEON. I initiated and led the working group, conceived of the manuscript idea, led the writing of the manuscript, wrote and edited large sections of the manuscript, created figures, and edited and reviewed the final manuscript

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2. Variability in Periphyton Community and Biomass over 37 years in Lake Tahoe (CA-NV)

2.1. Abstract

Nuisance periphyton blooms are occurring in oligotrophic lakes worldwide, but few lakes have documented changes in biomass through periphyton monitoring. For decades periphyton has caused concern about oligotrophic Lake Tahoe's nearshore water quality. To determine whether eulittoral periphyton increased in Lake Tahoe, measures of biomass and dominant communities at 0.5 m below lake level have been monitored regularly at nine shoreline sites starting in 1982, with up to 54 additional sites monitored annually at peak biomass. Lake-wide, this metric of periphyton biomass has not increased since monitoring began. Biomass decreased at many sites and increased at one. Periphyton biomass peaked in March and was low in the summer lake-wide. The northern and western shores had higher biomass than the eastern and southern shores. Biomass varied with lake level. High biomass occurred at sites regardless of urban development levels. As increasing periphyton at Lake Tahoe was first cited in scientific literature in the1960s, it is possible that periphyton increased prior to our monitoring program. A dearth of published long-term monitoring data from oligotrophic lakes with reported periphyton blooms makes it difficult to determine the extent of this issue worldwide. Long-term nearshore monitoring is crucial for tracking and understanding periphyton blooms.

2.2. Introduction

The nearshore regions of lakes are directly connected to the upland watershed. As a result, nearshore environments are influenced by land-use change, pollutant loading, erosion, and resource overuse which can all lead to eutrophication (Beeton, 2002). Peri-phyton serve as indicators of ecosystem function in the littoral zone and, along with phytoplankton, are the base of the food web in freshwater lake systems (Hecky & Hesslein, 1995; Yoshii, 1999). Periphyton are often easily visible from the shoreline, react rapidly to changing conditions, and play a critical role in many lake processes including nutrient cycling, energy flow, and food web interactions (Axler & Reuter, 1996; Vadeboncoeur & Steinman, 2002; Denicola & Kelly, 2013). Changes in benthic algal biomass can be used to distinguish areas of environ-mental stress, where biomass in a part of the lake shoreline deviates from the normal range of variability (Lambert et al., 2008; Spitale et al., 2014). Due to their role as an indicator and their importance for lake-ecosystem health, it is important to evaluate temporal and spatial variability in this community.

Nuisance periphyton blooms are large growths of mostly filamentous periphyton in the littoral zones of oligotrophic lakes that create undesirable ecological, economic, or aesthetic outcomes. These blooms have been observed in pristine lakes worldwide. These periphytic blooms occur in high light nearshore environments and are often dominated by cyanobacteria and chlorophytes. For example, in Lake Baikal, benthic blooms have mostly consisted of chlorophytes such as Ulothrix and Spirogyra (Kravtsova et al., 2014). In New Zealand, blooms have been observed in Lake Taupo, where the shallow assemblage was dominated by cyanobacteria Scytonema and Dichothrix, and filamentous chlorophytes (Hawes and Smith, 1994). Some blooms are also caused by invasive algae such as Didymosphenia in Lake Hövsgöl, Mongolia (Cantonati et al., 2016). In the USA, blooms have been observed in Lake Chelan, WA, and were primarily composed of diatoms including Achnanthes and Gomphonema and filamentous green algae including Ulothrix and Cladophora (Jacoby et al., 1991). Despite wide-spread periphyton blooms over the past several decades, there are few long-term littoral monitoring programs. Lake Baikal and the Laurentian Great Lakes are examples of lakes with littoral monitoring programs capable of detecting changes in the periphyton biomass and community composition (Higgins et al., 2008; Kravtsova et al., 2014). As a result of the rarity of this type of program, the extent to which benthic algal blooms are occurring and their characteristics remain under reported and poorly understood.

No scientific data on periphyton in Lake Tahoe exists before major anthropogenic disturbance reached the lake in the 1950s and 60s in the form of large-scale development of infrastructure, homes, ski resorts, and the expansion of the casino industry. Inputs of sediments and nutrients from widespread land development and insufficient sewage treatment and disposal practices initiated anthropogenic eutrophication of the lake (e.g., Goldman, 1974). Epilithic periphyton was first observed at nuisance levels in the eulittoral zone (0–2 m depth) in the mid-1960s by Goldman (1967); he also noted there was little periphyton on the rocks when he began studies of the lake in the late 1950s. Initial studies of periphyton were conducted in the 1970s and 1980s (e.g. Goldman & De Amezaga, 1975; Loeb, 1980; Loeb et al., 1983; Aloi et al., 1988; and others). Communities were made up of mixed taxa, which followed spatial and temporal patterns. In the eulittoral zone stalked diatoms (e.g. Gomphoneis) and green filamentous algae (e.g. Ulothrix) predominated (Fig. 1) (Loeb & Reuter, 1984). This community, that was subject to both high ambient light levels and the sloughing potential of wave action.

In the sublittoral zone (greater than 2 m depth), nitrogen-fixing cyanobacteria such as Tolypothrix, Calothrix, Scytonema, and Nostoc dominated (Loeb, 1980; Reuter et al., 1986a, b). These communities, that survived at lower light levels and were protected from direct wave action, were only intermittently sampled during drought periods when lake levels fell by up to 2–3 m, thereby allowing them to be sampled using the 0.5 m depth protocol.

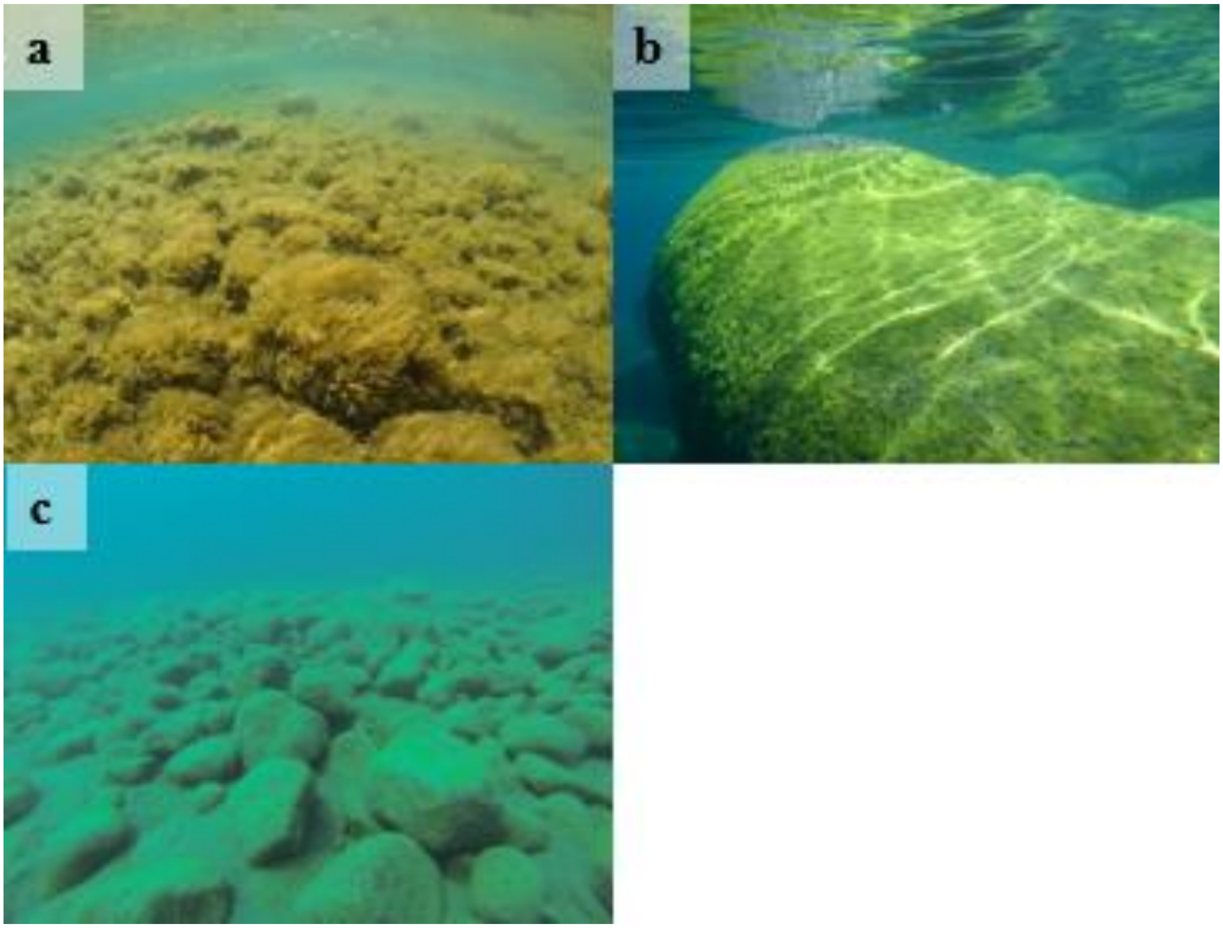

Fig. 2.1. Periphyton a) diatoms b) green filamentous algae, and c) cyanobacteria on rocks in Lake Tahoe.

Lake managers considered periphyton an important indicator of thresholds in the lake's environmental status based on these early studies, and routine monitoring began in 1982. These data initially showed that periphyton biomass increased near the locations of urban development (Loeb, 1980; Aloi, 1986). This review of the entire long-term Lake Tahoe periphyton monitoring data set addresses variability in nearshore periphyton from the early 1980s to the present day. In most cases funding for explanatory data for assessing potential drivers was not provided.

This paper evaluates long-term trends in periphyton growth in the splash zone of Lake Tahoe over a period of decades and addresses several questions: (1) Has periphyton biomass increased since monitoring began in 1982? (2) Is there a seasonal component to biomass accumulation? (3) Is the largest periphyton growth occurring near highly developed areas? (4) Is the peak yearly biomass that is visible from the shore affected by various periphyton communities that exist at different lake levels? Compared to many systems, Lake Tahoe has a long record of consistent periphyton measurements, making it ideal for evaluating long-term periphyton variability.

2.3. Methods

2.3.1. Lake characteristics

Lake Tahoe is nestled in the Sierra Nevada mountain range, straddling the states of California and Nevada, USA at an elevation of 1898 m amsl. It is deep, with a maximum depth of 501 m and a mean depth of 313 m. It has a surface area of 499 km^2 and a shoreline of 116 km. The watershed surrounding the lake is 800 km^2 with 63 inflowing streams defined by their watershed boundaries (Fig. 2) and is composed of granodiorite and andesitic volcanic rock (Hyne et al., 1972). The basin was formed by a double graben fault and therefore has steep, rocky side-slopes. The bottom substrate of the lake’s south shore is almost exclusively sand. Lake Tahoe is considered oligotrophic with an average Secchi depth of 21.6 m in 2018, largely due to the granite basin and small watershed to lake ratio (TERC, 2019).

With a dam moderating its single outflow, Tahoe’s lake level fluctuates within a total range of 2.5 m, oscillating around 0.5 to 2 m/year, largely dependent on natural meteorological cycles. The lake’s water levels cycle up and down annually with the maximum around early summer’s flowing snowmelt and the minimum around early winter prior to the wet season. Drought cycles influenced the magnitude of Lake Tahoe’s water level cycles during our monitoring (TERC, 2018). California experienced droughts from 1986–1992, 2006–2010, and 2011–2019 (National Drought Mitigation Center, 2020). Dry periods were also observed in the Lake Tahoe region within these periods with some wet years occurring (i.e. 1986, 2006, 2011, and 2017). The west side of the basin generally receives more precipitation and inputs of nutrients from runoff than the east side (LRWQCB and NDEP, 2010). The prevailing wind direction is out of the southwest (Roberts et al., 2019).

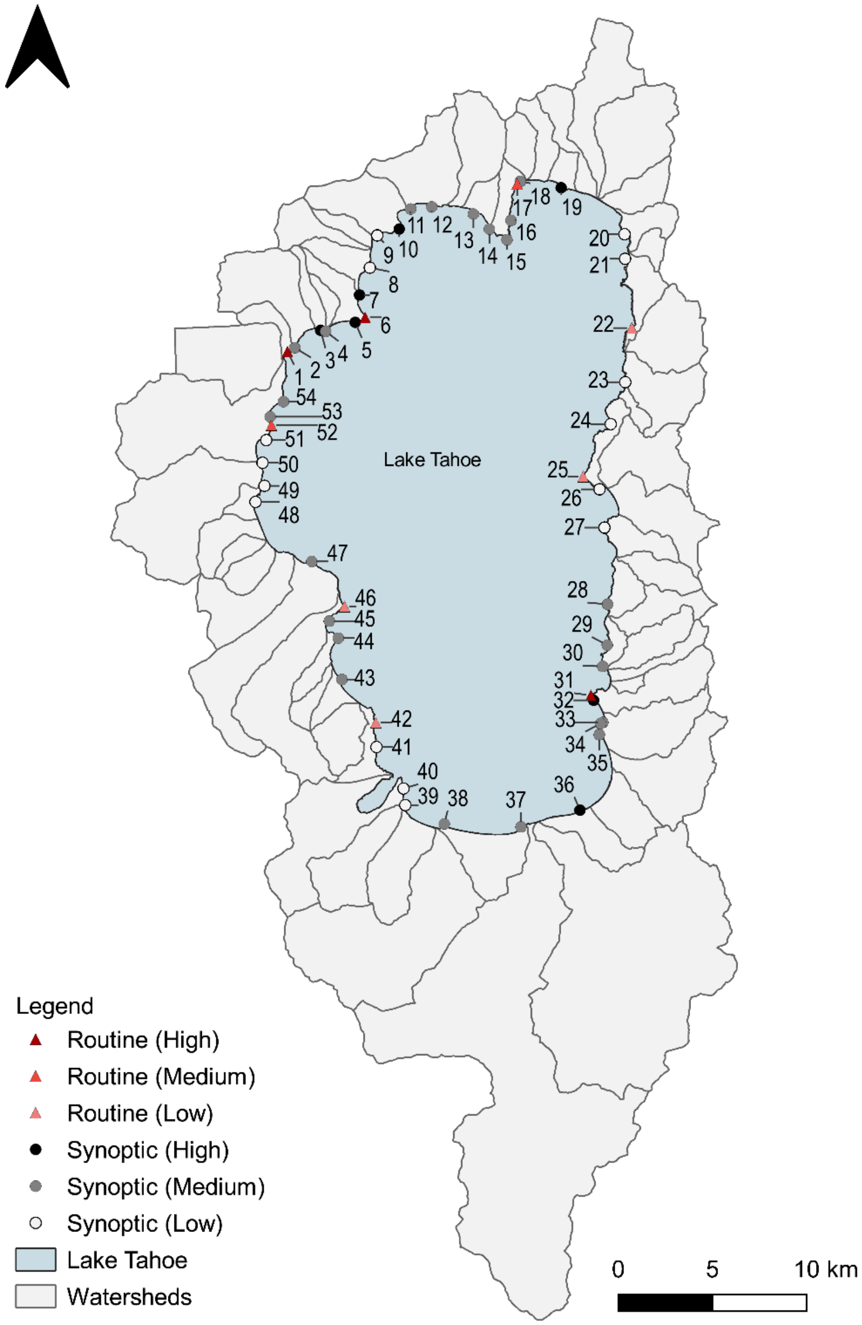

Fig. 2.2. Periphyton sampling locations around Lake Tahoe and their site development level. The watershed boundaries of the 63 inflowing streams are indicated in gray.

From the beginning of periphyton monitoring, Lake Tahoe has changed. Clarity, as measured by Secchi depth, was decreasing during the 1980s and 1990s but plateaued in the 2000s and 2010s (Tahoe Environ-mental Research Center, 2019). Similarly, mid-lake phosphorus levels were decreasing in the earlier period and began to increase around the year 2000 (Tahoe Environmental Research Center, 2019). Mid-lake nitrogen levels have been increasing since the 1980s (Tahoe Environmental Research Center, 2019).

2.3.2. Field and laboratory methods

To quantify periphyton in lakes, taxonomic, biomass, and metabolism analysis are commonly used. While community metabolism can be used as a proxy for growth rates in periphyton and can be useful for understanding the mechanisms of algal growth, biomass was used for monitoring at Tahoe because it was considered more relevant to biomass accumulation (Biggs & Kilroy, 2000). Enumeration of algal genera and species was not included in this monitoring due to limited resources. Instead, gross observations of predominant periphyton types at each site were made during snorkel surveys beginning in the early 2000s.

Routine monitoring was designed to track periphyton biomass throughout the year at developed and undeveloped areas, measure algal standing crop, and evaluate long-term variability. Monitoring was con-ducted 29 of the past 37 years: 1982–1985, 1989–1993, and 2000–present. Surveys occurred at six to nine routine shoreline sites (Fig. 2 and Table 1), chosen to provide a range of development levels and previously observed amounts of periphyton growth. The number of monitoring events varied through time, ranging from 3 to 15 times per year, but occurred approximately monthly between February and June which is typically the period when biomass peaks. As the exception, in the year 2004 monitoring only occurred once in October.

Routine sampling included collecting data about algal biomass; percent cover; filament length; and predominant algal types present.

An increased number of synoptic sites were added to coincide with the spring biomass peak, beginning in 2003, for enhanced resolution of biomass distribution. The additional 45 synoptic sites were visited once annually to measure percent cover and algal filament length (Fig. 2 and Table 1). As a result of the spring peak occurring at slightly different times around the lake, and weather constraints on sampling, the synoptic effort may not have captured the exact peaks at all sites but generally was close to maximum biomass.

Two measures were used to assess biomass in this study: chlorophyll-a (chl-a) and ash-free dry mass (AFDM). Chl-a is considered an indicator of autotrophic organism biomass. We did not measure other pigments more specific to larger taxonomic groups of autotrophs. AFDM is a measure of total organic material and was included in monitoring starting in 1989. At each site, epilithic periphyton samples were collected from natural rocky substrates at a depth of 0.5 m below the water surface. As lake level changed, the sampling point remained 0.5 m below the surface. Samples of three replicates before 2000 and two replicates after 2000 were collected using two-syringe brush samplers (Loeb, 1981). These samplers collect periphyton from an area of 5.3 cm^2. After collection, material was transferred from the syringes into centrifuge tubes and returned to the lab for processing the same day. Samples were centrifuged to concentrate the material, allowed to dry for an hour or more to a uniform damp consistency and then weighed, yielding total wet mass (TWM). Each sample was then rapidly split, and weighed, to provide subsamples for AFDM and chl-a analysis. Chl-a subsamples were stored frozen at a temperature of 24ºC for later analysis, and AFDM subsamples dried overnight (the drying temperature used was either 105ºC (for data from 1989 to 1992) or 60ºC (for data from 1992 to present). Use of different drying temperatures had only a small impact on AFDM estimates, as a comparison for 50 subsamples showed slight differences (median of 3.3% difference).

Table 1. Site names, locations, frequency, geographic region, and level of development of the Lake Tahoe periphyton monitoring program. Point is abbreviated as Pt. Synoptic sites were monitored annually around the time of peak biomass, whereas routine sites were monitored approximately monthly. Site development level was based on the percent impervious coverage for nearby shore runoff sub-basins.

Site #	Site Name	Monitoring Frequency	Lake Region	Dev Level	Site #	Site Name	Monitoring Frequency	Lake Region	Dev Level
1	Tahoe City	Routine	North	High	28	Cave Rock	Synoptic	East	Medium
2	Tahoe City Tributary	Synoptic	North	Medium	29	Lincoln Park	Synoptic	East	Medium
3	TCPUD Boat Ramp	Synoptic	North	High	30	N. Zephyr Cove	Synoptic	East	Medium
4	Lake Forest	Synoptic	North	Medium	31	Zephyr Pt.	Routine	East	High
5	S. Dollar Pt.	Synoptic	North	High	32	S. Zephyr Pt.	Synoptic	East	High
6	Dollar Pt.	Routine	North	High	33	Marla Bay	Synoptic	East	Medium
7	S. Dollar Creek	Synoptic	North	High	34	N. Elk Pt.	Synoptic	East	Medium
8	Cedar Flat	Synoptic	North	Low	35	S. Elk Pt.	Synoptic	East	Medium
9	Garwoods	Synoptic	North	Low	36	Timber Cove	Synoptic	South	High
0	Flick Pt.	Synoptic	North	High	37	Tahoe Keys Entrance	Synoptic	South	Medium
11	Stag Avenue	Synoptic	North	Medium	38	Kiva Pt.	Synoptic	South	Medium
12	Agatam	Synoptic	North	Medium	39	Cascade Creek	Synoptic	South	Low
13	Kings Beach	Synoptic	North	Medium	40	S. Eagle Pt.	Synoptic	South	Low
14	Brockway Springs	Synoptic	North	Medium	41	E. Bay/Rubicon	Synoptic	West	Low
15	N. Stateline Pt.	Synoptic	North	Medium	42	Rubicon Pt.	Routine	West	Low
16	Stillwater Cove	Synoptic	North	Medium	43	Gold Coast	Synoptic	West	Medium

Site #	Site Name	Monitoring Frequency	Lake Region	Dev Level	Site #	Site Name	Monitoring Frequency	Lake Region	Dev Level
17	Incline West	Routine	North	Medium	44	S. Meeks Pt.	Synoptic	West	Medium
18	Incline Condo	Synoptic	North	Medium	45	N. Meeks Bay	Synoptic	West	Medium
19	Burnt Cedar Beach	Synoptic	North	High	46	Sugar Pine Pt.	Routine	West	Low
20	Hidden Beach	Synoptic	East	Low	47	Tahoma	Synoptic	West	Medium
21	Observation Pt.	Synoptic	East	Low	48	S. Fleur Du Lac	Synoptic	West	Low
22	Sand Pt.	Routine	East	Low	49	Blackwood Creek	Synoptic	West	Low
23	Chimney	Synoptic	East	Low	50	Kaspian Pt.	Synoptic	West	Low
24	Skunk Harbor	Synoptic	East	Low	51	Ward Creek	Synoptic	West	Low
25	Deadman Pt.	Routine	East	Low	52	Pineland	Routine	West	Medium
26	S. Deadman Pt.	Synoptic	East	Low	53	N. Sunnyside	Synoptic	West	Medium
27	S. Glenbrook	Synoptic	East	Low	54	Tavern Pt.	Synoptic	West	Medium

Sub-samples were thawed for a few minutes, then chl-a was extracted by boiling a subsample of periphyton for two to three minutes in reagent grade methanol (Spectranalyzed^{TM}, Fisher Chemical^{TM}) while being manually ground with a glass rod in a centrifuge tube. The subsample was then centrifuged to clarify the extract solution, transferred to the 4 cm spectrophotometer cell, and optical density was measured on a dualbeam Shimadzu UV1700 series spectrophotometer at 653, 666, and 750 nm. A methanol blank was used in the reference 4 cm cell. A wavelength of 750 nm was used to correct for turbidity. The amount of chl-a was calculated applying the equation from Iwamura et al. (1970):

$$\text{Chl-}a = 17.12 * \text{O.D.}_{666} - 8.68 * \text{O.D.}_{653}$$

where chl-a is in lg/ml, O.D._{666} is the optical density at 666 nm and O.D._{653} is the optical density at 653 nm. Sample site chl-a (mg/m^2) was determined by accounting for sampling area (m^2), extract volume (ml) and total sample wet weight relative to subsample wet weight.

The wet weight was taken on the AFDM subsample (SWM). After drying in an oven at 60 LC for at least 10 h, the subsample was weighed to provide a dry weight (SDM60), then combusted at 500 LC for an hour. After removal, the subsample was weighed again (SCM500). AFDM was calculated as:

$$\text{AFDM } (g/m^2) = (\text{TWM}/\text{SWM})*(\text{SDM60}-\text{SCM500})/\text{area sampled } (m^2)$$

Less than 1 percent of data were censored based on several factors. Extremely high or low outliers among replicates were identified and censored when comparison with other replicate values at the time of collection and in the samplings prior to and following the sampling date indicated them as anomalous. Heavy sand content which contributed to high variation among replicates also led to censoring of a few replicates. Finally, where biomass was extremely heavy and possible drawing of material into the sampler from outer edges was suspected, these samples were also censored.

An ‘‘Autotrophic Index’’ (AI) was calculated as the ratio of AFDM (mg/m^2) to chl-a (mg/m^2) (Biggs & Kilroy, 2000). A high AI indicated more organic material than chl-a materials.

Algal percent cover was estimated at a depth of 0.5 m as an additional measure of biomass accrual. Predominant periphyton communities (i.e. stalked diatoms, filamentous green algae, and cyanobacteria) were noted while snorkeling. To verify the identification of predominant communities, a microscope was used to confirm the snorkel identification some of the time. In 2015 this laboratory confirmation became more standard and was conducted for roughly half of the monitoring events in order to permit training of new sampling staff. In these audits, the dominant group was usually found to be consistent with the snorkel identification, particularly when there was high biomass present. Lake level data were obtained from the United States Geological Survey station near Tahoe City (USGS, 2019).

2.3.3. Statistical methods

To assess monthly biomass, Kruskal–Wallis tests were performed followed by Dunn's test with p adjusted using Bonferroni's method (Bonferroni, 1936; Kruskal & Wallis, 1952; Dunn, 1964; Abdi, 2007). A Mann–Kendall test was used to evaluate monotonic trends within the time series data. Specifically, this method was used in place of parametric linear regression analysis because the test does not require that the trend be linear and it assumes independence between sampling events (Mann, 1945; Kendall, 1975). The test produces the Kendall's Tau which indicates the strengths of the variable's association; the S-statistic which compares each point's relation to the following points; the z-score which is the normalized test statistic; and the P-value which indicates the significance level. A positive S-statistic indicates an increasing trend while a negative value points to a decreasing trend. A P-value of 0.05 or smaller was considered a significant trend. Though 0.05 is the standard accepted P-value, some notable additional results with higher P-values were included in the tables for the reader's consideration of ecological significance. All statistical tests were performed with R (version 3.6.2, R Core Team, 2013). Mann–Kendall tests incorporated all data including outlier values because maximum values are viewed as important features of annual biomass cycles.

To analyze spatial data, all sites were grouped into north, south, east and west based on their location around the lake (Table 1). In addition, the level of human development associated with each of the sites was quantified using QGIS analysis. Runoff subbasins were delineated based on United States Geological Survey digital elevation model topography (Arundel et al., 2015). The subbasin delineation was used to clip a raster layer containing land use information from the National Land Cover Database 2011 survey (MRLC, 2011). The resulting polygons were used to calculate percent impervious coverage for runoff subbasins. While only 30% of the watershed area is considered impervious (or urban), approximately 67% of the nutrients are derived from this area (Sahoo et al., 2013). The 33rd and 67th percentiles were used to divide percent impervious cover data into the categories of low (0–9% impervious cover), medium (10–19% impervious cover), and high development (> 19% impervious cover) (Table1). Much of the Tahoe basin landcover is either housing developments or forest so this measure of urbanization encapsulated our land uses of interest.

Data were separated into the time periods of years 1982 to 1993 and 2000 to 2019 to assess long-term historic versus variability over 20 years. The year 2000 was chosen as the break point because there was a change in the trend of lake clarity and phosphorus levels around that year (Tahoe Environmental Research Center, 2019). These changes suggest a shift in the overall lake ecosystem occurring around this time that could potentially affect periphyton. For the earlier 1982–1993 period, chl-a data was available from 1982–1985 and 1989–1993 and trends from those times were analyzed together. For AFDM, data was available and analyzed for 1989–1993.

2.4. Results

2.4.1. Temporal variability and trends

Statistically significant temporal trends for data from all routine sites combined around the lake at 0.5 m, were found for AFDM but not for chl-a (Table 2). A Mann–Kendall test showed that there was no significant long-term trend in periphyton chl-a when all sites data were combined during the entire period of record (1982–2019), or the more recent 2000–2019 period (Table 2).

However, there was a negative lake-wide trend ($P = 0.01$) in AFDM for all available years (1989–2019) and for the more recent period 2000–2019 ($P < 0.01$). Mann–Kendall tests based on the limited data from 1982 to 1993 showed increasing periphyton AFDM and chl-a at 0.5 m (both $P < 0.01$). However, these results were based on an incomplete data set that did not include the period of 1982–1987 (Fig. 3). A Mann–Kendall test, run on the peak biomass, synoptic dataset, showed no significant trends at 0.5 m.

Individual routine sites showed a mixture of statistically significant trends at 0.5 m for chl-a and AFDM through time. There was a statistically significant increase in periphyton chl-a at one site (Incline West) on the northwest shoreline (Table 2). Three other sites (Zephyr Pt., Dollar Pt., and Sugar Pine Pt.) showed statistically significant declines in chl-a. These sites are dispersed around the lake: Dollar Pt. is on the northwest shore, Zephyr Pt. is on the southeast shore, and Sugar Pine Pt. is along the southwest shore. Both Dollar Pt. and Zephyr Pt. are adjacent to developed areas. Sugar Pine Pt. is adjacent to a state park (Table 1, Fig. 2). Five sites that ranged from low to high in levels of development (Deadman Pt., Incline Condo, Rubicon Pt., Sand Pt., and Zephyr Pt.) showed statistically significant ($P < 0.05$) declines in AFDM. The other sites showed no significant trend in AFDM over each of the periods of record analyzed.

Table 2. Mann-Kendall Test Results for Lake Tahoe AFDM and chl-*a*. In some cases, all available sampling was tested, in others only data from cyanobacteria or diatom dominated water years were tested. Data from 1986-1988 and 1994-1999 were not collected. Significant and interesting not significant results were included for the lake-wide tests, while only the significant individual site results were included. Note that p-values denoted with ** are significant to the 0.01 level and those denoted with * are significant to the 0.05 level.

Location	**Dominant Community**	**Years**	**Constituent**	**Tau**	**S**	**z**	**p**
Lake-wide	All	1982-2019	Chl-*a*	-0.02	-2586	-1.34	0.18
	All	1982-1993	Chl-*a*	.34	3856	10.07	<0.01**
	All	2000-2019	Chl-*a*	-0.03	-1416	-1.29	0.2
	All	1989-2019	AFDM	-0.16	-8439	-7.4	<0.01**
	All	1989-1993	AFDM	0.24	434	4.13	<0.01**
	All	2000-2019	AFDM	-0.06	-2231	-2.58	0.01**
	Cyanobacteria	1989-2019	AFDM	-0.19	-0.19	-3.19	<0.01**
	Cyanobacteria	1989-2019	Chl-*a*	-0.09	-877	-2.06	0.04*
	Diatoms	1989-2019	AFDM	0.01	46	0.19	0.85
	Diatoms	1989-2019	Chl-*a*	-0.03	-148	-0.6	0.55
Deadman Pt.	All	1989-2019	AFDM	-0.28	-1776	-4.41	<0.01**
	Cyanobacteria	1989-2019	AFDM	-0.29	-165	-2.43	0.02*
Dollar Pt.	All	1982-2019	Chl-*a*	-0.13	-1747	-2.51	0.01**
	Cyanobacteria	1989-2019	Chl-*a*	-0.26	-340	-2.68	0.01**
	Cyanobacteria	1989-2019	AFDM	-0.28	-129	-2.18	0.03*
Incline West	All	1982-2019	Chl-*a*	0.28	2665	4.85	<0.01**
	Cyanobacteria	1989-2019	Chl-*a*	0.24	277	2.38	0.02*
	Diatoms	1989-2019	AFDM	-0.51	-40	-2.38	0.02*
Sugar Pine Pt.	All	1982-2019	Chl-*a*	-0.19	-1461	-3.15	<0.01**
Rubicon Pt.	All	1989-2019	AFDM	-0.16	-1034	-2.53	0.01**
Sand Pt.	All	1989-2019	AFDM	-0.29	-1966	-4.69	<0.01**
Zephyr Pt.	All	1982-2019	Chl-*a*	-0.19	-2491	-3.54	<0.01**
	All	1989-2019	AFDM	-0.37	-2668	-6.05	<0.01**
	Cyanobacteria	1989-2019	AFDM	-0.33	-164	-2.64	0.01**

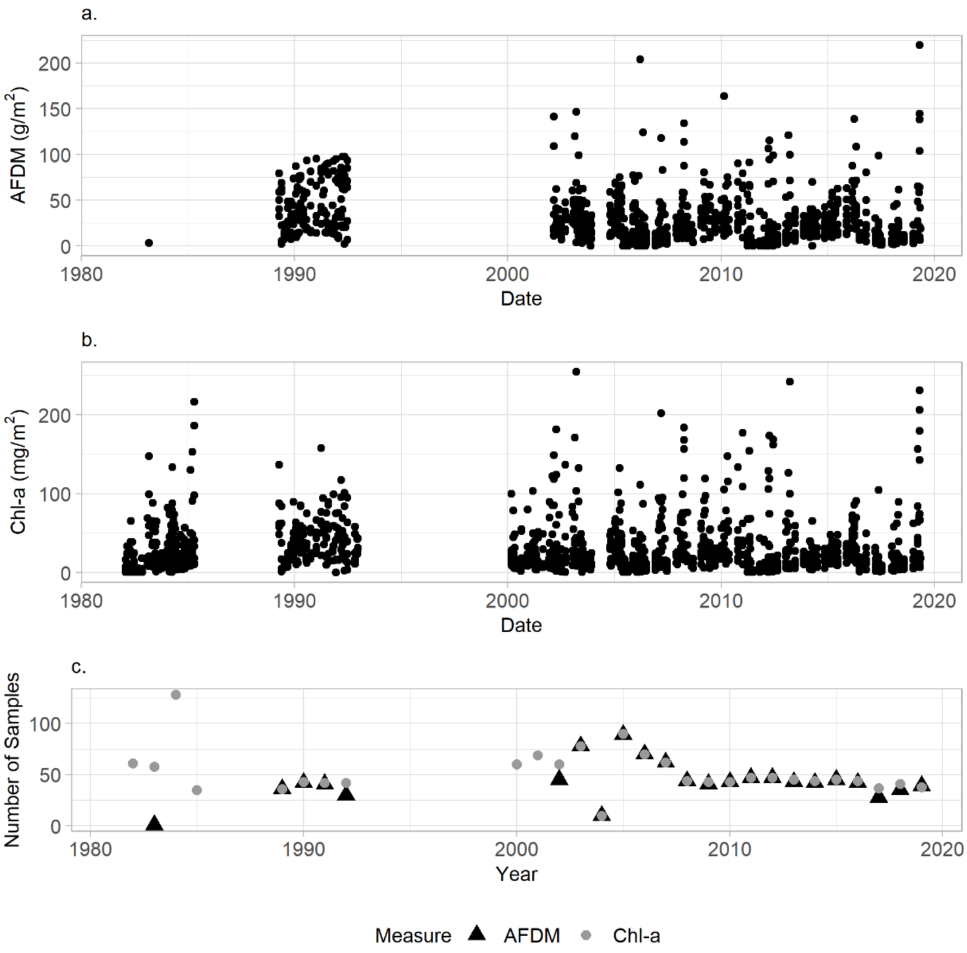

Fig. 2.3. Routine site periphyton a AFDM, b chl-a c and instances of AFDM and chl-a measurement per year at 0.5 m. Instances per year sometimes coinside for AFDM and chl-a. There are large data gaps in the first 20 years of the dataset.

Periphyton community biomass exhibited clear seasonal patterns (Fig. 4). Data from all routine monitoring sites show that median biomass as both AFDM and chl-a tended to be lowest in summer (June through August) well after cessation of the spring snowmelt runoff, when water level was beginning to decline from summer high levels. Median AFDM and chl-a levels generally were highest during spring (March–April) when the water level was typically rising associated with winter storm inputs, prior to or during onset of the spring snowmelt. Some chl-a observations were over 100 mg/m^2 and as high as 254.7 mg/m^2 in months of highest biomass while maximum observations where under 100 mg/m^2 in the

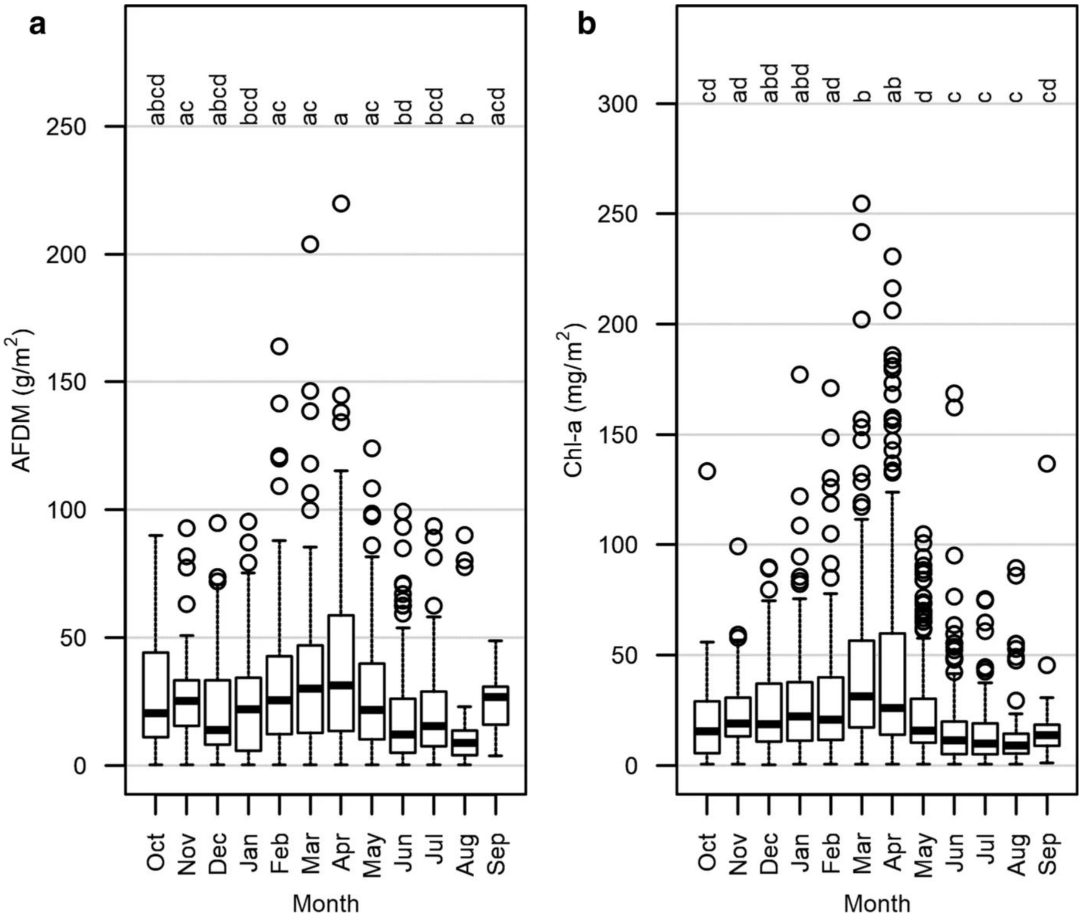

Fig. 2.4. Periphyton monthly biomass variability from 1982 to 2019 for a AFDM and b chl-a. The boxes represent the monthly interquartile range and the thick center lines represent the median. Whiskers represent 1.5 times the Interquartile range or if no data exceeds that value the whisker are the maximum or minimum. The circles indicate outliers that are defined by standard convention as outside of the whiskers. Different letters above each box represent significant differences between months at the 0.05 level using Dunn's test for multiple pair wise comparison. Months with the same letter above them are not significantly different from each other while months with different letters above them are significantly different from one another

months of low biomass. Many AFDW observations were well over 100 g/m^2 in the months of highest biomass and as high as 219.8 g/m^2 while they were generally under 100 g/m^2 in the low biomass months. In the months of high median biomass, there was a high ratio of live photosynthetic material to detrital or stalk material in the mat. Thus, median AI was lower, reaching its lowest monthly median of 731 in March. AI reached its median monthly maximum of 1496 in September.

2.4.2. Community variability and trends

Epilithic periphyton communities, which were classified by the dominant taxonomic division(s) visible in the periphyton mat, showed patterns over time and space. The frequency that a community was observed was calculated from the routine data as a ratio of the times a community was observed each year to the total number of yearly observations. Each year, either stalked diatoms or cyanobacteria were most frequent and there were no years where filamentous green algae were the most frequent (Fig. 5). The water level cycles influenced the type of periphyton community. Cyanobacteria were primarily found at 0.5 m when lake levels were stable or declining while diatoms mostly dominated when lake levels increased (Fig. 5). Additionally, cyanobacteria mostly dominated in the 15 years with low water level while stalked diatoms dominated in the eight years with high waters (Fig. 5). As lake level fluctuated, the bottom substrate either became exposed and desiccated as lake level dropped, or conversely, previously exposed rock was submerged as the lake rose. At a few sites such as Pineland and Tahoe City, stalked diatoms might still be dominant in what were otherwise characterized as cyanobacteria dominated years (based on lake-wide characterization of dominant algae at 0.5 m). A prevalence of cyanobacteria at east shore sites and some sites along west and north shores may account for the cyanobacteria dominance in ‘‘cyanobacteria dominant’’ years.

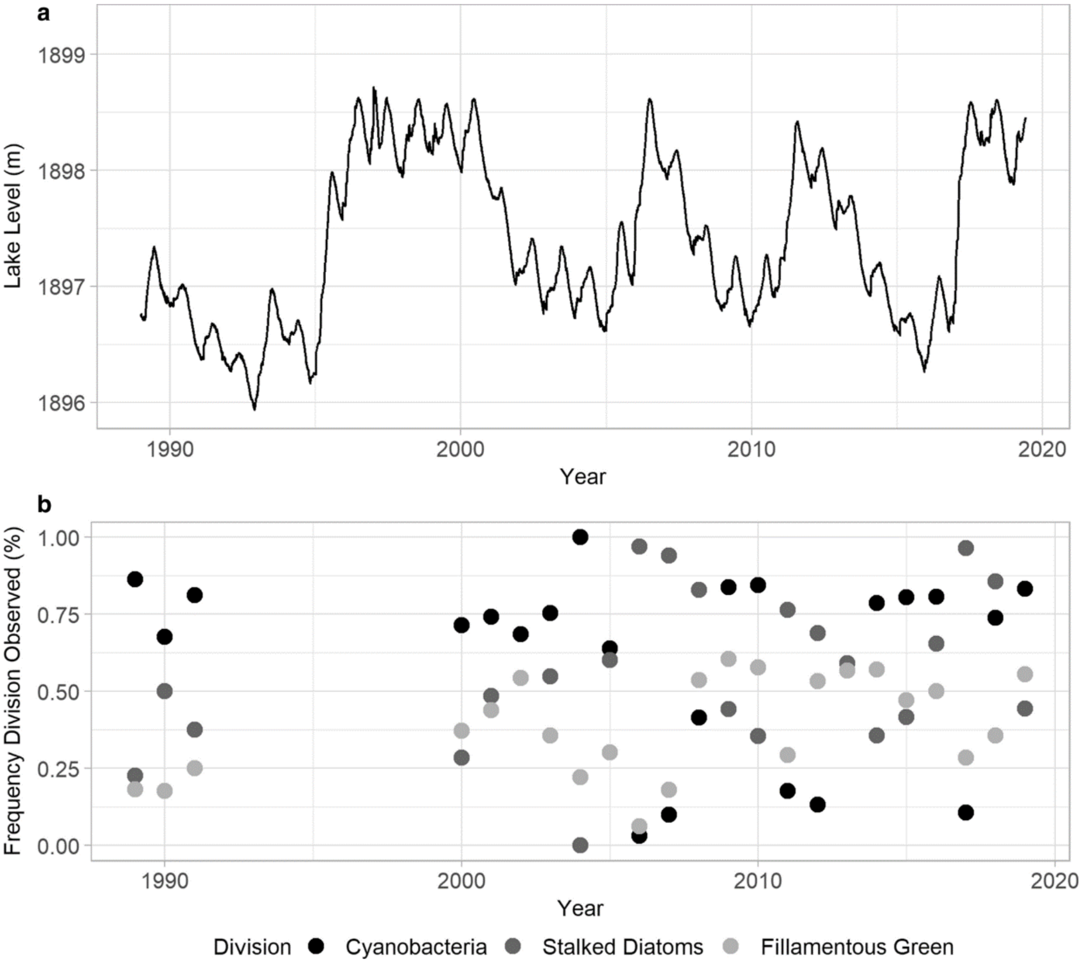

Fig. 2.5 Lake level change affected what communities were observed at 0.5 m. Plot a shows a lake level change over time and b shows annual percentage of the time that each periphyton community was observed.

Summary statistics for chl-a and AFDM levels at 0.5 m varied in years when stalked diatoms dominated compared with years when cyanobacteria dominated. In years in which stalked diatoms dominated, chl-a (Q1 = 6.7 mg/m^2, median = 13.6 mg/m^2, max = 241.8 mg/m^2) was significantly different ($P < 0.01$) compared with years when cyanobacteria were most abundant (Q1 = 11.2 mg/m^2, median = 19.2 mg/m^2, max = 254.7 mg/m^2). Similarly, years where stalked diatoms dominated had significantly lower ($P < 0.01$) AFDM (Q1 = 4.5 g/m^2, median = 10.7 g/m^2, max = 203.9 g/m^2) than years where cyanobacteria dominated (Q1 = 13.8 g/m^2, median = 26.2 g/m^2, max = 163.9 g/m^2). Maximum values and standard deviations showed that stalked diatom-dominated years had larger ranges of biomass. The AI calculated for observations in which only a single community was visually observed showed that stalked diatoms and filamentous green algae had a median ratio of 731 (Q1 = 518, max = 7277), and 865 (Q1 = 485, max = 7084), respectively, whereas cyanobacteria had a higher median ratio of 1248 (Q1 = 961, max = 2662).

At each site, the maximum chl-a concentration was higher in cyanobacteria dominated years than in stalked diatom dominated years, though sometimes by a small amount (Table 3). Similarly, at all sites but Pineland, median chl-a was higher in cyanobacteria dominated years than in stalked diatom dominated years. These patterns of higher maximum and median values in cyanobacteria dominated years held true in the AFDM measurements at all sites with the exceptions of Dollar Pt. which had lower maximums and means on cyanobacteria dominated years and Tahoe City and Pineland which had lower maximums in cyanobacteria dominated years. To identify trends specifically within the stalked diatom and filamentous green algal communities, which tended to be spatially intermixed, the Mann–Kendall trend test was also conducted on data for Water Years (October 1 to September 30) in which diatoms dominated in field identifications. Data from 1982 to 1988 were not included in this analysis since there was limited or no information on predominant algal types for this period. The results indicated that for years when diatoms were predominant, generally in higher lake level years, there was no significant lake-wide trend in algal biomass over time for either AFDM or chl-a (Table 2). When the data for individual sites were examined, only one routine site (Incline West) showed a significant trend and this was for AFDM (Table 2). This site showed a decreasing trend. No significant trends were found for chl-a at individual sites.

Table 3. Biomass summary statistics of routine periphyton sites for all years combined, years where community was documented and cyanobacteria were most frequently observed, and years where community was documented and stalked diatoms where most frequently observed for a. AFDW and b. chl-*a*.

a. AFDM (g/m^2)									
	All Years			**Cyanobacteria Dominated Years**			**Stalked Diatom Dominated Years**		
Site	**Q1**	**Median**	**Max**	**Q1**	**Median**	**Max**	**Q1**	**Median**	**Max**
Deadman Pt.	8.98	28.99	97.33	26.71	39.00	95.32	0.08	6.35	26.48
Dollar Pt.	10.90	18.42	134.25	13.01	18.49	109.20	8.08	19.51	134.25
Incline Condo	7.44	19.38	70.7	21.08	31.74	70.70	4.05	7.81	17.25
Incline West	8.67	27.29	108.36	23.30	34.35	108.36	6.03	8.59	66.09
Pineland	14.39	28.05	219.77	14.68	28.59	99.85	12.30	24.90	115.14
Rubicon Pt.	12.47	25.49	144.67	17.60	27.14	144.67	4.71	8.36	113.79
Sand Pt.	6.33	29.71	97.42	20.59	32.96	93.59	1.02	4.24	34.81
Sugar Pine Pt.	2.70	8.38	70.9	7.02	14.24	70.90	1.68	3.36	18.83
Tahoe City	15.46	33.57	203.86	16.49	33.64	163.90	14.65	33.57	203.86
Zephyr Pt.	8.55	15.06	59.2	12.30	18.21	59.20	3.40	8.09	31.91
Chl-*a* (mg/m^2)									
	All Years			**Cyanobacteria Dominated Years**			**Stalked Diatom Dominated Years**		
Site	**Q1**	**Median**	**Max**	**Q1**	**Median**	**Max**	**Q1**	**Median**	**Max**
Deadman Pt.	5.75	14.88	66.92	14.24	24.30	66.92	2.95	6.94	22.58
Dollar Pt.	12.54	24.07	157.71	12.52	25.35	157.71	10.48	19.90	156.52
Incline Condo	9.14	15.03	98.93	8.89	13.66	67.94	7.30	12.80	31.90
Incline West	8.93	15.18	69.59	13.26	19.28	69.59	7.61	13.94	62.46
Pineland	15.27	31.96	241.77	16.53	32.14	241.77	9.72	49.57	241.77
Rubicon Pt.	9.62	19.51	216.28	14.82	21.98	179.37	4.20	14.19	168.62
Sand Pt.	6.08	13.90	100.74	10.57	19.24	99.24	2.62	6.22	40.24
Sugar Pine Pt.	5.15	11.20	130.14	5.48	10.83	66.35	2.44	6.57	37.18
Tahoe City	16.49	32.05	254.68	16.14	32.12	254.68	18.03	31.68	202.09
Zephyr Pt.	9.89	14.50	87.42	10.91	14.14	87.42	6.67	9.88	76.45

Where cyanobacteria dominated the community observations, generally in lower lake level years, a Mann–Kendall test showed temporal trends towards decreasing biomass. The results of the test for these data showed a significant decrease lake-wide in AFDM and chl-a (Table 2). The results for individual sites using this analysis showed Dollar Pt. had a significant decreasing chl-a trend over time and Incline West had a significant increasing trend. Deadman Pt., Dollar Pt., and Zephyr Pt. had significant decreasing AFDM trends over time (Table 2).

2.4.3. Spatial variability and trends

Routine site data showed that there was great variation between sites (Table 3). Sites such as Pineland had high levels of periphyton by every summary statistic while sites like Zephyr Pt. and Sugar Pine had relatively low amounts of periphyton.

The spring synoptic surveys showed that, sites on the eastern side of the lake tended to have lower annual peak biomass (Table 4). The highest peak biomass was in the northern and western parts of the lake with the highest found at the Tahoe City Public Utility District Boat Ramp, Ward Creek, Garwoods, Gold Coast, and Tahoe City Tributary sites (Fig. 6). Around the lake, the largest chl-a biomasses recorded were predominantly associated with stalked diatoms and filamentous green algae.

Table 4. Periphyton abundance metrics including median, first quartile (Q1), and the number of sites from 2003 to 2019 synoptic surveys by geographical region.

Region	**AFDM ± Q1 (# sites) (g/m^2)**	**Chl-*a* ± Q1 (# sites) (mg/m^2)**	**% Cover ± Q1 (# sites)**
North	30.84 ± 15.46 (19)	34.13 ± 13.94 (19)	70 ± 60 (20)
East	12.00 ± 6.27 (16)	13.32 ± 7.33 (16)	70 ± 50 (19)
South	14.05 ± 5.16 (5)	21.13 ± 7.05 (5)	60 ± 40 (5)
West	29.61 ± 9.27 (13)	37.97 ± 11.75 (13)	75 ± 60 (14)

The northern region had the highest median algal percent coverages for spring synoptic sites. Individual sites with the highest percent coverage included Kaspian Pt., Lake Forest, E. Bay/Rubicon, Tahoe City Tributary, and Ward Creek.

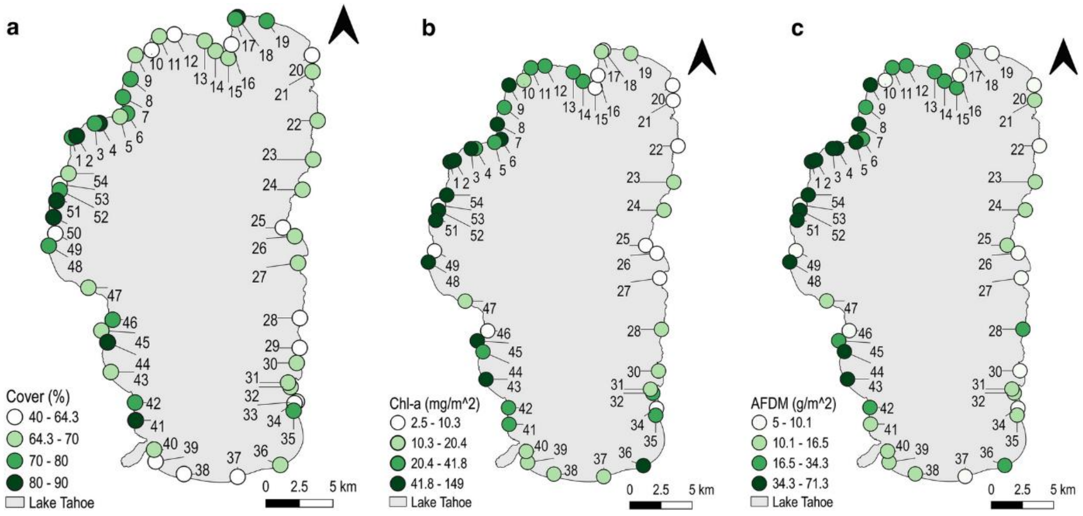

Fig. 2.6. Map of median a percent cover, b chl-a, and c AFDM at all sites. Marker color represents quantile ranges. All biomass measures are higher on the north and west sides of the lake as compared to the south and east sides of the lake

2.5. Discussion

2.5.1. Temporal variability and trends

Over the last three decades, periphyton biomass at 0.5 m has not significantly changed lake-wide; however, a significant decline was observed at several sites. Lake-wide, chl-a showed no trend, while AFDM declined. We attribute these divergent trends in the indices of periphyton biomass to the fact that AFDM measures live and detrital organic matter within the periphyton mat from the entire benthic community and can accumulate over multiple years, while chl-a pigment degrades and sloughs off the substrate after senescence. Further, the long strands that are found in the stalked diatom community are not pigmented as the stalks are composed of carbohydrates (Kilroy & Bothwell, 2014). This may indicate that the divergent trends since 2000 are due to a change in species composition. The increasing trend found in data from 1982 to 1993 is based on incomplete data but chl-a was higher in 1993 than in 1982.

When compared to other oligotrophic lakes with periphyton blooms, Lake Tahoe's periphyton biomass at 0.5 m depth falls on the low end of the reported range. For example, Lake Taupo in New Zealand regularly produces periphyton chl-a biomasses over 500 mg/m^2 and has recorded values over 1500 mg/m^2 between 0 and 2 m depth (Hawes & Smith, 1994). Other lakes, such as Lake Chelan, have biomass levels more comparable to Lake Tahoe's biomass at 0.5 m with periphyton chl-a biomass reaching 140 mg/m^2 at 2 m depth (Jacoby et al., 1991).

Changes relevant to periphyton biomass may have begun prior to our monitoring. The Signal Crayfish [Pacifastacus leniusculus (Dana, 1852)] was introduced in the 1930s and 1940s. These crayfish graze on the periphyton and excrete nutrients in a more bioavailable form which may contribute to growth of the periphyton (Flint & Goldman, 1975). Anthropogenic impacts associated with rapid development of the Tahoe basin occurred in the 1950s and 1960s. Periphyton were noticed to be visibly higher in the spring of 1967 compared to the late 1950s (Goldman, 1967). Shortly after these observations, the Tahoe Research Group began monitoring of periphyton (Goldman, 1974), however, the monitoring focused on the use of artificial substrates suspended above the bottom and results were not directly comparable with later monitoring of periphyton on rocks in the nearshore. Their results showed that chlorophytes and diatoms dominated the periphyton species with low species diversity. They also found periphyton growth rates were highest near the stream mouths and primary production ranged from 0.343 mg C/m^2/day in the south of the lake to 1.010 mg C/m^2/day in the northeast. Limited anecdotal and photographic evidence suggest there was likely less periphyton along the shoreline before the period of rapid population growth and development in the 1950s and 1960s (TERC, unpublished). Many Tahoe developments were on septic systems prior to the 1970s. All residences were on sewer lines by the early 1970s, and all sewage was exported from the basin. This could have reduced problems associated with overloaded septic systems during storms and eventually resulted in less nutrient inputs to the lake. However, it is unknown how long septic system nutrients affected the quality of the natural subsurface groundwater flow entering the lake or if this septic plug still effects water quality today.

There were no clear patterns linking temporal biomass trends with levels of development. Two of the sites with decreasing chl-a were adjacent to areas of high development (Zephyr Pt. and Dollar Pt.) while one (Sugar Pine Pt.) was near an area of low development. Five of the sites, near areas with levels of development ranging from low to high, showed a decrease in AFDM. One of the sites, Zephyr Pt., showed a decrease in both chl-a and AFDM despite being in a high development subbasin. These findings suggest that our measure of development level alone does not explain temporal trends in algal biomass and may not have a direct relationship with nutrients, which are likely an important influence in periphyton biomass. Thus, other influences, such as additional sources of nutrients must be considered. Decreases in periphyton at some developed areas may be the result of watershed remediation projects designed to decrease erosion and associated nutrients from entering the lake. Data on site specific reductions are lacking so direct correlations cannot be made.

Periphyton biomass at 0.5 m shows a clear seasonal pattern with increases as early as December in some years lasting through April, as water levels rise. The highest values during the period of record were typically found in March and April. This signals that peak accumulation occurs in the early spring between December and April. The spring peak in biomass may be due to a combination of factors. In winter, water levels rise as high runoff from storms and early snowmelt contributes both surface and subsurface discharge of nutrients into the lake (Leonard, 1979; Naranjo, 2019). Increases of solar radiation provide more light for photosynthesis. Lake mixing contributes nutrients to surface waters in late winter. Although the development of the periphyton mat can vary with the predominant community, observations suggest that in months of high biomass much of the live material in thick stalked diatom mats resides in the upper portion of the mat (attached to tips of stalks), while the basal layer of the mat is senescent due to reduced irradiance resulting in weaker attachment to the substrate (Johnson et al., 1997; Clark et al., 2004). Photosynthetic oxygen bubbles produced in the upper portion of the mat lift the periphyton, increasing wave-induced shear and making the periphyton more susceptible to sloughing (Biggs & Thomsen, 1995). The rate of periphyton growth may also decline later in the spring as lake level begins to near its maximum. In months of low biomass, much of the biomass is non-photosynthetic senescent material, increasing AI.

2.5.2. Biomass trends in periphyton communities

There are currently two dominant periphyton communities in Lake Tahoe, unchanged from the 1980s. One community comprises filamentous green algae [such as Mougeotia genuflexa (Dillwyn) C. Agardh and Ulothrix zonata (Weber et Mohr) Ku¨tzing] and stalked diatoms [such as Gomphonema parvulum (Ku¨tzing) Ku¨tzing and Gomphoneis herculeana (Ehrenberg) Cleve] and shows no significant upward or downward temporal trend in biomass. Though there is interannual variation, it grows and colonizes quickly and is often found in the eulittoral zone (Reuter et al., 1986a, b). The second community, predominantly cyanobacteria, such as Calothrix scopulorum (Weber & Mohr) C. Agardh and Nostoc entophytum Bornet & Flahault, shows a decline in biomass over time. These cyanobacteria take longer to accumulate biomass and typically grow deeper, in the sublittoral zone (Loeb, 1980). Cyanobacteria dominated mats are primarily observed at our 0.5 m deep sampling sites during times of rapid lake level decline, such as the three drought periods within our dataset. Much of the reduction in biomass over time appeared to occur in water years when cyanobacteria dominated community observations, the years that also had the highest biomass measurements. In contrast, the stalked diatom and filamentous green algae dominated water years did not show statistically significant reductions in biomass over time. This may be related to the impact of repeated low water levels from the 1990s to the 2010s exposing and causing senesence in once stable cyanobacterial mats. The observed changes could be due solely to the position of lake level because of droughts rather than actual changes in community biomass. In addition, the rate of runoff and therefore position of the 0.5 m level can change rapidly or slowly depending on runoff patterns. A high runoff rate could result in a low periphyton biomass at 0.5 m.

All three AI ratios are high relative to ratios found in many periphyton communities. For example, Rosenberger et al. (2008) measured three deep oligotrophic lakes in the USA with mean AIs ranging from 2 to 151. Our high AI values agree with those found in other Lake Tahoe periphyton studies (Naranjo et al., 2019) and are likely due to the predominant type of algae present in Lake Tahoe's periphyton. To overcome shading by neighbors, the stalked diatom, Gomphoneis herculeana secretes stalks of extracellular polymeric substance that can constitute much of their biomass (Hoagland et al., 1993; Bothwell & Kilroy, 2011). Therefore, the relatively high AI ratios found in cyanobacteria and stalked diatoms could be a combination of high AI values in the live community and indicative of a buildup of senescent mat material (Weitzel, 1979). We do not believe the high ratios necessarily indicate impacts of organic matter pollution, as has been shown in other systems (e.g. Collins & Webber, 1978).

2.5.3. Spatial variability and trends

Based on our data, the southern and eastern sides of Lake Tahoe experience lower peak chl-a and AFDW biomass on average than the north or west sides of the lake. Various studies have shown the importance of groundwater inflow on periphyton growth in Lake Tahoe (e.g. Loeb, 1987; Naranjo et al., 2019). A basin-wide evaluation of nitrogen and phosphorus shows lower nutrient load for the east and south shores (USACE, 2003). The changing water table depth can affect the groundwater inflow of nutrients to the lake. Tahoe groundwater nutrient data are limited but these inflows may be responsible for much of the periphyton biomass variability including the high temporal and spatial heterogeneity in periphyton (Naranjo et al., 2019).

In addition to groundwater, multiple factors could contribute to this pattern. In addition to nutrient loads on the east side, southwesterly winds mean that the east side of the lake is more prone to a higher wave climate and wind-induced currents, which could induce the removal of algae by sloughing (Roberts et al., 2019). Constant abrasion from and movement of predominately mobile sandy substrate in the southern portion of the lake does not allow for a buildup of epilithic periphyton. This wind also causes water movement, leading to higher availability of nutrients and increased periphyton nutrient uptake (Reuter et al., 1986a, b).

2.5.4. Further factors contributing to observed trends

Many factors likely affect the observed periphyton spatiotemporal patterns for biomass, although limited explanatory data accompany our periphyton monitoring program. Stormwater can deliver water with high nutrient concentrations. Monitoring of stream discharge, sediment and nutrient concentrations and loading has been conducted on multiple streams in the Lake Tahoe basin since the early 1980s. Streamflow inflow can influence periphyton growth near the mouths of some streams while a more generalized impact of stream inputs of nutrients may be tempered by the fact that stream inflows are cold relative to the lake, so their nutrients often plunge deeper down the steep shoreline rather than move toward our 0.5 m sites along shore.

Nutrient inputs from surface and subsurface (groundwater) discharge, proximity to anthropogenic sources of nutrients and development, lake mixing and upwelling, lake-level changes, grazing, and exposure to waves may all contribute to observed biomass levels. Changes to these factors in Lake Tahoe since long-term monitoring began in the 1980s may have contributed to variability in periphyton growth. Compared to the 40 years before our study, the study period had highly variable lake levels (TERC, 2019). From the 1980s to the 2020s several periods of drought caused lower lake levels, as well as prolonged periods of stratification with reduced mixing-derived nutrient movement. Lake temperature has increased (TERC, 2019) and lake clarity was declining in the 1980s and 1990s and then began to level off in the 2000s. Since the 1980s, pelagic photic zone phosphorous has declined and nitrogen has increased, making Tahoe algae co-limited by these nutrients (Goldman et al., 1993). Mid-lake primary productivity more than quadrupled since 1970 (TERC, 2019). Additionally, stringent environmental regulations have helped to reduce inputs of sediments and nutrients associated with surface runoff. A combination of these factors could contribute to the reduction in periphyton AFDM seen at many sites around the lake.

2.6. Conclusion

Statistically significant trends at 0.5 m depth from all sites combined around the lake were absent for chl-a, but a trend of decreasing AFDM was found. Monitoring of periphyton at Lake Tahoe began after significant changes had been made to the watershed in the 1960s. It is possible that the primary period of change in periphyton biomass was associated with the environmental shifts during this period, however, no comparable monitoring data is available from this period or the years preceding it.

Data showed that periphyton at the 0.5 m depth was affected by seasonality and lake level. The periphyton biomass was highest in spring and lowest in summer. Periphyton community and biomass was affected by lake level changes. At 0.5 m, cyanobacteria mostly dominated low water level years with while stalked diatoms dominated high water level years. Biomass was significantly higher when cyanobacteria dominated than when stalked diatoms dominated the observed community. Somewhat surprisingly, periphyton biomass was not correlated with level of development adjacent to the sites.

In the specific case described here, where a long-term dataset was collected in a consistent fashion over a 37-year span, our conclusions are limited by the nature of the sampling protocol adopted and maintained. With the benefit of hindsight, far more could have been learned if sampling had taken place in stationary positions in both the eulittoral and sublittoral zones and if community dynamics had been more consistently monitored. However, that would have required more time and resources than were available. Given limited monitoring budgets, technologies such as remote sensing may allow new opportunities in the future.

Periphyton blooms are occurring in oligotrophic lakes across the globe, and it is difficult to prove whether these blooms are changing due to a dearth of long-term monitoring data. To prove a change in the periphyton biomass, monitoring programs must begin data collection early and choose their monitoring design carefully, with an emphasis on the nearshore environment. Documenting conditions before and after periphyton blooms begin may be crucial for understanding the underlying causes of periphyton blooms in oligotrophic lakes and creating protocols to control future blooms.

2.7. Acknowledgements

Many individuals have participated in the monitoring of this long and unique periphyton data set at Lake Tahoe over the last 30-40 years and their collective contributions are recognized. Stanford Loeb initiated the synoptic monitoring program and Jane Aloi was a key researcher as the program began. Our current sampling team members include Katie Senft and Brandon Berry. This study was financially supported by the David and Dana Loury Foundation, the Boyd Foundation, and the University of California, Davis. Funding for the collection and analysis of the long-term periphyton data set was supported by various resource agencies in the Tahoe basin, most notably the Lahontan Regional Water Quality Control Board and the Tahoe Regional Planning Agency.

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3. Bayesian Modeling of Periphyton Biomass Drivers in an Oligotrophic Lake

3.1. Abstract

Periphyton blooms, rapid increases in benthic algae biomass, are occurring in many oligotrophic lakes worldwide. Periphyton blooms occur in the microhabitats of the benthic nearshore, but lake monitoring programs often measure midlake variables. To understand if the data collected in a typical lake monitoring program are sufficient to understand periphyton drivers, we modeled periphyton using the longterm dataset available at oligotrophic Lake Tahoe, where blooms have been observed since the 1960s. Using a Bayesian statistical model, we investigated the effects of a range of measured and calculated variables on periphyton biomass. We found that light intensity, mid-lake nitrate concentration, and the time since the substrate was last exposed significantly affect the biomass of periphyton. Midlake total hydrolyzable phosphorous was not a significant driver. Overall, we found that these variables, typical to lake monitoring programs, explained 32% of the variance in periphyton biomass at Lake Tahoe. Space and time variable groundwater nutrient influx and periphyton grazer data were unavailable but may have improved the model. To better understand periphyton blooms, we may need data on finer spatial and temporal scales—matching the explanatory variables' scales and their patterns. Biological conditions in the midlake are distinct from the microhabitats in the nearshore and should be monitored, especially in systems at risk of periphyton blooms.

3.2. Introduction

Worldwide, scientists are beginning to observe a phenomenon of filamentous algal blooms in oligotrophic lakes (Vadeboncoeur et al., 2021). Not surprisingly, periphytic algae appear to have similar growth requirements to planktonic algae. Water temperature, nutrient availability, light availability, and grazing contribute to periphyton biomass levels (Marks and

Lowe, 1993; Kilroy and Bothwell, 2014; Reuter, 1983; Hackley et al., 2016; Hillebrand et al., 2001). However, it is also known that periphyton blooms are not caused by the same set of eutrophying conditions that lead to planktonic algae blooms (Vadeboncoeur and Steinman, 2002). All else the same, as lakes become more eutrophic, production shifts from benthic periphyton to pelagic phytoplankton (Vadeboncoeur et al., 2003).

Periphyton compete with phytoplankton for both nutrients and light (Hansson, 2006; Sand-Jensen and Borum, 1991). In conditions of ample nutrients, planktonic algae remain buoyant near the surface, blocking out light for deeper periphyton. Phytoplankton's faster uptake rates limit the availability of water column nutrients for periphyton (Reuter et al., 1986; Reuter and Axler, 1992; Hwang et al., 1998). However, case studies have shown that periphyton have the advantage of direct access to benthic nutrients. As such, periphyton blooms often appear in clear water where periphyton have direct access to nutrients such as rich groundwater influxes (Naranjo et al., 2019) and sewage (Timoshkin et al., 2018). Unlike planktonic algae, however, periphyton are bound to the conditions of the specific location where they are attached. Bed shear stress from wave action can contribute to biomass reduction through sloughing and buildup of new algal growth, detritus, and sediment can bury lower layers of the mat, causing increased mortality (Cattaneo, 1990; Scheifhacken et al., 2007). Yet, these conditions do not explain all instances of periphyton blooms.

Due to the limited understanding of periphyton's niche, the causes of the widespread periphyton blooms are still largely unknown. While monitoring efforts to understand periphyton blooms have increased in some lakes, these programs are limited by resources and often face challenges in capturing spatial and temporal heterogeneity. Single component studies on periphyton rarely explain biomass patterns (Hillebrand et al., 2001). Consequently, research aimed at understanding the cause of periphyton biomass trends must examine multiple influences. A seemingly important influence, the influx of groundwater nutrients, is not typically monitored in lakes, even though they are thought to be primary drivers of periphyton blooms. Groundwater is difficult to access and both spatially and temporally heterogeneous making it complicated or costly to observe. Therefore, even at highly monitored lakes, researchers may not be equipped to understand the root causes of periphyton blooms and thus recommend successful management solutions.

In this paper, we use the case study of Lake Tahoe, CA-NV, USA, to see if a whole lake monitoring program supplies adequate data to improve our understanding of periphyton blooms. We use 26-years of biological, chemical, and physical data to understand the drivers of periphyton trends. A Bayesian hierarchical model combined multiple datasets and evaluated which variable(s) played significant roles in explaining the variation in periphyton biomass. While the ecological and limnological communities have widely utilized Bayesian modeling (Hobbs and Hooten, 20015; Cheng et al., 2010; Wu et al., 2017; Bertani et al., 2016), this is its first implementation for periphyton known to the authors.

3.3. Methods

Measured nutrient and water temperature data collected from multiple sites around Lake Tahoe were combined to reflect the conditions surrounding periphyton. The bed shear was modeled based on the measured wind data and the bathymetry of the lake. Data was as spatially and temporally relevant to the periphyton observation as was available. Where data were collected at or near periphyton monitoring stations, that data was used with its corresponding periphyton measurement. When near periphyton data were not available, where possible, we used models to estimate near periphyton site conditions. For some parameters, there was no information to estimate conditions on a site-by-site basis.

Field location

Lake Tahoe is located at 1898 m amsl in the Sierra Nevada Mountains on the border of California and Nevada, USA. The oligotrophic lake is 501 m deep and has a 116 km shoreline. Lake Tahoe is dammed at its outflow, but lake level variation ranges about 0.5 to 2 m/yr within a range of 2.5 m and is mainly controlled by precipitation and evaporation.

Periphyton at Lake Tahoe is primarily composed of a mixed stalked diatom and charophyte community near the lake surface, and a deeper cyanobacteria dominated community. Documented reports of increasing periphyton biomass began in the 1960s (Goldman, 1967). A time-series analysis showed that periphyton biomass at 0.5m depth has not significantly increased from 1982 to 2019 (Atkins et al., 2021). At some parts of the lake, periphyton biomass had declined over time.

Periphyton Monitoring

Lake Tahoe periphyton was monitored from 1982-1985, 1989-1993, and 2000-present. Monitoring was conducted 3~15 times per year (on average six times a year) and centered around the peak spring biomass. During each sampling event, six to nine sites were surveyed (Figure 1). These sites were selected to include a range of periphyton biomasses and provide sites near high, medium, and low development levels onshore. Periphyton samples were always collected at 0.5 m depth, meaning that as lake level changed, the elevation of the samples moved accordingly. Periphyton samples were gathered using Lobe two brush samplers (Loeb, 1981). For each sample, three replicates were collected before 2000. After 2000, two replicates were collected. Routine samples were analyzed for ash-free dry mass (AFDM) and chlorophyll-*a*. Additional details about the Lake Tahoe periphyton monitoring scheme and laboratory analysis can be found in Atkins et al. (2021).

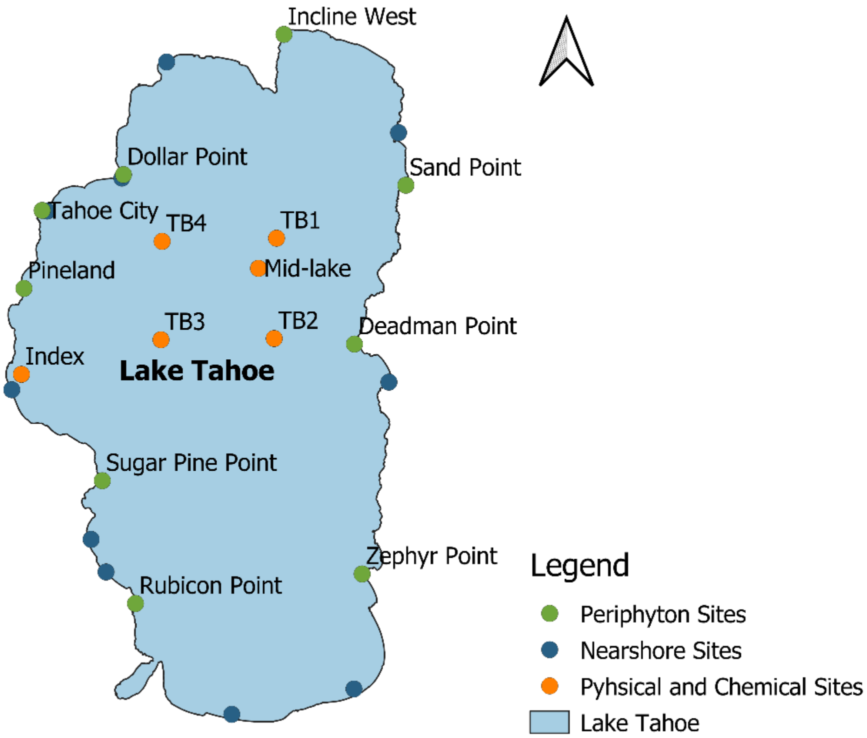

Fig. 3.1. Map of Lake Tahoe monitoring sites labeled with monitoring site names. The map shows locations for periphyton monitoring (green points), nearshore temperature monitoring (blue points), and physical and chemical monitoring (orange points). PAR was measured in Incline Village, just north of the lake.

Monitoring Nutrients

Nutrient data included nitrate-nitrogen (NO_3-N) and total hydrolyzable phosphorous (THP). NO_3-N was collected approximately weekly from 1982 until 2019. THP was collected approximately monthly from 1982 until 2019. On any given nutrient sampling date, nutrients were collected alternatively from the Midlake site or the Index site (Figure 1). A Van Dorn Sampler was rinsed with lake water from the surface of the collection site. The bottle was lowered to the appropriate depth and closed to collect a water sample at or above 1 meter. For the THP samples, the water was then transferred directly to a Nalgene sample bottle that had been cleaned with acid and phosphorus-free lab soap. For NO_3-N samples, the water was filtered before being bottled. To filter the samples, the collection bottles were mixed by inversion. The contents were then poured through a 25 mm GF/C Microfiber filter with a pore size of 1.2 µm into a sidearm flask. The samples were then transferred to an acid-washed bottle. All samples were kept in a cool dark cooler and transferred to a laboratory for analysis.

In the lab, THP was determined using a sulfuric acid digestion method with detection limit of 2.0 ug/L. Samples were analyzed within a month of collection. Sulfuric acid was added to the sample to release the soluble phosphorous from insoluble inorganic phosphates, organic phosphorus compounds, and pyrophosphates. After acid hydrolysis occurred, the samples were adjusted for pH. At this point, the orthophosphate levels were proportional to their color intensity, and a spectrophotometer was used to determine the orthophosphate concentration.

A total amount of nitrate and nitrite was determined using a hydrazine method with a detection limit of 2.0 ug/L. This method reduced nitrate to nitrite using a hydrazine-copper reducing solution. Then a diazotization-coupling reaction created a color intensity based on the nitrate and nitrite concentration. Finally, a spectrophotometer was used to determine the final concentration.

While groundwater N and P estimates are available for the Tahoe region, none known and available to the authors, were spatially and temporally robust enough to improve the model. Further, most lake monitoring programs do not include groundwater flow or nutrient monitoring. Thus, this modeling exercise did not include groundwater nutrient inputs, which are known to control at least some Lake Tahoe periphyton biomass (Naranjo et al., 2019).

Physical Processes Monitoring

PAR at depth was measured with a Biospherical radiometer (attached to a Seabird SBE25 Plus profiler) and inferred from Secchi disk data using Beer's Law. Short wave radiation was collected every 10 minutes using three instruments in Tahoe City. Data from one instrument was used to gap fill for the others to create a complete dataset. Data from the instruments were prioritized as follows: (1) a Kipp & Zonen CNR1 Net Radiometer collected short wave radiation in the spectral range of 305-2800 nm from 2003-6-11 to present; (2) a Kipp & Zonen CM21 Pyranometer collected data within the spectral range of 305-2800 nm from 1997-10-30 to present; and (3) a Li-Cor LI190SB Short Wave radiometer with a spectral range of 400-700 nm collected data from 1997-10-30 to 2003-1-30. Gap filled short wave data were used to calculate PAR at depth, assuming that PAR was 45% of shortwave data and using the following equation:

$$I(z) = I_0 e^{-kz}$$

in which z is depth, I_0 is short wave radiation, and k is the light attenuation coefficient calculated as:

$$k = \frac{a}{d_s}$$

where a is the light attenuation conversion factor (1.7) and d_s is the Secchi depth. Secchi depth was measured at the MLTP monitoring site (Figure 1) approximately monthly for the entirety of our periphyton dataset. PAR data from before 1997 was estimated using multiple imputations. The gap-filling method, multiple imputations, accounts for the uncertainty of missing data by generating multiple data sets with different plausibly filled gaps. The Bayesian model is run for each imputed dataset, and the model results are combined into one result at the end.

Estimates of nearshore temperature were made by fitting correlations between the midlake temperature and temperature collected at 11 nearshore sites around Lake Tahoe as was done in Roberts et al., 2018 (Figure 1). For the Midlake Site, we utilized a record that spanned the time of the periphyton dataset with twice weekly surface temperature from the LTP monitoring location. Temperature data from 11 nearshore stations around the lake was used for the lake periphery temperature (Figure 1). These stations were located at approximately 2 m depth and collected at a 30 sec interval. Where data from the nearshore stations were missing, records were gap-filled using data from 24 hours earlier. Temperature was time-averaged to a daily timescale. When both midlake and nearshore data were observed, the two locations' difference was found for each nearshore station. The mean littoral to pelagic temperature difference of each Julian day was calculated for every nearshore site. Means of temperature differences were smoothed using spline interpolation. These temperature differences for each nearshore station were then applied as a correction to the longer LTP temperature dataset to approximate long-term temperature near each nearshore site. The average r^2 for these correlations was 0.86, but the strength of these relationships varied by site. The modeled temperatures tended to overestimate low temperatures. Thiessen polygons were drawn around each nearshore site using QGIS. Periphyton monitoring stations within a polygon were assigned to the temperature approximation for that nearshore station.

Bed shear stress was calculated by using wind speed and direction data, as well as bathymetric data, as input to the STWAVE nearshore wave model (Roberts et al., 2019). The STWAVE model uses the wave action balance equation under steady-state conditions to convert wind conditions into depth-specific wave conditions. Wind data from 4 midlake buoys (TB1 – TB4) were utilized (Figure 1). Data from each buoy's two anemometers were averaged. For missing periods when instruments were not functioning correctly, TB1 data was gap filled with TB3, TB 2, and then TB4. Data at these buoys were collected from the year 2000 to 2019 at a 5 min time interval. Wind data were averaged to hourly means using vector averaging for the wind direction and scalar (normal) averaging for wind speed. Wind means were calculated using the 'openair' package version 2.7-2 in r. Wind was further downscaled to a two-week period using the max hourly wind mean for each two-week period prior to the periphyton sampling event. Periphyton takes one month to cycle from a clean surface to a mature community (Aloi, 1986). Half of that time was used to capture the largest shear event that would still affect periphyton biomass. Overall, this approach simulated the largest steady-state wind event occurring in the lake within that period. In addition to wind data, the node nearest to each periphyton sampling site closest to 0.5 m depth and between the 0.2 m and 2 m depth was chosen to represent each site in the wave model. The Lake Tahoe STWAVE model (Roberts et al., 2019) then yielded the maximum daily bed shear stress at each selected node. Bed shear data from before 2000 was estimated using multiple imputations.

The strength of correlations between measured and modeled wave height based on wind data binned to one hour ranged from an r^2 of 0.68 to 0.86 at different sites. Particle resuspension from the lakebed is one outcome of shear that can be used to understand the model's accuracy. The modeled time that exceeded a critical particle resuspension threshold was compared to the observed turbidity. This measure showed root-mean-square errors between 1-7%, depending on the site. The model tended to overpredict smaller waves.

Time since last exposed, or the time since the lake depth measured was last exposed to air, was calculated using measured depths of sampling and lake level measurements. Lake level measurements were based on the USGS gages at Tahoe City (USGS, 2019).

Statistical Analysis

The physical and chemical parameters described above were evaluated using a statistical model. Data for the explanatory variables were centered (the variable's means was subtracted from each value) and scaled (centered variables were divided by the variable's standard deviations) using the "scale" function in R version 4.0.3 to make parameters comparable. Missing data in the days since the sample site was last exposed above water parameter represented an area that had not been exposed since the recording of lake measurement began. Thus, it was missing not at random, and the standard multiple imputation method was not an acceptable method to fill these missing data. Instead, we modeled this variable as a monotonic variable. We categorized these data into five ordered categories: the first four were binned in quadrats, and the last bin was unfilled data. The bins were from 1-329 days, 330-864 days, 865 - 2954 days, and 2955 days to 20,301 days, and not exposed since 1900. The data for explanatory variables was temporally matched with the dates of periphyton sampling resulting in the same timescale of periphyton sampling. THP was indexed by site for better spatial understanding. All remaining data gaps were filled using the mice package to create 100 imputations. The Bayesian model was constructed and solved using the *brms* package (Bürkner, 2017) in R. Periphyton chlorophyll-a was modeled using the following equations:

$$Chlorophyll_i \sim norm(\mu_i, S_i)$$

$$\mu_i = (b0_{site}) + \left(b1_{wateryear}\right) + (b2)Shear_i + (b3)Temperature_i +$$

$$(b4)DaysSinceLastExposed_i + (b5)PAR_i + (b6)PAR_i{}^2 + (b7)NO3_i + (b8)THP_{site(i)} +$$

$$(b9)LakeSurfaceElevation + (\mathrm{b10}) \sum_{j=0}^{days\ since\ exposed_i - 1} \zeta_j + P_i$$

where i was site- and time-specific sampling record, $b0_{\text{site}}$ and $b1_{wateryear}$ are random effects capturing the effects of sampling sites and sampling year. $b_{1\ldots n}$ was the coefficient of the corresponding variables, the deviation from b_0. We used the mildly informative prior of lognormal(0,1) for standard deviations and normal(0,5) for the coefficients in the model. The monotonic parameter, days since last exposed, was modeled such that ζ is a simplex, j is the number of elements, and a Dirichlet prior with the distribution concentration set to α_1, $\alpha_{2,}$ α_3, and α_4 equal 1.

An intrinsic conditional autoregressive model (iCAR) was used to model spatial autocorrelation between adjacent sites. The iCAR model assumed one smoothing term variance between sites and was appropriate because the periphyton is heterogeneous even within sites, implying relatively local spatial autocorrelation (Cramb et al., 2017). The spatial random effects component (P_i) was modeled using the following equation:

$$P_i | p_{\backslash i} \sim \mathcal{N}\left(\frac{1}{\sum_j w_{ij}} \sum_j w_{ij} p_j, \frac{\sigma_p^2}{\sum_j w_{ij}}\right)$$

where a spatial weights matrix w contains the element w_{ij} with i sample sites as rows and j sample sites as columns (Besag et al., 1991, Besag, 1974, Lee, 2011, Best et al., 2005). W determines the spatial proximity between the random effects, and it is defined as a binary, first-order, adjacency matrix, whereby

$$w_{ij} = \begin{cases} 1 & if\ i\ and\ j\ are\ adjacent \\ 0 & otherwise \end{cases}$$

The model was run for 10000 iterations with a 5000-iteration warmup and a thinning of 10. The model was considered converged when $1.00 \leq \hat{r} \leq 1.03$ and when trank plots showed well-mixed chains for each imputed model (McElreath, 2018).

Analysis was completed using relevant *brms* functions. R^2 was calculated based on the method described in Gelman et al., 2008. The predicted values' variance was divided by the sum of the expected variance of the errors and the predicted values' variance using the bayes_R2 function in *brms*. Posterior conditional effects plots were created using the conditional_effects function in *brms*.

3.4. Results

The converged model's estimate of chlorophyll-a had an R^2 of 0.32, explaining 32% observed variance in >30 years of periphyton chlorophyll-a. All results were considered significant if they fell within a 95% credibility interval. Results showed that temperature had a significant negative relationship with periphyton chlorophyll-a (Figure 2). The effect of lake surface elevation, shear stress, and THP did not have significant effects. NO_3 had a significantly positive effect on periphyton. PAR shows a linear effect with chlorophyll-a increasing when PAR is low, but PAR's quadratic term was not significant.

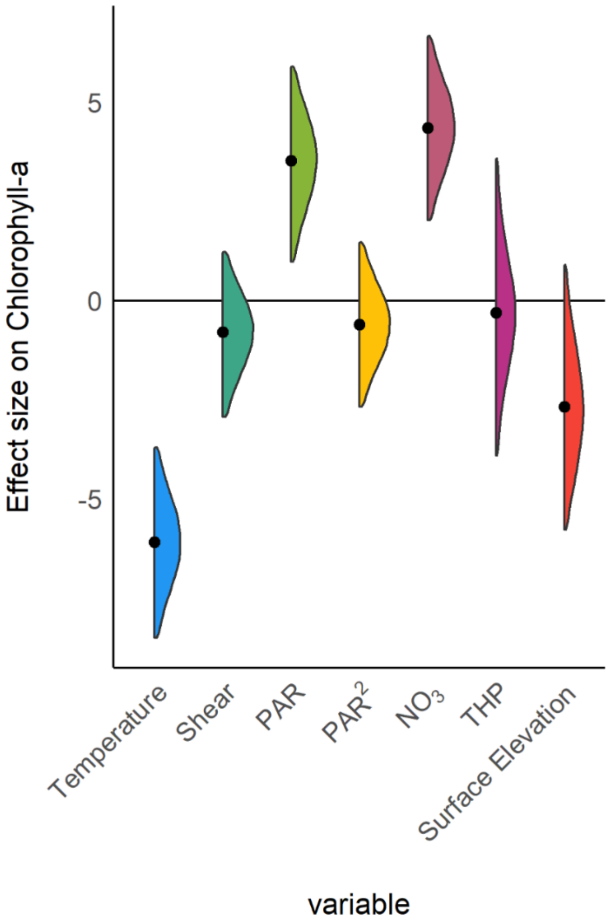

Fig. 3.2. Constituent beta half violin posterior distribution plots. Distributions are shown to the 95% credible interval.

When broken down by site, THP effects were not significant at any individual location. Midlake THP had the largest effect size on chlorophyll-a at Sugar Pine Point (which had very low biomass) and Pineland (which had high biomass) (Figure 3). At some sites, midlake THP had a negative effect size, including Tahoe City, Incline West, Sand Point, and Deadman Point.

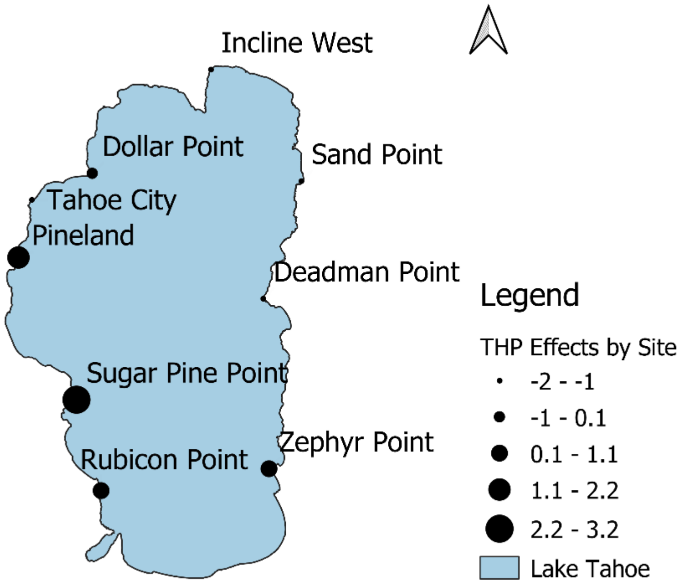

Fig. 3.3. Map of mean midlake THP effect sizes for each site. THP effects were not significant to the 95% credibility interval at any site.

Random effects were defined as group-level effects that are not attributable to the fixed predictors included in the model. The random effects of sites and years mainly were not significant, yet they showed patterns of interest. The random effects of the water year (the 12 months from October 1-September 31 of the following year) show a periodic oscillation pattern (Figure 4). Every 4 to 5 years, the water year or variables associated with water years go from negatively impacting the periphyton biomass to positively affecting the periphyton. The random effects and their pattern account for a factor affecting periphyton unaccounted for in the model. Only two years had significant negative impacts on chlorophyll-a and one year had a positive impact.

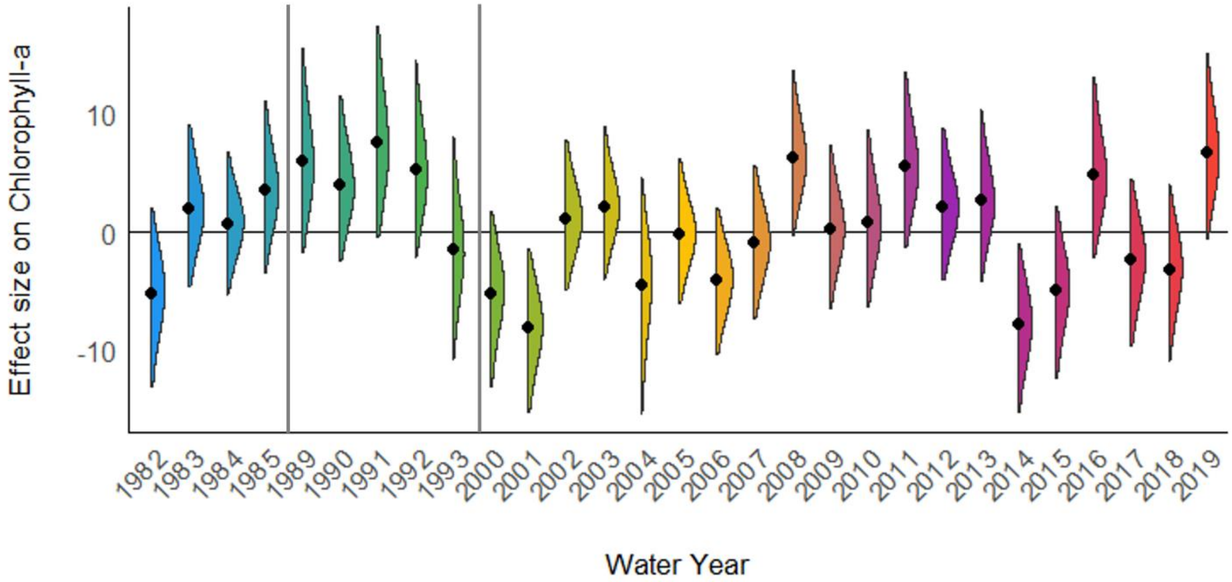

Fig. 3.4. Half violin posterior distribution plots for yearly random effect. Distributions are shown to the 95% credible interval. The two gray vertical lines show breaks in the data record.

Site-specific random effects also showed broad distributions of effects on chlorophyll-a (Figure 5). Dollar Pt., Pineland, Rubicon, and Tahoe City all had significant positive effects on chlorophyll-a. These sites were all on the western side of the lake. Sugar Pine Pt. was the only site on the lake's western side that did not have a significant positive effect. The rest of the sites, on the northern and eastern side of the lake, did not show a significant relationship with Chlorophyll-a. The iCAR model results showed that no site had a significant effect on its neighboring sites.

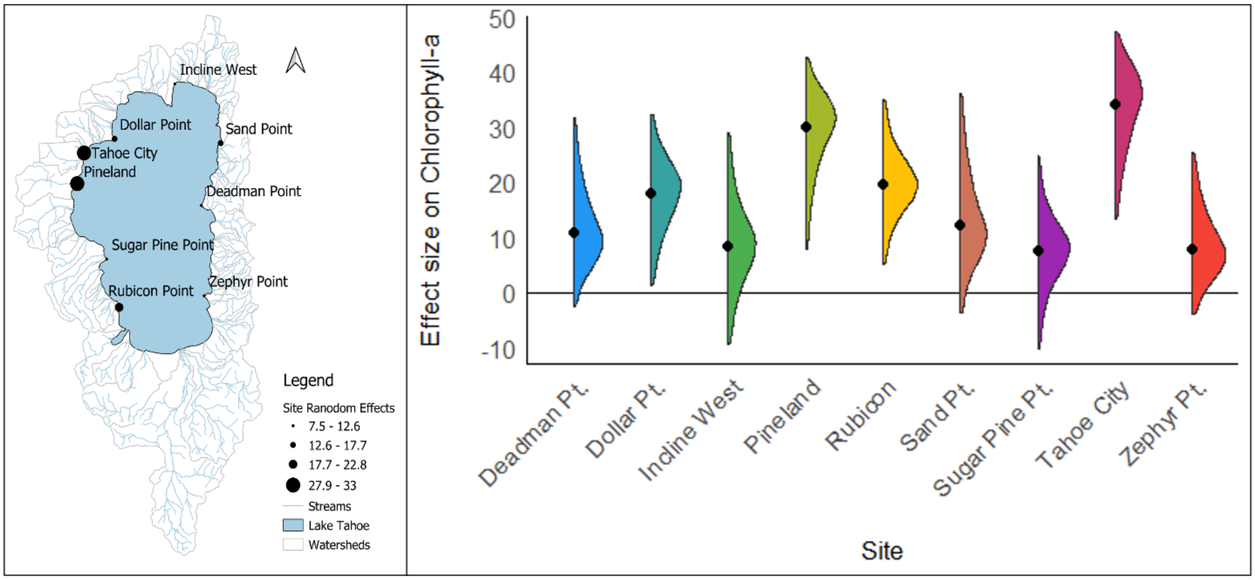

Fig. 3.5. a. Map of mean site-specific random effects. b. Half violin posterior distribution plots for site-specific random effect. Distributions are shown to the 95% credible interval.

A posterior conditional effects plot of the monatomic variable days since last exposed showed that if all else were the same, periphyton chlorophyll-a would increase as the time since the substrate was last exposed to the air (Figure 6). In category 1, the lowest number of days since last exposed, chlorophyll-a was low and the effect of days since last exposed showed low variability. Category 1 had the highest mean posterior, the most influential impact of any of the inputs to the model. A large biomass increase occurred between the first and second categories of days. The effect of days since last exposed also showed a more extensive range in the second category than in the first. Between each of the second to the fifth categories, the mean biomass increased.

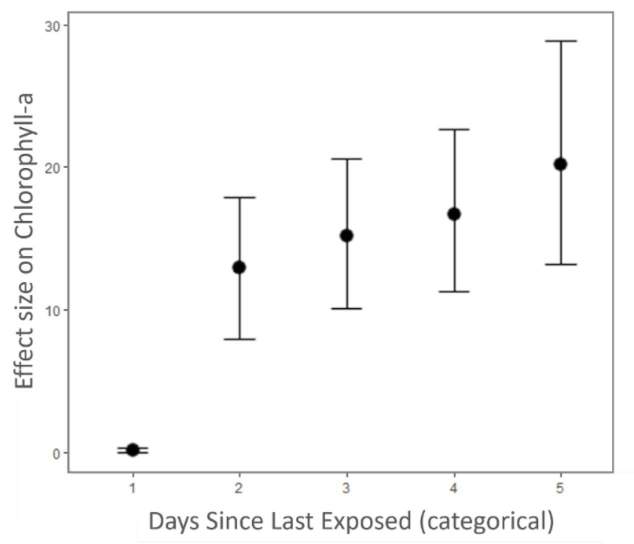

Fig. 3.6. Posterior conditional effects plot of days since last exposed.

A conditional effect plot further showed that PAR influenced chlorophyll-a levels linearly (Figure 7). Chlorophyll-a levels increased more or less evenly as PAR increased. The range of the credibility interval is wide on this metric toward the PAR extremes due to having fewer data in this range.

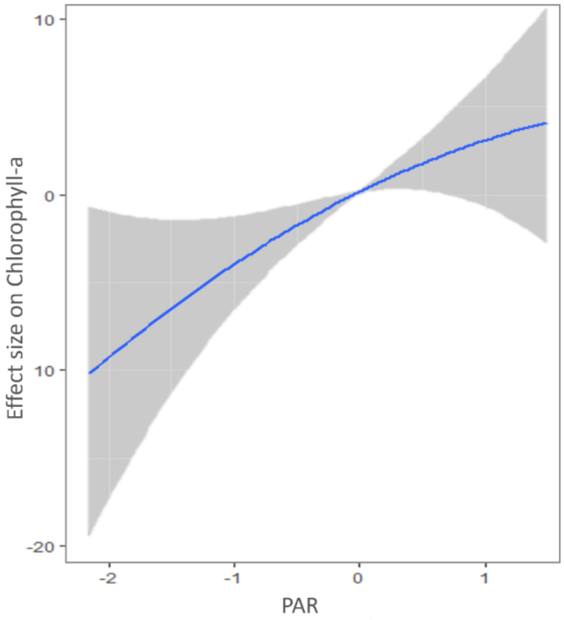

Fig. 3.7. Predicted conditional effects plot of PAR.

3.5. Discussion

The inputs to this model explained a third of the variability in periphyton biomass in Lake Tahoe. Temperature correlated negatively with biomass. PAR, and days since last exposed, correlated positively with periphyton biomass. Midlake NO_3 correlated positively with biomass, while midlake THP was not significantly correlated with biomass. Patterns in the water year posterior showed an unknown multi-year process that was not accounted for by our model.

This model could likely be improved if new relevant factors were added and constituents were measured in the modeled locations. In addition, processes should be monitored at a relevant spatial and temporal scale.

The Effects of Modeled Factors

Temperature had a negative impact on periphyton growth (Figure 2). This finding was contrary to the prevalent phytoplankton trope in which warm eutrophic lakes cause algae blooms. Periphyton biomass may only respond to warming temperatures if nutrients are available (Cao et al., 2017). Nitrogen and phosphorus input primarily occurs during winter rainstorms, spring snowmelt, and spring groundwater influx. Consequently, Lake Tahoe's cool temperature blooms are inextricably linked to the timing of nutrient inputs when water temperature is seasonally low.

The impacts of bed shear stress were perhaps surprisingly small (Figure 2). The model did show that shear reduced biomass but not to a significant level. While powerful shear events can remove large clumps of periphyton from substrate, these areas can fully restore their previous community within a month (Aloi, 1986). Considering that our sampling interval is approximately monthly, we are not resolving the impacts of shear events. Sloughing mostly occurs as the age of periphyton increases and its health declines, making shear’s effects time specific. Additionally, shear typically removes periphyton in a patchy manner. Our measurements of periphyton biomass as chlorophyll-a do not fully capture this patchiness as we are limited to two to three replicates per site. A better measure of shear at each site would be our percent cover estimate, but this measure does not fully reflect biomass.

PAR significantly affected periphyton chlorophyll-a linearly (Figure 7). In Lake Tahoe, the model showed that low levels of light corresponded to lower periphyton biomass. Periphyton biomass at 0.5 m does not appear to decline even at the highest ranges of Lake Tahoe's typical light inputs. Rapid light attenuation within mats is thought to contribute to protecting periphyton from the effects of overexposure to light.

Mid-lake NO_3-N had a significant positive association with periphyton biomass (Figure 2). The positive relationship may be due to a correlation in the input timing of nutrients to the nearshore and the midlake. Unlike phosphorous, most of Lake Tahoe's nitrogen comes from atmospheric deposition (TERC, 2020). Yet, near-surface nitrate tends to be low (< 5 µg Nitrate-N /L) year-round unless full lake turnover occurs. Turnover can quadruple midlake surface nitrate levels. However, full turnover only occurs in some years, on average every eight years since 2000, and tends to occur in late winter, after periphyton growth peaks. Deep lake nitrate reaches its annual height in January. Perhaps, upwelling events contribute to periphyton biomass by bringing nutrient-rich water from the bottom of Lake Tahoe to near-surface locations (Roberts et al., 2021). It is also possible that the mechanisms that increase nearshore nutrients, such as river inflows and groundwater input, also correlate with the timing of midlake nutrient contributors.

On the other hand, midlake phosphorous was not correlated to periphyton biomass at the entire lake scale (Figure 2). This finding was surprising because Lake Tahoe phytoplankton are co-limited by nitrogen and phosphorous, and periphyton was thought to be similarly limited. Unlike nitrogen, most of Lake Tahoe's phosphorous comes from non-urban runoff (TERC, 2020). There are several possible explanations of why THP was not correlated with biomass. One is that midlake phosphorous does not correlate with the nearshore phosphorous readily available for periphyton uptake. This explanation is compelling because periphyton nutrients, at least at some locations around the lake, are received primarily from groundwater (Naranjo, 2019), while planktonic algae receive nutrients from midlake water. Thus, nutrient limitations could differ between planktonic and periphytic algae. Another possible reason that periphyton did not appear to be phosphorous limited is that periphyton is not actually phosphorous limited. Periphyton was nitrogen and phosphorous co-limited in the 1980s (Aloi, 1986) and was assumed to have remained co-limited like phytoplankton. Chlorophytes tend to require higher bioavailable N:P ratios (Vadeboncoeur et al., 2021), but Chlorophytes are the minority of periphyton in Lake Tahoe compared to diatoms and cyanobacteria (Atkins et al., 2021). In any case, to understand the THP component of periphyton blooms, we may need nearshore THP data on finer spatial and temporal scales—matching of the scales of the THP's patterns.

The days since last exposed results showed when substrate is newly submerged, for approximately the first year, periphyton biomass increases slowly as it colonizes (Figure 6). The greatest growth occurs between 330-864 days since last exposed. Surprisingly, biomass continues to accrue over time, though more slowly, after this initial growth period.

Finally, lake surface elevation had a negative relationship with periphyton biomass (Figure 2). This result is somewhat surprising. Periphyton data for this project was measured at 0.5 m. Thus, as lake level declines, our measurements go from sampling the diatom and green algae communities near the lake's surface to measuring the cyanobacteria communities located deeper in the lake. Previous analysis of this dataset showed that periphyton biomass was higher when cyanobacteria dominated periphyton communities than when stalked diatoms dominated the community at 0.5 m (Atkins et al., 2021). However, we do not have direct evidence that this is the cause of this biomass difference. The previous work described analyzed this information as a single correlation while this work was multivariate. Some of the lake surface elevation correlation may have been assigned to the related days since last exposed term, making this term less significant.

An oscillation in the yearly random effects results reveals a parameter not included in the input data (Figure 4). This pattern begs the question- What was not included in the model that is creating this pattern? One idea was that drought was not fully represented in the lake level input, but drought years did not match well with the cycling shown. Precipitation levels were also a possibility, but those data do not line up with this pattern either. This pattern is likely based on a constituent that we do not have data about. For example, perhaps this pattern has to do with populations of periphyton grazers such as snails and crayfish. This pattern could also have to do with groundwater nutrient levels.

3.6. The Missing Components

The r^2 for this model shows the complexity of the ecological system. We believe that several factors are important to driving periphyton in Lake Tahoe that are not included in this model. These drivers were not included because we do not systematically collect these monitoring data in Lake Tahoe. We do not have information on the population or grazing rates of crayfish over time at these sites.

Perhaps most importantly, we do not have near periphyton nutrient levels. Midlake nutrients are not the nutrient supplies driving periphyton, but they were the nutrient data available for this research. Naranjo et al. showed that periphyton biomass near Ward Creek is stimulated by groundwater nutrient levels (2019). However, we also know that groundwater inflow and nutrient contents are highly spatially and temporally variable (Naranjo et al., 2019). Further, in the most recent periphyton nutrient limitation tests, which took place in the 1980s, periphyton was variably N, P, or N and P limited around the lake and through time (Loeb, 1987). These results are distinct from the phytoplankton in the 1980s, which were more uniformly P limited and then transitioned to N and P limitation. Changes in groundwater nutrient ratios may have also changed in the past decades, leading to changes in periphyton nutrient limitations. Aside from groundwater influence on periphyton nutrient levels, periphyton receive nutrients from surface inflows. Particularly, runoff from developed areas and stream water inflows may contribute to periphyton growth. We do not monitor how extensively these inflows influence periphyton growth. Upwelling events may also contribute to periphyton biomass (Roberts et al., 2021).

3.7. Management Implications

The modeled results show that we already measure some of the components key to understanding periphyton growth. Light appears to be a limiting factor for near-surface periphyton. Periphyton generally thrive under warmer conditions, so Lake Tahoe periphyton thriving under cool conditions seems more circumstantial than explanatory.

Midlake NO_3 levels are high around times of high periphyton biomass. Small increases in midlake nutrient levels may correlate to periphyton biomass increases but are likely not driving the periphyton growth. Naranjo et al. showed that groundwater drove periphyton around the Ward Creek inflow (2019). Typical groundwater nitrate levels around Ward Creek were on average 20 times higher than in the midlake.

Groundwater flow and nutrients should be monitored regularly in Lake Tahoe to further our understanding of periphyton drivers. However, groundwater is temporally and spatially patchy and may not be driving periphyton growth around the lake. Thus, strategic monitoring of groundwater is required to understand the variability of this system. Similarly, periphyton nutrient limitations should be reevaluated.

The fact that none of the spatial autocorrelation results were significant showed yet again that periphyton processes occur on a localized scale. Thus, we can improve our understanding if we focus on learning about periphyton on a scale relevant to the processes occurring within the microhabitat.

For generations, oligotrophic lakes have been monitored in much the same ways as eutrophic lakes. In a system so devoid of nutrients, microhabitats are created in areas of high nutrient inputs. At many lake monitoring programs, the midlake is relatively well studied. However, nearshore habitats of oligotrophic lakes, which are vastly different from their midlake neighbors, are hardly monitored. While this monitoring and research disparity is changing, many lake programs attempt to fill the deficit by applying midlake instrumentation and methods to the nearshore. These methods are limited. With a new habitat, we must ask new questions and seek their answer in new ways. Thus, the monitoring programs to understand the nearshore should focus on monitoring that which influences the nearshore, particularly groundwater nutrients and periphyton.

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4. Envisioning Climate Change Impacts on Periphyton in Lake Tahoe

4.1. Abstract

Periphyton blooms, or a rapid increase in periphyton biomass, occur in oligotrophic lakes worldwide, and many of their drivers are affected by climate change. The outputs from a series of models were used to project future conditions of periphyton biomass drivers in Lake Tahoe, including water temperature, lake level change, nutrient concentration, light environment, and precipitation. The model output variables were analyzed to determine their impacts on Tahoe's periphyton communities. Overall, the climate is projected to be hotter and wetter, with more cloud cover leading to less incoming shortwave radiation. The models predicted higher nitrate fluxes from streams but no significant increase in soluble reactive phosphorous fluxes. Lake level will likely change at a higher frequency in the future. Analysis of each condition's effect on periphyton led to the synthesis of two potential outcomes for periphyton in Lake Tahoe. In one scenario, a projected increase of lake temperature and higher N:P ratio leads to a shift in Tahoe littoral periphyton blooms from diatom dominance to green algae dominance. In the second scenario, the climate change conditions lead to increased biomass, but the littoral blooms remain diatom dominant. As the effects of climate change continue to affect oligotrophic lakes, managers should limit littoral nutrient influxes and monitor the community composition of periphyton.

This paper was co-written by Karen S. Atkins, Thomas P. Shannon, Michael F. Meyer, Isabella A. Oleksy, Nicholas T. Framsted, Deviyani Gurung, and Robert Ladwig,

4.2. Introduction

Attached algae, known as periphyton, provide essential ecosystem functions and can be used as an early indicator of environmental stress in lakes. Periphyton can account for a large portion of whole lake production, especially in smaller and more oligotrophic lakes (Vadeboncoeur and Steinman, 2002; Sadro et al., 2011). By fixing nitrogen, some periphyton also play an important role in lake nutrient cycling (Reuter et al., 1986). Periphyton actively uptake nutrients from substrate and groundwater influxes and concentrate them, making them important to the assimilation of subsurface solutes into the lake food web (Hecky and Hesslein, 1995). Alongside the production by macrophytes and phytoplankton, periphyton primary production adds redundancy and thus stability to the base of lake food webs (Bondavalli and Bodini, 2014). Even in large and deep lakes, many aquatic fauna, including fish, benthic invertebrates, and turtles, feed on periphyton (Chessman 1986; Jin et al. 2003; Vadeboncoeur and Steinman, 2002). Periphyton's role as a food source for these generalists increases the quantity of weak interactions within the food web and helps form a resilient food web (de Mazancourt et al., 2013; Pimm, 1984). The food web interaction creates chemical and energetic connectivity between littoral and benthic regions (Hecky and Hesslein, 1995; Vadeboncoeur and Steinman, 2002; Vadeboncoeur et al., 2003). Furthermore, periphyton communities respond rapidly to environmental conditions making atypical blooms or community composition useful as an early indicator of change within the system (Lambert et al., 2008; Spitale et al., 2014).

Large-scale periphyton biomass increases that occur over a short period, periphyton blooms, have been observed in oligotrophic lakes worldwide (Kravtsova et al., 2014; Hawes and Smith, 1994; Cantonati et al., 2016). Lakes can experience gradual changes in biomass, press or rapid blooms, pulse. The blooms often occur seasonally and are caused by combinations of increased nutrient loading, changed lake hydrodynamics, and changed food web dynamics

(Vadeboncoeur et al., 2021). All these bloom-forming conditions can be impacted by climate change. Specifically, lake climate change models project differences in lake level fluctuations, light availability, water temperature, nutrient supply, and predation. As a result of climate change's influence on its drivers, periphyton blooms are likely an early sign of the ecological effects of climate change within lakes.

Climate change could alter periphyton biomass and production due to projected and observed changes in temperature, nutrient inputs, and light in lakes. In experiments where water temperatures were elevated by 3 °C and 4.5 °C, periphyton biomass increased (Cao et al., 2017; Baulch et al., 2005), especially when combined with nutrient pulses. Nutrient availability often limits periphyton biomass and production. Climate change is expected to shift the quantity and timing of nutrients available for periphyton uptake (Sahoo et al., 2013). Lake nutrient influx rates are determined by hydrologic factors such as snowmelt timing, lake level fluctuations, groundwater inflow rates, and stream discharge rates which are shifting under climate change conditions (Naranjo et al., 2019; Cao et al., 2017). Periphyton biomass and production at depth is also affected by light penetration (Hansson, 1992; Vadeboncoeur et al., 2001). PAR increases periphyton biomass and production until photosynthetic saturation is reached (Hill 1996; Kilroy and Bothwell, 2014; Marks and Lowe, 1993). However, periphyton is sensitive to excessive ultraviolet radiation (UVR), which can contribute to photoinhibition, smaller biomasses (Higley et al., 2001), and weaker attachments to substrate (Kilroy and Bothwell, 2014). These factors that control periphyton biomass and production are shifting due to climate change.

The distribution of periphyton within a lake could also change due to climate change. Lake levels will fluctuate more with climate change (Gunn et al., 2001). When lake level fluctuates, habitat near the surface may be lost, and periphyton attached to the newly exposed substrate may desiccate (Morison and Sheath, 1985; Gray et al., 2007). Deeper parts of a lake may become habitable as light penetrates deeper. Lake level change can also result in a shift of hydraulic head between the lake's surface and the surrounding watershed. This change in pressure alters nutrient-rich groundwater influx or outflow to lakes (Krabbenhoft et al., 1990). By altering growth conditions in lakes, climate change will modify the distribution of periphyton within.

Climate change could alter periphyton community composition. Increasing temperature has been shown to cause a shift in the community composition (Baulch et al., 2005). While specific species vary between locations, diatoms generally dominate when water is below 20 °C, chlorophytes dominate between 15 °C and 30 °C, and cyanobacteria dominate at high temperatures (DeNicola, 1996). Further, specific periphyton species are adapted to and can acclimate to ranges of light intensity. However, light conditions are shifting due to climate change. Therefore, periphyton communities may experience range shifts as they migrate to regions corresponding to their light niches (Marks and Lowe, 1993; Vadeboncoeur et al., 2014).

The predation of periphyton will be important to periphyton under climate change conditions (Baulch et al., 2005). Top-down control by grazers such as snails, caddisflies, crayfish, chironomids, and mayflies is an important factor in regulating periphyton biomass (Hillebrand and Kahlert, 2001; Vadeboncoeur and Stienman, 2002). In mesocosms that simulated climate change conditions, benthic grazers were responsible for reducing periphyton biomass to pre-climate change levels (Kazanjian et al., 2018). In some lakes, grazing may regulate periphyton biomass under climate change.

Modeling can provide scientists and managers with insights into mechanisms governing periphyton and the ability to forecast future conditions. Downscaled General Circulations

Models (GCMs), sometimes referred to as global climate models, can provide inputs for hydrologic models and lake physical models. The outputs from those lake models may provide insights into both the nature and the magnitude of plausible future lake conditions. While this approach falls short of explicitly modeling periphyton, it is not widely implemented in part because data collection of periphyton and its drivers is inadequate at most lakes (Atkins et al., 2021). However, by modeling the future lake conditions and understanding the drivers of periphyton, we can infer the future response trajectories and thereby help scientists and managers prepare for the changes.

This study uses modeled climate change scenarios at Lake Tahoe to understand potential impacts on periphyton in deep lake oligotrophic systems. Using two widely adopted climate change scenarios in four GCMs that both California and Nevada have adopted, we use the meteorological outputs to produce time series of hydrologic variables and lake variables. These are then used to infer how periphyton in Lake Tahoe may change in the future and discuss the implications of our findings for scientists and managers. We hypothesize that climate change will: (1) increase nutrient input to Lake Tahoe, increasing periphyton biomass; (2) warm nearshore waters and alter species composition; (3) increase the frequency of lake level fluctuations, altering substrate availability; and (4) decrease inputs of shortwave radiation, altering photosynthetically active radiation (PAR) and ultraviolet radiation (UVR), decreasing periphyton growth.

4.3. Methods

4.3.1. Study Site

In the Sierra Nevada mountains in California and Nevada, USA, Lake Tahoe has a surface area of 499 km^2, has a shoreline length of 116 km, and is 501m deep. The depth of the photic zone (one-percent light level) had annual averages ranging from 94 m to 77 m in the 1970s but declined to 46 m to 61 m in the 2010s. Tahoe periphyton blooms were first described in 1967 (Goldman, 1967). Monitoring data spanning from 1982 to 2019 showed that periphyton biomass at 0.5 m did not increase over time, though biomass may be changing at other depths (Atkins et al., 2021). The periphyton blooms reach peak biomass in spring and minimum biomass in summer. Two periphyton communities dominate the littoral: one contains stalked diatoms with some patches of filamentous green algae, including *Gomphoneis herculeana, Gomphonema parvulum*, *Mougeotia genuflexa*, and *Ulothrix zonata*, and the other contains cyanobacteria, including *Calothrix scopulorum* and *Nostoc entophytum*. The diatom and green algae community generally occupies the eulittoral and the cyanobacteria community tends to habitate in the deeper sublittoral zone. However, lake level changes within a 2 m span complicate this pattern as algae are desiccated or inundated for periods varying from months to years. Most periphyton blooms worldwide have green algae dominant eulittoral zones (Vadeboncoeur et al., 2021), so Tahoe's diatom-dominated eulittoral blooms are unusual and of great interest.

4.3.2. Modeling Methods

The Scripps Institution of Oceanography's Southwest Climate Center (SCC) produced the climate results for four GCMs: HadGEM2-ES, CNRM-CM5, CanESM2, and MIROC5 for two Representative Concentration Pathways (RCPs) RCP 4.5 and RCP 8.5where the earth's radiative forcing stabilizes around 4.5 W/m^2 or 8.5 W/m^2 before 2100. The state of California has also adopted these models and scenarios as they are believed to best embrace the likely climate change impacts in the western US (https://cal-adapt.org).

The GCMs had an approximate grid size of 1° (110 km). The SCC used the Localized Constructed Analogues (LOCA) (Pierce et al., 2014) method to downscale daily precipitation, temperature, and wind data to a 1/16° (about 6 km) grid size, and results were adjusted using a frequency-dependent bias correction (Pierce et al., 2015; Maurer et al., 2002). Corrected LOCA data was input into a Variable Infiltration Capacity (VIC) model (Liang et al., 1994; Hamman et al., 2018; Pierce et al., 2018). The VIC model is a macroscale hydrologic model that solves water and heat energy balances to estimate 23 hydrologic and meteorological parameters, including incoming shortwave radiation and precipitation. To evaluate model accuracy, the historical period from 1950-2005 was modeled. 2006-2099 were projected as future estimates for each model and scenario combination.

The Lake Tahoe Watershed Model (Tetra Tech 2007; Lahontan and NDEP 2010) was rerun with the predicted climatological variables to produce daily stream discharge and concentrations of suspended sediment, total Nitrogen, and total Phosphorus. This model had been developed for use in the Lake Tahoe Total Maximum Daily Load (TMDL) Program and had been previously calibrated.

These model outputs from the GCMs, VIC, and the Watershed Model were used to run the Lake Clarity Model (LCM) (Sahoo et al., 2010) to estimate Lake Tahoe's response to climate change. LCM is a one-dimensional horizontally mixed Lagrangian layer model that simulates inflows, mixing, stratification, and vertical particle transport. In this application, only the hydrodynamic parts of the model were run. As was done for the Total Maximum Daily Load calculations for Tahoe, a constant groundwater input of 1.34 x 10^4 m^3/day was applied (U.S. EPA, 2016). The future daily outflows from the Lake Tahoe Dam cannot be estimated, so the minimum flows in the Truckee River Operating Agreement were used at a constant discharge

(ORCC, 2008). Thus, the predicted output for absolute lake level should not be relied upon. However, while the lake level itself was partially controlled by the assumed dam release, the rate of change in lake level is primarily influenced by meteorological factors, mainly evaporation and stream inflows and was examined. The absolute value of summed monthly lake level increases and decreases were used to create the lake level fluctuation metric. The absolute value was used to measure the rate of lake level changing rather than assess whether the lake level was rising and falling, which had little certainty given unknown dam operations. More details on the modeling can be found in Trommer et al., 2021.

To estimate nearshore temperatures from the modeled midlake temperatures, correlations of midlake to nearshore temperatures were applied using data from Lake Tahoe (Roberts et al., 2018). These relationships were based on the average difference for each Julian day between measured temperature at a midlake lake buoy and at ten nearshore stations located around the lake's periphery at a depth of approximately 2 m. The average strength of correlation was r^2= 0.86 but varied by site and tended to overestimate the lowest temperatures. These correlations were applied to the LCM output temperatures at 0.5 m depth, estimating nearshore temperatures around the lake. The lake was split into northeast and southwest sections for statistical analysis because shore temperatures in the northeast are on average warmer than those in the southwest.

Nitrate and soluble reactive phosphorous (SRP) load data were generated. Nutrient loads were compiled for seven major stream inflows to Lake Tahoe: Incline Creek, Ward Creek, Blackwood Creek, Third Creek, Glenbrook Creek, Upper Truckee River, and Trout Creek. The correlations that had previously been developed for nutrient loads for those streams were based on measurements for the last 30-40 years. As future streamflows are predicted to be significantly higher, those nutrient loads may prove to be underestimated.

4.3.3. Statistical Methods

Mann-Kendall trend tests were used to analyze monotonic trends within the modeled time series data. Mann-Kendall tests assume independence between sampling events but do not assume linearity in the trend (Mann, 1945; Kendall, 1975). The tests were performed using the “MannKendall” function in the “Kendall” R package version 2.2. The tests resulted in the following test statistics: a Kendall Score (S), which evaluates each point’s relation to the following points and indicates an increasing or decreasing trend with its positivity or negativity; a two-sided p-score which assesses the significance level; a Kendall’s Tau which evaluates the strengths of the variable’s association; and a z-score which is a standardized test statistic. Following standard scientific convention, a two-sided p-value of 0.05 or smaller was considered a significant trend.

4.4. Results

The modeling results showed that under both scenarios, but especially under the RCP 8.5 scenario, Lake Tahoe’s biostimulatory conditions, the environmental conditions that stimulate periphyton growth, will change. The Mann-Kendall results of the modeled RCP 4.5 and the RCP 8.5 scenario showed a small but significant reduction in incoming shortwave radiation over time due to increased cloud cover (Figure 1, Table 1). In the RCP 4.5 scenario, incoming shortwave went from an average of 18,368 kW/day from 2006 to 2026 to an average of 18,266 kW/day from 2080 to 2100, a 102 kW/day decline. In the RCP 8.5 scenario, the average incoming shortwave went from 18,316 kW/day to 17,844 kW/day, a 472 kW/day reduction within these time ranges. Shortwave penetrating to the periphyton at depth may be further affected by lake clarity changes, which were not modeled.

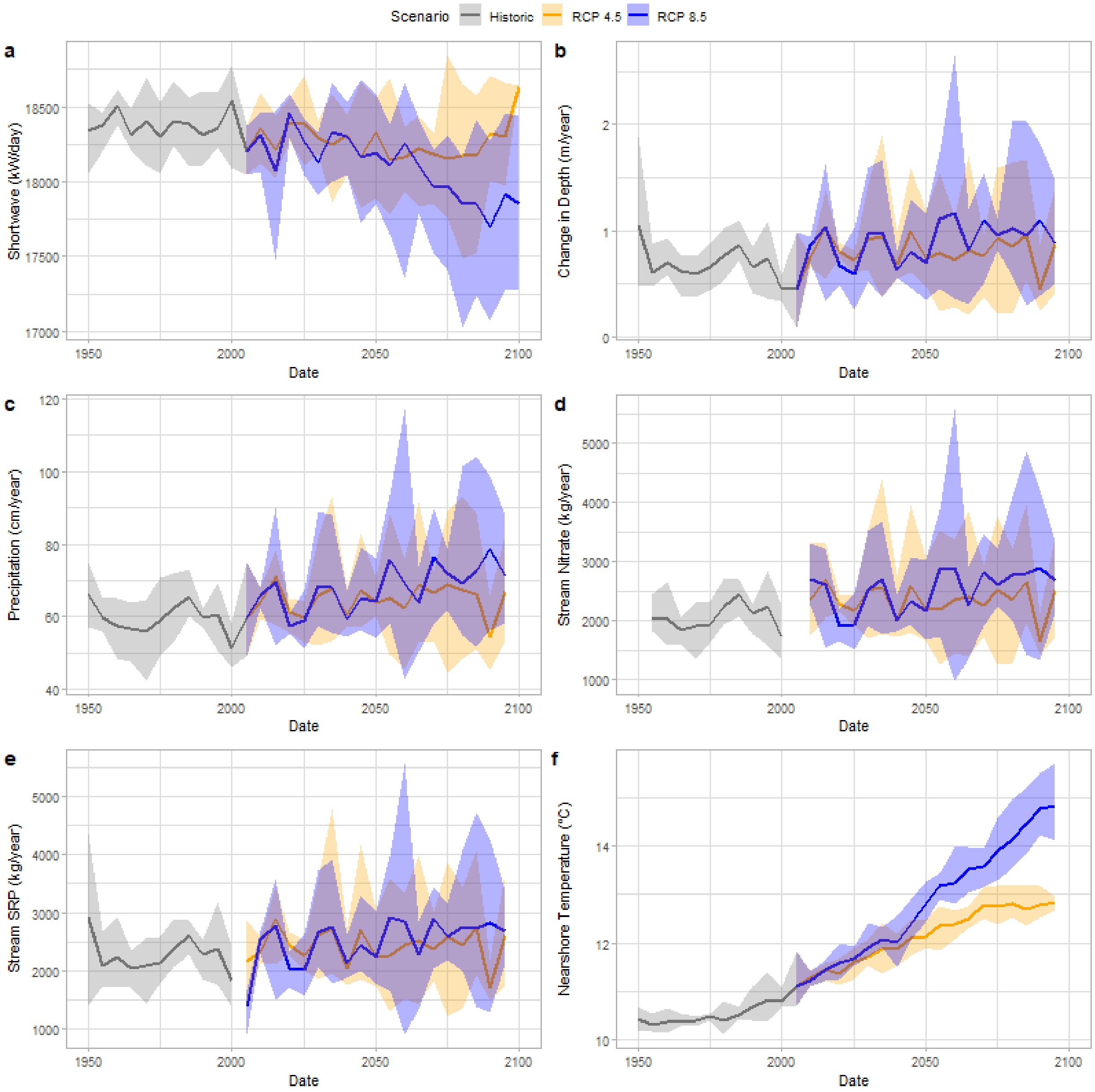

Fig. 4.1. Model results for historical and projected RCP 4.5 and RCP 8.5 scenarios from 1950 to 2100 for a) incoming shortwave radiation, b) rate of lake level change, c) average annual precipitation, d) nitrate and, e) SRP loads from stream inflows and, f) average lakewide nearshore temperature. For plot readability, all data was averaged over five years. Shading around means represents the range of predicted averages between models.

For the rate of lake level fluctuations, Mann-Kendall results showed that there would be a significant increase in monthly variation over time under the RCP 4.5 scenario (Figure 1, Table 1). In this scenario, Tahoe lake level changed an average of 0.12 m from 2007-2027 and increased to an average of 0.13 m, a 0.01 m increase, in the last twenty modeled years of 2080 to 2100.

Table 1. Mann-Kendall Trend Test results for modeled data averaged from the CANESM2, CNRM, HadGEM2, and MICRO5 models. Modeled data begins in 1952 and extends to 2099. Note that *p*-values denoted with ** are significant to the 0.01 level, and those marked with * are significant to the 0.05 level.

Constituent	**RCP Scenario**	**Mann-Kendall**			
		Tau	**S**	**z**	**p**
Shortwave Radiation	4.5	-0.01	-1E+07	-2.40	0.02*
Shortwave Radiation	8.4	-0.02	-2.6E+07	-6.08	<0.01**
Lake Level Flux	4.5	0.04	55882	2.26	0.02*
Lake Level Flux	8.4	0.03	42040	1.70	0.09
Precipitation	4.5	0.00	4787222	1.127	0.26
Precipitation	8.4	0.01	21316305	5.02	<0.01**
Nitrate	4.5	0.04	12642	1.84	0.07
Nitrate	8.4	0.08	22558	3.28	<0.01**
SRP	4.5	0.02	5730	0.78	0.44
SRP	8.4	0.04	12118	1.63	0.10
Temperature All Sites	4.5	0.10	60347037	28.96	<0.01**
Temperature All Sites	8.4	0.19	1.12E+08	53.65	<0.01**
Temperature NE Sites	4.5	0.16	2.32E+08	56.03	<0.01**
Temperature NE Sites	8.4	0.23	3.28E+08	79.24	<0.01**
Temperature SW Sites	4.5	0.16	2.28E+08	55.17	<0.01**
Temperature SW Sites	8.4	0.22	3.22E+08	77.87	<0.01**

Model results showed that precipitation in the Tahoe region will increase due to climate change. While the increase in precipitation is not significant in the RCP 4.5 scenario, it is significant in the RCP 8.5 scenario (Figure 1, Table 1). The RCP 8.5 scenario went from getting an average of 0.17 cm/day to 0.20 cm/day. The Eastern side of the lake will continue to receive less precipitation than the western side of the lake, and there will be no significant change in the timing of the bulk precipitation. However, more precipitation will come as rain rather than snow. The averaged RCP 4.5 scenarios predicted a 1.5% reduction in snow per decade over the next hundred years. Similarly, the averaged RCP 8.5 scenarios predicted a 3.4% reduction in snow per decade (Trommer et al., 2021). The timing of peak runoff from this precipitation will shift from June to May in the RCP 4.5 scenario and to January in the RCP 8.5 scenario.

Nutrient influxes from river inflows are predicted to change as well. Under RCP 4.5, river nitrate was not expected to change significantly (Figure 1, Table 1). However, under RCP 8.5, a significant increase in nitrate is expected. Under the RCP 8.5 scenario, nitrate went from an average of 2,281 kg/year in the first five years of the simulation to an average of 2,803 kg/year in the last five years, a 522 kg/year increase. The flow rates expected in these climate change scenarios will produce streamflows beyond the range the model was calibrated for. Thus, these results are likely underestimates, particularly in extreme flow years. Further, these lakewide load estimates do not explain what portion of nutrients will remain local to the nearshore and accessible to periphyton. SRP did not show a significant change in either scenario.

Mann-Kendall trend tests showed that there was a significant increase of nearshore temperature over time lakewide. In the RCP 4.5 scenario, Tahoe nearshore temperatures averaged 11.4 °C from 2007-2027 and increased to an average of 12.8 °C, a 1.4 °C increase, in the last twenty modeled years (Figure 1, Table 1). In the RCP 8.5 scenario, average nearshore temperatures went from 11.4 °C to 14.5 °C in the same period, a 3.1 °C increase. Mann Kendal tests on each region of the lake showed that the northeast part of the lake will heat more than the southwest portion of the lake.

4.5. Discussion

Climate change is affecting lakes and their biota in complex and interrelated ways. We modeled climate change conditions at Lake Tahoe to evaluate future shifts that could affect the structure and function of periphyton (Fig 2). Projections showed that climate change will impact Lake Tahoe in much the same way that it will affect many lakes. Periphyton blooms may change in biomass and community composition over time. The prediction of increased nutrient input from climate change could lead to more periphyton biomass, especially at locations of increased nutrient inputs, such as around river mouths and areas of groundwater inflow. The increase of nutrients paired with the warming of the littoral nearshore could further increase biomass and may favor green algae over the diatoms that currently dominate the eulittoral zone. Likely, changing biostimulatory conditions will either increase periphyton biomass or push lakes over a critical nutrient and temperature threshold into a green alga dominated stable state. Based on the modeled data, we 1) examined the implications of each modeled output to periphyton separately, 2) imagine combined outcomes of these conditions and discuss possible scenarios for periphyton in the future, and 3) considered the implication of our findings to the scientific and management communities.

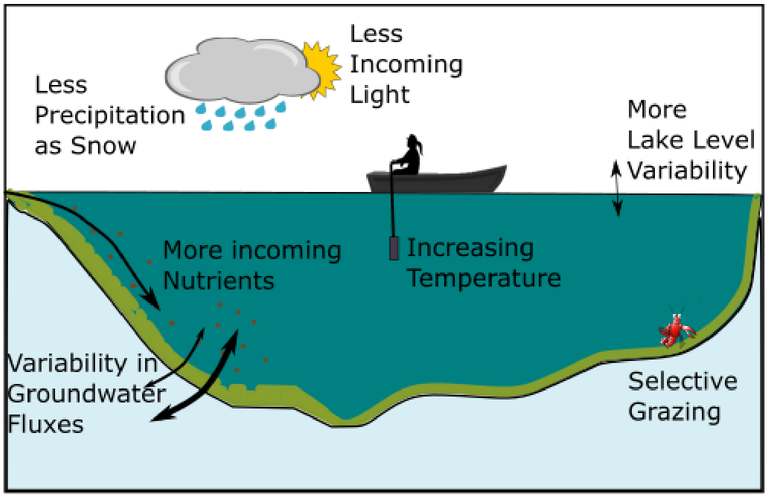

Fig. 4.2. Visual representation of the conditions that impact periphyton considered in this paper.

4.5.1 How Climate Change Conditions Effect Periphyton

4.5.1.1. Light

Under both scenarios, periphyton biomass may decrease due to the predicted reductions in shortwave radiation. The reduction of shortwave radiation was small, though it was significant. Periphyton tends to acclimatize to high ambient light intensities in summer such that near-surface periphyton photoinhibition from high irradiance was not found at ambient light levels in a study across lakes sizes (Vadeboncoeur et al., 2014). For blooms that tend to peak in times with seasonally reduced light, a further reduction in incoming PAR due to climate change would reduce biomass. While not explicitly modeled, a change in lake photic zone depth could further shift the depth of periphyton communities as species move toward their light niches (Kraemer et al., 2017). This shift could change the lake's overall periphyton biomass, especially in the already light-limited deep lake periphyton.

However, a change in incoming shortwave radiation could also increase cyanobacteria's access to nutrients. High UVR exposure may currently be inhibiting growth in nitrogen-fixing species such as *Anabaena circinalis*, as was found in nearby meso-oligotrophic Castle Lake (Higley et al., 2001). Thus, a reduction in incoming shortwave radiation, including UVR, as was predicted by our climate models, could increase cyanobacteria's access to limiting nitrogen.

4.5.1.2. Lake Level Change

An increase in the rate of lake level fluctuation will make periphyton biomass in littoral zones more spatially and temporally variable. Lake level change is an essential driver in the variation of periphyton biomass (Atkins et al., 2021). Increasing lake levels shift niches higher in elevation and open new substrate for periphyton to colonize. Periphyton succession in these new habitats is such that in Tahoe, newly wetted areas are quickly colonized with small pennate diatoms followed by Synedra and stalked Gomphoneis at two weeks. A fully mature community of primarily stalked Gomphoneis and some green algae occur after one month (Aloi, 1986). This succession varies in other lakes. Lake level change leads to sediment wetting and drying cycles that alter nutrient mineralization conditions within sandy soil, causing rising lake levels to release nutrients to the lake (Steinman et al., 2012; Birch, 1964).

Conversely, lake lowering desiccates periphyton communities that were previously underwater and shifts ideal niches lower in elevation. Unlike the littoral communities, deeper periphyton communities will likely not be highly affected by relatively small lake-level changes. Overall, with a significant increase in the monthly lake level variation, biomass levels in the eulittoral zone will likely become more variable as the new substrate is wetted and dried, disturbing periphyton.

With more lake level change, variations in groundwater flux will also increase, affecting periphyton nutrient availability. The LCM groundwater influx rate was held at a constant. However, as Naranjo et al. (2019) showed, measured groundwater influxes to Lake Tahoe vary with lake level and significantly drive periphyton growth. In that study, Lake Tahoe groundwater influx rates were measured as high as 0.8 m/d. The water was rich in nitrate and dissolved phosphorous compared to the oligotrophic midlake water. Groundwater influx rates are dependent on hydraulic gradients that vary with lake level within a seasonal timeframe. When lake levels are low, high hydraulic gradients cause groundwater influxes near the lake’s surface elevation, and in Tahoe, groundwater discharge increased. Conversely, when lake levels are high, reduced hydraulic gradients push groundwater influx deeper and, in some lakes, can even cause seepage out of the lake to the groundwater. With increased lake level fluctuation, we can expect to see more variability in nutrients available to periphyton. While the implications for this are largely unknown, unstable nutrient supply may affect community composition and biomass.

4.5.1.3. Precipitation

Models predicted a small increase in precipitation, a greater ratio of rain to snow, and earlier runoff peaks affecting biostimulatory conditions leading to temporal changes in the influx of nutrients that drive periphyton. When rain hits bare earth, it can cause splash erosion

(Edwards and Burney, 2005) and contribute to lake nutrient inflow. Snow is a protective layer to the ground reducing this erosion. Snow falls to the earth with less potential energy reducing erosion on impact. Thus, a shift from rain to snow may lead to higher splash erosion and more nutrient runoff during precipitation events. Further, a greater rain to snow ratio shifts the timing of runoff, carrying nutrient-rich erosion into lakes. Rain results in more immediate runoff than snow, and extreme rain events can lead to high runoff and stream flows that cause erosion. On a longer scale, the shift from snow to rain is driving peak runoff estimates from spring to winter. The shift in this flux of nutrients will cause it to align more closely with the peak periphyton growth season, perhaps encouraging more periphyton growth.

4.5.1.4. Temperature and nutrients

Predicted warmer nearshore waters combined with increased nitrate input are expected to increase lake periphyton biomass. The shift to earlier runoff would mean more nutrients entering the lake in winter rather than spring. This shift, combined with accelerated metabolism from increased temperature (Phinney and McIntire, 1965), could lead to greater nutrient uptake levels and increased nutrient scarcity in spring. Peak runoff inflows rich in nutrients will still arrive after the current peak periphyton bloom, though it will be more temporally aligned. As a result of the added nutrient availability around peak periphyton growth, blooms may become larger. However, the blooms may also be shorter-lived because the runoff nutrient influx will decline sooner after peak periphyton bloom. The timing of groundwater inflow is likely more influential to periphyton bloom timing (Naranjo et al., 2019). How climate change will affect the quantity and timings of groundwater pulses into Lake Tahoe is yet unclear. If higher temperature results in earlier groundwater influx, this will likely have a large impact on shifting periphyton bloom timing earlier.

Periphyton at Lake Tahoe are co-limited by nitrogen and phosphorous (Domagalski et al., 2020; Hatch et al., 2001; Goldman et al., 1993; Jassby et al., 1995). Thus, warmer nearshore temperatures will likely not affect biomass unless additional nutrients are available. This relationship was demonstrated in an oligotrophic lake mesocosm study by Cao et al., which was dominated by the filamentous Chlorophytes Cladophora sp. and Oedogonium sp. also found in Lake Tahoe (2017). At elevated temperatures alone, there was no change to periphyton biomass. However, periphyton biomass was higher at elevated temperatures (+3°C and +4.5°C) than at ambient temperatures when excess nitrogen (200 μg L^{-1} KNO_3) was added. Similarly, Bothwell found that in conditions of excess phosphorous (3-4 μg L^{-1}SRP), periphyton growth rates were controlled by temperature in the early stages of seasonal growth. However, the temperature effects diminished when seasonal nutrient limitation was at play (1988). To contextualize nutrient availability, a recent study reported that average Tahoe groundwater has 51 μg L-1 SRP, Ward Creek inflow has 6 μg L-1 SRP, and midlake water has 3 μg L^{-1} SRP (Naranjo et al., 2019). Average Tahoe groundwater has 60 μg L^{-1} NO_3 , Ward Creek inflow has 48 μg L^{-1} NO_3, and midlake water has 3 μg L^{-1} NO_3 (Naranjo et al., 2019). Thus, a 1.7 °C increase in nearshore temperatures resulting from RCP 4.5 or a 3.7 °C increase from the RCP 8.5 scenario combined with a nutrient influx would lead to higher periphyton biomass if nutrients were available.

The magnitude of warming we model under both scenarios is not expected to result in internal loading of phosphorus. As temperature increases, water is saturated at lower oxygen concentrations. Thus, as Tahoe heats, the lake can hold less oxygen. Under current conditions, Tahoe sediments typically do not become anoxic. In the unlikely scenario that rising temperatures lead to seasonal sediment anoxia, phosphorous release from sediments would increase (Jeppesen et al., 2009), likely causing periphyton biomass increases. Low oxygen levels caused by warming could also increase denitrification rates, reducing available nitrogen (Veraart et al., 2011). In the event of Lake Tahoe's anoxia, sediment uptake and release could be responsible for more available phosphorous and less available nitrogen.

As predicted by our models, nitrate may be provided from an increase in Tahoe's stream flows, contributing to a species shift and altering biomass. The significant increase in nitrate with no significant change in SRP may increase the N:P ratio. This metric is vital in determining the relative abundance of periphyton species within a lake. Chlorophytes require more ammonium and nitrate than the diatoms that currently dominate Lake Tahoe, so a shift to a higher N:P ratio from river inputs would favor these periphyton **(**Vadeboncoeur et al., 2021).

Rising temperatures and increased nutrients may increase the biomass of historically less dominant periphyton. Green algae have traditionally contributed less to periphyton biomass than diatoms and cyanobacteria in Lake Tahoe. Around the world, filamentous periphyton blooms are often dominated by green algae growth (Vadeboncoeur et al., 2021). In oligotrophic Rocky Mountain lakes that experience periphyton blooms, once diatom-dominated communities have shifted to chlorophyte dominance (Oleksy et al., 2020). This shift and similar shifts noted in lakes worldwide have mainly been attributed to changes in nutrient availability, sometimes paired with increasing temperatures (Oleksy et al., 2020; Oleksy et al., 2021; Lowe and Pillsbury, 1995). Compared to the diatoms that previously dominated these lakes, chlorophytes thrived under higher temperatures and require more ammonium and nitrate **(**Vadeboncoeur et al., 2021). In Tahoe, climate change driven temperature and nitrogen increases could lead to more periphytic green algae.

While nearshore water temperatures will increase, the average nearshore temperature of Tahoe will remain cool enough to favor diatom species (DeNicola, 1996; He, 2010). Periphyton species typically exhibit peak growth at an optimal temperature, and growth rates decline as they diverge from that temperature. This ideal temperature differs between species. Experimental research exploring optimal temperature for specific species is lacking. He (2010; master's thesis) grew periphyton, including several species found in Tahoe, in artificial streams at six different temperatures ranging from 13.5 °C to 38 °C. All Tahoe species— *S. minuta* had its highest growth rate at 13.5 °C, *S. ulna and N. palea,* had their highest growth rates at 16 °C; *F. crotonensis* had its highest growth rate at 23.5 °C; M. *varians* had its highest growth rate at 27 °C; and *Phormidium Sp.* and *Anabaena sp.* had their highest growth rates at 33 °C. Thus, a new average nearshore temperature of 12.8 °C under RCP 4.5 or 14.8 °C under RCP 8.5 would move Tahoe's nearshore temperature closer to the optimal growth temperatures that He measured for diatoms *S. minuta, S. ulna, N. palea, F. crotonensis,* and *M. varians,* and for cyanobacteria *Phormidium Sp. and Anabaena sp.* These findings further show that many of the Tahoe periphyton may increase their growth rates under a warmer temperature regime.

4.5.1.5. Grazers

While we do not know how benthic algae grazer populations will shift in Tahoe's future, changes to benthic grazing rates may affect biomass, and preferential grazing may affect the community composition of Tahoe's periphyton blooms. Benthic grazers control periphyton at low biomasses but have less effect on periphyton biomass once it has bloomed into late succession mats with large biomasses. Under climate change conditions, increased temperatures and nutrient availability may increase the rate at which periphyton mats go from low to high biomass, giving grazers a shorter opportunity to assert top-down control and reduce biomass (Vadeboncoeur et al., 2021). Grazers consume lipid-rich diatoms but tend to consume less high biomass like the filamentous green Zygnematales common to Lake Tahoe (Vadeboncoeur and

Steinman, 2002). Thus, grazers will continue to reduce early succession diatom biomass, reducing filamentous green algae's competition. However, this influence may become less important if the low biomass phase is shortened or if the grazer population shifts (Kazanjian, 2018).

4.5.2. Possible future scenarios

There is great uncertainty about how Tahoe periphyton will react to the combination of many climate change driven shifts. How will periphyton respond to variability in groundwater nutrient inputs? Which periphyton species will dominate under warmer conditions with higher nutrient availability? Will a change in Tahoe's clarity occur, resulting in a shallower photic zone and reducing the habitat of Tahoe periphyton? These answers remain unclear and are areas of potential future research. We do not know the precise tipping point conditions that lead to community and biomass change in Lake Tahoe periphyton. However, combining the information we do have, we propose two hypothesized scenarios for the future of periphyton in Tahoe.

In one scenario, lake conditions reach a threshold of major change in the periphyton biomass and community composition, as occurred in Oleksy et al. (2020). An increase in temperature and benthic nutrient availability leads to the green algae, such as *Zygnema,* or introduced *Spirogyra* becoming dominant in the benthic eulittoral zone. The stalked diatoms that are a significant contributor to littoral biomass become less prominent as conditions become less favorable. The community shift from a stable state of diatoms to green algae could also be a concerning reduction of a major food source for benthic grazers as predicted to occur in many lakes (Beisner et al., 1997; Petchey et al., 1999). Nutrient flushes, heavy in bioavailable nitrogen, coming in the winter support increased growth around the current peak growth in biomass. In addition to the community composition, this increase of nutrients and less top-down control would likely lead to higher biomass in the eulittoral zone.

In the second scenario, the same changes in lake temperature and nutrient inputs do not push the lake over a community composition threshold but increase biomass in the preexisting communities. As occurred in Baulch et al. (2005), in the eulittoral zone, cool water diatoms continue to thrive in warmer temperatures. With the addition of bioavailable nitrogen and temperatures closer to their optimal growth temperatures, diatom biomass increases. Green algae would continue to appear in patches within the diatom community but would not dominate that habitat. In this scenario, the shorter window of nutrient runoff in winter could lead to a shorter periphyton bloom season. Thus, top-down control of grazers would continue to control early-season periphyton levels.

Under both scenarios, the sublittoral zone would likely remain cyanobacteria-dominated but may increase in biomass. If clarity is reduced, the photic zone depth would move higher in the water column. In this case, periphyton habitat would not extend as deep into the lake. Further, with a reduction in UVR penetration, cyanobacteria may fix nitrogen in shallower regions of the lake, causing their range to move toward the surface. In addition to changes in light, more lake level variation and more rain will affect sublittoral periphyton. The highest groundwater nutrient input areas varying more regularly may mean that a higher biomass of sublittoral periphyton, mostly cyanobacteria, is supported as nutrients are distributed more evenly over time. Warmer temperatures could lead to higher cyanobacteria biomass overall. If more precipitation leads to higher lake levels and water is still clear enough for light to penetrate, we may expect the cyanobacteria communities of the deeper sublittoral to increase biomass because of deeper groundwater nutrient influxes. Thus, while cyanobacteria would still be dominant in the lower portions of the lake, their range would likely shift upward.

These scenarios can be thought of in terms of the alternative stable state hypothesis (Figure 3., Scheffer et al., 2001). Tahoe periphyton biomass and community structure have maintained a stable, diatom-dominated state for decades (Atkins et al., 2021). Yet, diatom-dominated oligotrophic lakes, like Tahoe, are being pushed toward a high-biomass green algae dominated stable state. While climate change is not the only reason for green algae periphyton blooms in oligotrophic lakes, it is a contributing cause. Given the lack of examples of lakes returning to diatom domination, a large shift in conditions may be required to push lake periphyton back to a diatom-dominated state if it transitions to filamentous green algae.

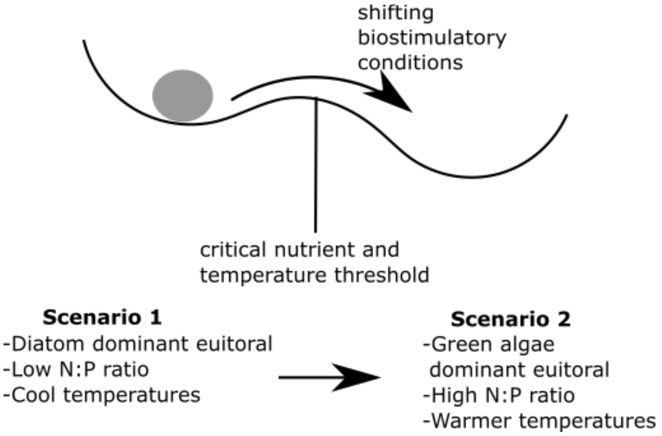

Fig.4.3. Cup-in-ball diagram showing that shifting biostimulatory conditions may push Lake Tahoe over a critical nutrient and temperature threshold, driving the ecosystems from one stable state to another. A smaller shift in conditions may be needed to push a diatom dominated periphyton bloom to a green algae bloom than to return from green algae bloom to diatom dominated bloom.

4.6. Implications for Scientists and Managers

Scientific understanding of the filamentous algae blooms occurring around the globe is still advancing. We do not know the causes of filamentous algae blooms in many oligotrophic lakes and are just beginning to arrive at theoretical frameworks that explain them (Vadeboncoeur et al., 2021). In some ways, Tahoe fits into this periphyton bloom story perfectly: increased nutrient loading, warmer water, and altered food webs have all occurred at Lake Tahoe. However, Tahoe's filamentous algae blooms are markedly different from other blooms because Tahoe's eulittoral blooms are diatom dominated while most other blooms are green algae dominated (Atkins et al., 2021; Vadeboncoeur et al., 2021).

Future research around periphyton in Lake Tahoe should include monitoring with the intent of understanding whether Tahoe's blooms are simply a different presentation of filamentous algae blooms or a precursor to the green algae dominated filamentous algae bloom. Researchers can do this by monitoring community composition and benthic nutrients, especially groundwater influxes, for changes in nutrient concentrations and N:P ratios (Atkins et al., 2021). Monitoring these processes would help the scientific community understand the inflection point of when lakes "go green."

To avoid future periphyton blooms with larger biomass, management of nutrients may need to be more stringent. Periphyton's biomass sensitivity to nutrients will increase as the temperature rises. Thus, Tahoe nutrient inputs, especially those entering through groundwater, will become even more tied to periphyton biomass. Especially, nitrogen inputs should be reduced to avoid high N:P ratios and a transition to green algae dominated blooms as the lake heats.

This paper's analysis of Tahoe periphyton considering climate change conditions highlights important considerations for managers and scientists. It is unclear whether Tahoe periphyton blooms are on the precipice of shifting toward green algae dominance or if diatoms will continue to be most abundant in the eulittoral zone. In either case, monitoring periphyton biomass and community composition is essential. Further, the monitoring and management of nutrients, particularly nitrogen, will be important as the effects of climate change progress.

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5. Integrating Periphyton and Surface Water-Groundwater Methods to Understand Lake Ecosystem Processes

5.1. Abstract

Groundwater-surface water (GW-SW) interactions represent an important, but less visible, linkage in lake ecosystems. Periphyton are 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 to 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 spatiotemporal 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.

5.2. Introduction

Groundwater-surface water interactions represent an important cross-ecosystem linkage that is hidden in plain sight. Since the late 19th century, scientists have highlighted how lakes can be used for studying interconnected physical, chemical, and biological processes (Forbes 1887; Lindemann 1942). Despite these connections, there is a disproportionate focus on the pelagic zone relative to the littoral (Vadeboncouer 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 groundwater-surface water (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 both monitoring work and paleolimnological investigations, periphyton are indicators of environmental change, chemical fluxes, and groundwater influence in lakes (DeNicola and Kelly 2014; Schneider et al. 2012; Battarbee et al. 2012). 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 oligo- 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 to 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 (Boulton et al. 2010, Gaiser et al. 2011, Krause et al. 2010, Lecher and Mackey 2018, Taniguchi et al. 2019, Valett et al. 1997). It is understandable why 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 (Lewandowski et al. 2015; Rosenberry et al. 2014).

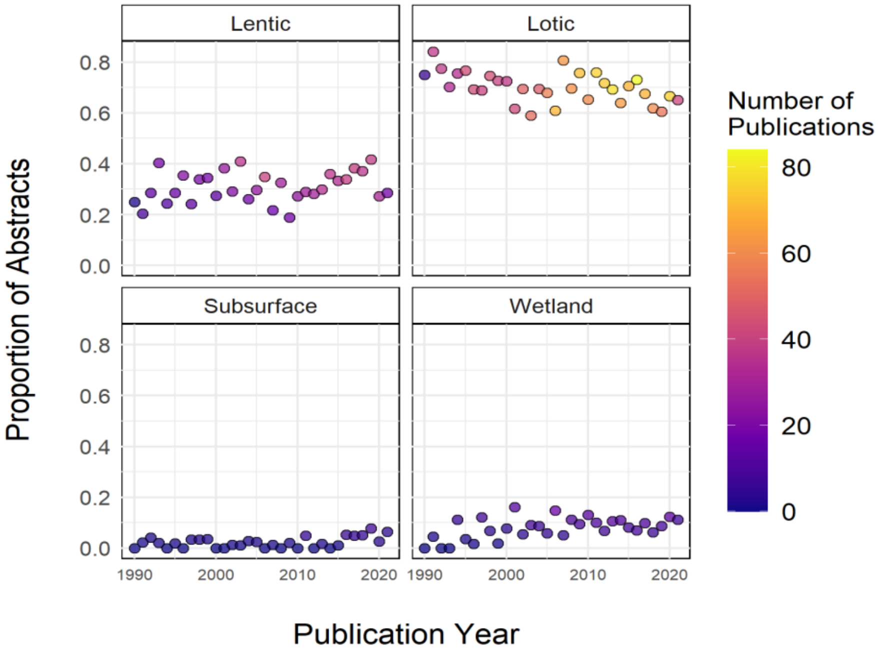

Fig. 5.1. Time series of proportion for lentic, lotic, subsurface, and wetland systems papers referencing "periphyton", "attached algae", or "benthic algae" in primary, peer-reviewed literature (n =2,482 abstracts; 49% of all total studies referencing any of our Web of Science search terms). Since 01 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 through 2020 suggest 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.

Our methods of monitoring groundwater discharge to streams and lakes has advanced in recent decades leading to greater understanding of these systems. Rather than siloing groundwater from surface water, researchers and managers 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, 3-D models and others 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

5.3. 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.

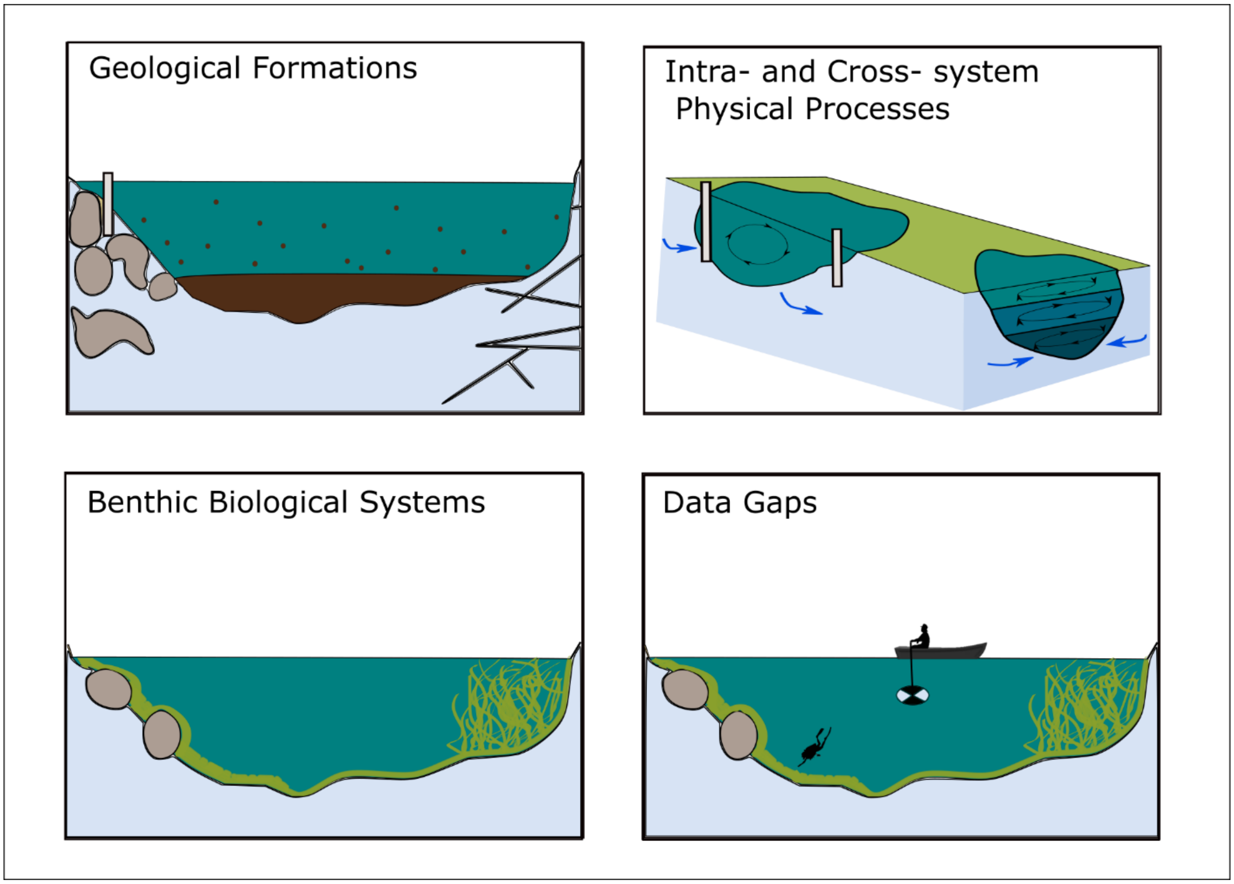

Fig. 5.2. Primary barriers to studying the benthic zone include a) the heterogeneity of geological formations and their properties; b) intra- and cross-system physical processes, c) the active role of benthic biological systems, and d) data gaps. Each panel depicts a characteristic example of how each 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.

5.3.1. 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 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 impacts 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.

5.3.2. 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 (Hagerthy and Kerfoot 1998), leading to spatial variability in periphyton structure (Hagerthy 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, tides, 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 nearshore 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 (Ward et al. 2017; Murphy et al. 2015). 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).

5.3.3. 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 colmation, 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 (Hansson 1990; Carlton and Wetzel 1988). However, periphyton likely compete for groundwater nutrients with rooted macrophytes which actively uptake solutes from porewater (Granéli and Solander 1988; Bristow and Whitcombe 1971). 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 Steveson 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.

5.3.4. 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 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.

5.4. 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 water 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 Cremans 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).

Table 5.1. Common groundwater methods

Groundwater Methods				
Method	Purpose	Strengths	Weaknesses	Literature Examples
Piezometers	Tool used to measure groundwater hydraulic gradients using pressure sensors located along the water table.	Allows for effective understanding of 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	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	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	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 2013; Genereux et al. 1993; Schmidt et al. 2010

Groundwater Methods (continued)				
Method	Purpose	Strengths	Weaknesses	Literature Examples
Temperature Profilers	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.	Only detects groundwater discharge, not recharge. 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
Watershed and Lake Water Budgets	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	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	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

With respect to periphyton methodologies and trade-offs in field sampling styles, others have offered insight into sampling and assessing natural substrates (Bergey and Getty 2006, Biggs and Kilroy 2000, Sawyers 2012, and Larson and Collyard 2019), and reviewed techniques for using nutrient diffusing substrates and devices to conduct controlled manipulations of periphyton responses to nutrient or chemical influx (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; Matlock et al. 1998). 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. Below, we briefly review some well established periphyton methods and also showcase these emerging methods at the forefront of periphyton research (Table 2).

Table 5.2. Common periphyton methods

Method	Purpose	Strengths	Weaknesses	Literature Examples
Rapid Assessments	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	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
Chlorophyll-*a*	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 chlorophyll-*a*: biomass relationship.	Sartory 1985; Harris and Graham 2015; Garrido and Zapata 2007
Pigment taxonomy	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

Method	Purpose	Strengths	Weaknesses	Literature Examples
eDNA metabarcoding	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
Biovolume estimates	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; Ugland et al. 2003; Hillebrand et al. 1999
Flow Cytometry	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	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

Method	Purpose	Strengths	Weaknesses	Literature Examples
Nutrient Diffusing Substrates (NDS)	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., BenthoTorch)	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

5.4.1. 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 non-organic 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.* The pigment chlorophyll-*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. Chlorophyll-*a* is commonly quantified via spectrophotometry, fluorometry, and high-performance liquid chromatography (HPLC) (Biggs and Kilroy 2000). Though chlorophyll-*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_2 or CO_2 gas exchange or consumption of ^{14}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_2 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 groundwater-surface water exchange and by extension periphyton processes (Rovelli et al. 2017). Berg et al. (2003) note that other devices aside from O_2 microelectrodes, such as sensors 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).

5.4.2. 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.

5.4.2.1. 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).

5.4.2.2. 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 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 dataset must be created. Samples are typically run within 24 hours of collection to ensure that cells remain intact (McCall et al. 2017). 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, Scarborough, Maine, United States), 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.

5.4.2.3. 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 chlorophyll-*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 (e.g., Tamm et al. 2015; Lauridsen et al. 2011; Schlüter et al. 2006). Since algal taxonomic groups differ in their major pigment production (e.g., chlorophyll-*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 (Louda et al. 2015; Browne 2010). 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 Oleksy et al. 2021; Hogan et al. 2014).

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 BenthoTorch (bbe Moldaenke GmbH, Germany) which was developed to measure periphyton biomass as chlorophyll-*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 BenthoTorch to cell counts and fluorometric and spectrophotometric quantification of algal pigments have shown poor to moderate agreement (Echenique-Subiabre et al. 2016; Harris and Graham 2015; 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 (Oleksy et al 2021; Kotalik et al. 2019) 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 (Lawrence et al. 2015; Thomas et al. 2013).

5.4.2.4. eDNA metabarcoding

Metabarcoding (or environmental DNA 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 environmental DNA (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 (OTUs) 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. Additionally, 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.

5.4.2.5. 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 and Winder 2015; Galloway et al. 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 (Guo et al. 2016; Cashman 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 α-linolenic acid (ALA) and linoleic acids (LIN) (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.

5.4.2.6. 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 (e.g., 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).

5.5. 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 spatio-temporal variation in ecological, biogeochemical, and physical processes is key. The hyporheic zone is defined as a three-dimensional (3-D) 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. Additionally, 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. Additionally, 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.

5.5.1. 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 (Birks 2010; Braak and Juggins 1993; DeNicola and Kelly 2014), although more sophisticated models can rely on computationally-intensive regression or Bayesian models (Rodriguez 1987; Auer and Canale 1982). 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 (Aseda 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 (SEM) 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). Further, 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 (Andersson 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 Simulation Program, WASP (Martin et al. 2006), CE-QUAL-R1 (Environmental 1995), Chesapeake Bay 3-D water quality model, CE-QUAL-ICM (Cerco and Cole 1994), 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., Water Quality Analysis Simulation Program (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, (i) periphyton do not move via advection by the water currents, (ii) 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 (iii) there is a maximum density for periphyton attachment to surfaces (e.g. sediment, macrophytes). The US 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.

5.5.2.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 (1-D) process-based models that solve the vertical heat transfer equation to account for the hydrodynamics of the system. A popular vertical 1-D 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 1-D lake models have successfully been applied to lakes across the world (Bucak et al. 2018; Hansen et al. 2017; Ladwig et al. 2018; Read et al. 2014; Yao et al. 2014).

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 open-source and open-access, 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 1-D 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. Further, vertical 1-D models do not account for the differences between littoral and pelagic conditions (Roberts, 2019); littoral temperatures and nutrient levels are assumed the same as pelagic. As a result of benthic and littoral variability, 1-D 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 three-dimensional model is critical for representing various locations and scenarios around the lake.

A prominent and state-of-the-art 3-D 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; Deltares 2021b). 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 3-D 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 σ 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, Sawyer et al. (2015) 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.

5.5.3. 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 (one to three dimensional) 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 US Geological Survey (MacDonald 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 three dimensions, 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. Additionally, 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 GUI (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 interspecies 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 1-D 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.

5.5.4. 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 1-D model. As in the 1-D 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 3-D groundwater model to a 3-D 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 3-D 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 Rodriguez-Escales 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 (Bocaniov et al., 2020, Farrell et al., 2020, Mi et al., 2020, Magee et al., 2019, Ladwig et al., 2021, Andersen et al., 2020). 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 (Ginder-Vogel et al. 2019; Hua et al. 2013). 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), Broecker et al. (2020), Wu et al. (2020)). 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) provides a conceptual model to get started on reactive transport modeling.

5.6. 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 (Hagerthy and Kerfoot 1998; Hagerthy 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.

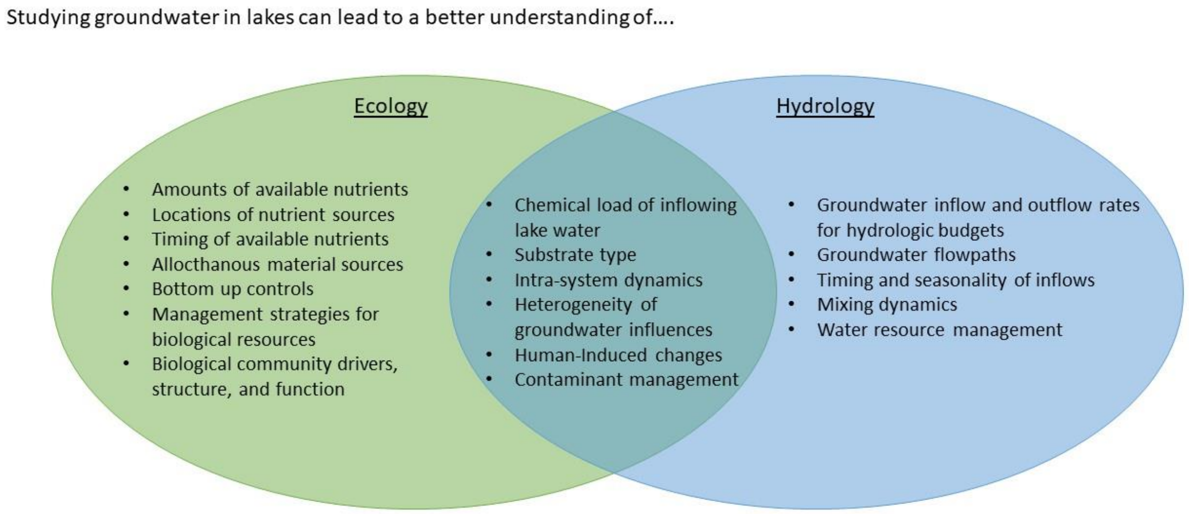

Fig. 5.3: Venn diagram delineating insights that ecologically- and hydrologically-focused studies can offer individually and when considered together.

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.

Table 5.3. 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, chlorophyll-*a*), 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, chlorophyll-*a*, pigment taxonomy, eDNA metabarcoding, biovolume estimates, benthic metabolism and production assessments, in situ pulse amplitude fluorometers, nutrient diffusing substrates, modeling	Piezometers, water isotopes (18O and dD), temperature profilers, watershed and lake water budgets, seepage meters, point-velocity probes

5.6.1. 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 substances, 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.

5.6.2. 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.

5.6.3. 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 (Hampton et al. 2017; Strasser and Hampton 2012; Barone 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.

5.8. Conclusions

Periphyton are important regulators and indicators of lake ecosystem function (Vadeboncouer and Steinman 2002; Vadeboncеour et al. 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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6. Conclusions and Recommendations for Future Work

6.1. Conclusions Summary

To understand the dynamics of periphyton communities, knowledge of the biological, chemical, and physical influences of periphyton should be generated and used to inform monitoring goals. Lake Tahoe has a long history of monitoring periphyton and some of its biostimulators. Despite public belief, from 1982-2019, eulittoral periphyton biomass at 0.5 m at Lake Tahoe did not significantly change though periphyton biomass may have increased before regular monitoring began in 1982 (Ch. 2). However, under future climate change conditions, there is a possibility that periphyton biomass will significantly increase and that community composition will change (Ch. 4). Lake monitoring programs collect some, but not all, of the data needed to understand periphyton biomass variability (Ch. 3). However, major drivers of periphyton, littoral nutrient inputs, are not measured at most lakes and are not measured at Tahoe. Knowing that groundwater is a littoral nutrient input essential to understanding periphyton biomass but difficult to monitor, innovative methods are required to monitor groundwater nutrients and periphyton (Ch. 5). This final chapter briefly summarizes the research findings of the chapters before and suggests logical next steps for future research on these topics.

6.2. A historical look at Periphyton in Tahoe

Lake Tahoe periphyton, measured at 0.5 m depth, did not show statistically significant lakewide biomass changes. However, the monitoring methods from 1982-2019 measured the eulittoral diatom and green algae community and the sublittoral cyanobacteria community depending on the lake level. While the diatom and green algae community showed no significant change in biomass, the cyanobacteria community showed a statistically significant reduction in biomass. Some sites, especially in the southern and eastern portions of the lake, showed less biomass than in the northern and western areas of the lake.

Improved monitoring practices at Tahoe will hold periphyton measurements stationary and not be reliant on lake level. This method will allow the eulittoral diatom and green algae community to be monitored individually from the sublittoral cyanobacteria community. This valuable new data should be analyzed regularly for indicators of further change. Further, the use of drone imaging to provide a detailed understanding of the spatial extent and taxonomic makeup of Tahoe's periphyton is a potentially powerful and efficient way to gain a detailed understanding of near-surface periphyton. The large amounts of spatial data can be especially useful in helping to identify biomass or growth rates if coupled with data essential for periphyton modeling.

To create further goals for Tahoe's protection, valuable information would be gleaned by understanding what Lake Tahoe's nearshore was like before major Euro-American settlement and its accompanying disturbances affected the watershed. Much of the basin was logged in the 1800s, and large-scale development occurred in the 1960s. We currently do not have information on periphyton before the Historical accounts of periphyton blooms began in the 1960s.

Using sediment core analysis to go "back in time" to see periphyton's history is possible. A core would need to be harvested thoughtfully. Too close to the surface and wave action would disturb the layers of sediment and detritus formed over time. Too deep, and periphyton would not have grown at depth. The location around the lake is also important, as substrate type and periphyton biomass vary around the lake. Previously, sediment cores have been analyzed for biogenic silica. While this gives a good sense of diatom frustules over time, it does not shed light on other types of periphyton and does not distinguish between periphytic algae and phytoplankton.

The cores should be analyzed for pigments and their derivatives as well as the composition of N and stable isotope ratios, as was done in Oleksy et al. (2020). Diatom frustules may be identified to determine what ratio of the algae present in the sample is periphytic and what is planktonic. Using these tools, we can get a better sense of periphyton dynamics in Tahoe's past.

6.3. Identifying the Drivers of Periphyton

Modeling showed that periphyton biomass is affected by temperature, nitrate, days since the substrate was last exposed to air, and photosynthetically active radiation. Periphyton live in microhabitats, and midlake data may not be indicative of nearshore total hydrolyzable phosphorus. We may need data on finer spatial and temporal scales—matching of the scales of the explanatory variable patterns. We could improve periphyton models by collecting data on other important biomass drivers.

While periphyton blooms themselves affect lakes by altering food web dynamics and littoral habitat, understanding periphyton bloom drivers allows for better management and prevention at their source. In many lakes, including Lake Tahoe, periphyton biomass is strongly influenced by nutrient-rich groundwater influxes (Loeb, 1987). In Lake Tahoe, and other lakes, much can be gained by monitoring groundwater influxes and their nutrients, but these nutrient sources are rarely monitored due to the difficulty and costly nature of their monitoring.

It is logical to collect groundwater nutrient data around the new periphyton monitoring points in Lake Tahoe. Establishing a correlation between groundwater nutrient influx and periphyton biomass could increase understanding that results in less required monitoring. This would give insight to surface influxes and provide information about groundwater nutrients at greater depth. Due to the time variable nature of the influxes, a few years of intensive groundwater monitoring could allow for a better understanding of seasonal patterns and flow rates around the lake that affect periphyton. In addition, nutrient monitoring would be required to track nutrient levels within these influxes.

Such groundwater data could be used to inform models further and lead to a greater understanding of the lake's nutrient budget, periphyton, and the lake's nearshore in general. As of now, the shortage of groundwater monitoring data available from Lake Tahoe translated to high uncertainty in groundwater modeling. With more data collection, time-variant groundwater nutrient or inflow data could be easily added to the Bayesian periphyton model presented in chapter 3, comparing the drivers of periphyton in Lake Tahoe in a more robust and therefore meaningful way.

6.4. The future of periphyton in Lake Tahoe under climate change conditions

Climate change will change many factors in Lake Tahoe, likely including periphyton community composition and biomass. Climate change has already begun to increase temperatures at Lake Tahoe. The warmer temperature, in combination with the possible increase of nutrient input, will likely increase biomass. An increase in the bioavailable N:P ratio could lead to the eulittoral zone of Tahoe transitioning from mostly diatoms with some green algae interspersed to becoming mostly green algae dominant. As the major primary producer in Tahoe's littoral habitat, change in biomass or community composition could impact Lake Tahoe as a whole. Periphyton indicates a shift in water quality with a rapid and visual change. Given an understanding that the driving factors of periphyton affect many aspects of the lake beyond periphyton itself, a shift in periphyton community composition or biomass should serve as a warning that great change may soon affect other parts of the lake.

Managers of Lake Tahoe should monitor the community composition of periphyton as shifts caused by climate change take hold and changes are emerging. Historically monitoring has consisted of visual community identification with microscopic confirmation. While this provides general presence/absence data down to three categories: diatoms, cyanobacteria, and green algae, it does not quantify the biomass or ratios contributed by each of these categories and thus could not be used to detect a shift in community composition. Emerging shifts, such as the white stalk filaments appearing on rocks in a circular pattern, first observed in the spring of 2020, are the initial signs of more change to come. With climate change’s impact increasing, now is an excellent opportunity to take a more rigorous approach at identification.

There are several ways that periphyton community composition could be quantified. The Tahoe Environmental Research Center monitors phytoplankton via light microscopy, and similar methods can be applied to Tahoe periphyton. Beyond these standard methods, using pigment analysis beyond chlorophyll-a to analyze community composition could be a less time-intensive way to quantify the relative amounts of periphyton groups in the sample. Up-and-coming flow cytometry technologies geared at identifying algae may be a way to get large quantities of accurate taxonomic and biovolume data with minimal time and effort. However, the cost of flow cytometry may currently be prohibitive to its application. No matter the method, it was essential to quantify the relative proportions of the major periphyton divisions found in the lake and, perhaps less rigorously, monitor the common periphyton species for new colonizations.

6.5. Focusing on groundwater as a major driver of periphyton growth

In lakes, monitoring periphyton and groundwater together could provide mutual insights. Many filamentous algae blooms in oligotrophic lakes are caused primarily by elevated levels of groundwater nutrient influxes. Yet, barriers including underlying geology, intra-lake and cross-lake landscape processes, and data gaps result in a dearth of both groundwater and periphyton investigations. This dissertation reviewed the many established methods of monitoring periphyton and groundwater individually. Suggestions are made of how to integrate these methods on a site-specific and landscape scale. Due to the many factors that drive periphyton biomass, modeling could effectively aid managers in planning around blooms.

Periphyton modeling lags behind other lake modeling. Many lake models are freely available and relatively easy to use. However, many do not have periphyton modules at all. The few periphyton modules available often require data that even lakes heavily monitored for periphyton do not typically have. Further, lakes are often modeled separately from groundwater systems making limiting the modeling of periphyton.

Module development and relevant data collection are required to further the integration of periphyton and groundwater methods. Some models, such as the very popular GLM, likely need relatively simple adjustments to existing modules to create periphyton models. These adjustments would account for such problems as “direct” access to groundwater nutrient inputs. To validate these models, laboratory experimentation is needed to fill coefficient data gaps that hold periphyton modeling behind. To drive the point home one more time, we need to monitor the drivers of periphyton, including groundwater.

6.6. References

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