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Phytoplankton Community as an Indicator of Cyanobacteria Harmful Algal Blooms in High Mountain Lakes

by

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A thesis submitted in partial fulfillment of the
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Abstract

Cyanobacteria blooms are a growing issue worldwide and can be harmful to both aquatic life and human health. Warm temperatures, nutrient loading, stable water columns, and selective grazing of zooplankton and phytoplankton can contribute to cyanobacteria bloom formation. In this study, I characterized the algal communities and water quality differences in two physiographically similar lakes with relatively little human influences, Odell and Crescent Lakes, Oregon, to better understand potential contributing factors to cyanobacteria harmful algal bloom formation (cyanobacteria bloom) in Odell Lake.

There are three hypotheses in this study:

1. If there was a cyanobacteria bloom in Odell Lake, but not Crescent Lake, then the algal community in Odell Lake would be representative of eutrophic conditions while Crescent Lake would not.
2. If temperature was a contributing factor to community shifts in either Odell Lake or Crescent Lake, then temperature would have significant changes associated with phytoplankton shifts and cyanobacteria abundance.
3. If nutrients were a contributing factor to cyanobacteria abundance, then the lake would experience increases in nutrient concentrations prior to cyanobacteria blooms formation.

Phytoplankton samples were collected from Odell and Crescent lakes on a weekly basis from June 2019 to September 2019 and characterized via microscopy. Multiparameter sondes were places in each lake at a fixed depth within one meter of the surface and recorded temperature (degrees C), pH, dissolved oxygen (mg/L and percent concentration), specific conductance (µS/cm), phycocyanin (relative fluorescence units; RFU), and chlorophyll-*a* (RFU) every 15-minutes throughout the study period. The phytoplankton community in Odell Lake was characterized by high abundances of eutrophic phytoplankton taxa, such as cyanobacteria, which had an average relative abundance of total density of 59.8 ± 30.3% (n=13; average ± standard deviation) throughout the sampling period. Crescent Lake was dominated by the phyla Bacillariophyta (diatoms) and Ochrophyta which had an average relative abundance of total density of 28.6 ± 14.0% and 20.9 ± 14.8%, respectively. Odell Lake transitioned from phytoplankton adapted to mesotrophic conditions and sensitive to stratification to phytoplankton found in eutrophic conditions and stratified water columns. Crescent Lake shifted from oligotrophic and mesotrophic algal taxa to a high abundance of cyanobacteria, however no visible bloom ever formed. A generalized additive mixed model of temperature data showed water temperature in Odell Lake was significantly warmer, on average 0.72 ± 0.92°C, than that of Crescent Lake as the bloom approached, which supported my second hypothesis. Nutrient measurements also supported the third hypothesis, as phytoplankton abundance in Odell Lake was significantly correlated with total phosphorus (TP; R-squared = 0.97; $p < 0.05$) and total nitrogen (TN; R-squared = 0.99; $p < 0.05$). Concentrations of orthophosphate peaked prior to cyanobacteria bloom formation, which when coupled with potential silica limitation in Odell Lake was likely responsible for promoting cyanobacteria abundance and cyanobacteria bloom formation dominated by N-fixer due to favorable nitrogen limiting conditions (TN:TP < 7) and reduced competition between cyanobacteria and diatoms due to silica limitation. Overall, this study found temperature was correlated with cyanobacteria bloom presence and intensity in Odell Lake, and nutrient conditions were more favorable to cyanobacteria dominance in Odell Lake versus Crescent Lake. The information provided in this study can be used with additional information could be used with additional information, such as lake orientation, wind patterns, and food web dynamics, to better understand factors contributing to cyanobacteria bloom formation in high mountain lakes.

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1. Introduction

Harmful algal blooms are the exponential growth of algae in a waterbody, that can often result in discoloration of the water and the production of toxins. In freshwater systems, these are often dominated by cyanobacteria and are referred to as a Cyanobacteria Harmful Algal Bloom or cyanobacteria blooms. Cyanobacteria are photosynthetic bacteria that date back to 3.4 billion years ago (Schopf 2000; Allen and Martin 2007). Bloom forming cyanobacteria have several different characteristics that allow them to out-compete other algal species, leading to exponential growth and bloom formation. Cyanobacteria, such as *Microcystis*, *Dolichospermum*, *Aphanizomenon*, and *Oscillatoria*, have maximum growth rates at high temperatures (Paerl et al. 2011; Carey et al. 2012). Low nitrogen to phosphorus ratios favor diazotrophic cyanobacteria, which have the capacity to fix nitrogen from the atmosphere (Reynolds 1998: Paerl et al. 2011; Carey et al. 2012; Cottingham et al. 2015). Nutrient rich environments and stratified water columns favor non-nitrogen fixers (Paerl et al. 2001; Huisman et al. 2018; Newell et al. 2019). Cyanobacteria can avoid predation due to toxicity, unpalatability, and low nutritional status by grazers and planktivorous fish (Paerl et al. 2001). Despite the several competitive advantages that cyanobacteria possess, these organisms are not dominant in every lake because the variables that trigger cyanobacteria blooms are many and can vary from lake to lake (Dokulil and Teubner 2000; Paerl 2018).

Cyanobacteria blooms can cause an array of problems to human health, economic losses, and wildlife and aquatic ecosystems. The green waters that result from a bloom can cause an unpleasant odor near lakefront communities and homes. Dodds et al. (2009) estimated that the U.S. loses approximately $3 billion (2023 USD) as a result of issues caused directly and indirectly by algal blooms in freshwater systems. This cost comes from protection and recovery of wildlife, losses in recreational activities in water bodies, property value loss on waterfront real estate, and hazards presented in drinking water supplies (Dodds et al. 2009; Bechard 2020). Cyanobacteria blooms can pose a significant risk to humans, pets and wildlife due to their ability to produce toxins, which can produce side effects as mild as skin irritation to as extreme as kidney or liver failure (Table 1; Carmichael 1994; Carmichael 1997; Chorus and Bartram 1999; Carmichael et al. 2001; Stewart et al. 2006).

The detrimental effects of cyanobacteria blooms have been documented around the world and exposure to cyanotoxins from cyanobacteria blooms has become a large public health concern. Within the state of Oregon, several cyanobacteria bloom events have appeared in headlines and have caused a growing interest in cyanobacteria blooms. According to the Oregon Health Authority (OHA), recreational advisories for cyanotoxins have been reported in 60 lakes across Oregon (DEQ 2011; OHA 2019; OHA 2023). In 2017, a cyanobacteria bloom in a reservoir located in Lakeview, Oregon led to the death of 32 cattle, a total loss of over $60,000 (2023 USD). A cyanobacteria bloom in Detroit Lake, located outside of Salem, Oregon and serves as the city's main drinking water source, led to a drinking water advisory for vulnerable populations and pets in the city of Salem in 2018 due to the cyanotoxin microcystin found in the finished drinking water. This drinking water crisis ultimately led to the declaration of a state of emergency in Oregon, which lasted about a month and a half (KATU 2018). Since the occurrence of these events, there has been a greater push from scientists, interested parties, and local and state government for proactive monitoring of water bodies that have histories of cyanobacteria blooms or are especially susceptible to eutrophication and bloom formation, as well as increased need in understanding the lake specific triggers of cyanobacteria blooms across Oregon.

This project is a paired study of two Oregon lakes, Odell and Crescent lakes, located in the High Cascades. Studying these lakes offers a unique opportunity to examine how algal community structures changed from a baseline/no-bloom condition to bloom condition by using Crescent Lake as a reference lake and Odell Lake as an impacted lake. This natural experimentation is possible because Crescent and Odell lakes have neighboring watersheds and share similar watershed characteristics, geomorphologies, and natural histories (Figure 1; Table 2). However, despite their similarities, Odell Lake has a history of algal blooms while Crescent Lake does not (Jacoby and Kann 2007; OHA 2023). In this study, I (1) characterized the changes in phytoplankton community composition and abundance in Odell Lake and Crescent Lake and (2) related changes in phytoplankton communities with available water quality data. I hypothesized that if there is a cyanobacteria bloom in Odell Lake, but not Crescent Lake, then the algal community in Odell Lake would be representative of eutrophic conditions while the one in Crescent Lake would not. Regarding water quality characteristics, I hypothesized that if temperature was a contributing factor to community shifts in either Odell Lake and Crescent Lake, then temperature would have significant changes with associated changes in phytoplankton shifts and cyanobacteria abundance. I also hypothesized that if nutrients were contributing factors to cyanobacteria abundance, then the lake would experience increases in nutrient concentrations prior to cyanobacteria bloom formation.

2. Background Information

2.1 Cyanobacteria Blooms

Cyanobacteria are some of the oldest life forms on Earth, possibly dating back to 3.4 billion years ago (Allen and Martin 2007; Rassmussen et al. 2008; Schirrmeister et al. 2011). Cyanobacteria are prokaryotic, photosynthetic bacteria most commonly known for contributing to the creation of the oxygenated atmosphere we live in (Kasting and Siefert 2002; Bekker et al. 2004; Rassmussen et al. 2008). Cyanobacteria are a critical component of global primary production, and many cyanobacteria contribute to the nitrogen cycle through nitrogen fixation (Chorus and Bartram 1999; Carey et al. 2012), however the components that make cyanobacteria such an important player in our global cycles also makes cyanobacteria an ecological and human health concern when cyanobacteria become prevalent in the form of toxic algal blooms. An algal bloom can be defined as a visible change in water quality, due to the discoloration of water, that is the result of excessive and exponential algal growth (CDC 2022; EPA 2022). The World Health Organization (WHO) defines a cyanobacteria bloom when cell counts exceed 100,000 cells per milliliter (Chorus and Bartram 1999; WHO 2003).

Freshwater algal blooms are often dominated by cyanobacteria and are therefore referred to as cyanobacteria blooms. Many cyanobacteria can fix atmospheric nitrogen (Fay 1992; Böhme 1998; Adams 2000; O'Neil et al. 2012), many bloom-forming cyanobacteria grow well at higher temperatures than other phytoplankton (Konopka and Brock 1978; Robarts and Zohary 1987; Paerl and Huisman 2008; Mehnert et al. 2010), and several taxa can control their buoyancy which allows them to access light and nutrients (Carey et al. 2012; Cui et al. 2016; Huisman et al. 2018), ultimately leading to cyanobacteria outcompeting other phytoplankton and forming an algal bloom (Figure 1). Cyanobacteria blooms can be odorous and obnoxious to lake goers and lake-side businesses. The effects of cyanobacteria blooms go beyond the lack of aesthetic appeal, as cyanobacteria blooms are associated with large economic costs, are an environmental and water quality hazard, can result in toxic and dangerous waters, and are a large public health concern.

Cyanobacteria blooms are considered "harmful" because of the detrimental effects that they have on water quality in recreational and drinking waters (Falconer 1999; Stone and Bress 2007; Salls et al. 2018), their effect on aquatic ecosystems and wildlife (Rodger et al. 1994; Paerl and Otten 2013; Huisman et al. 2018; Dreher et al. 2019), and their impact on human health (Carmichael et al. 2001; Stewart et al. 2006; Stone and Bress 2007). Cyanobacteria blooms can create monocultures that shade out other phytoplankton communities. The decomposition of the outcompeted phytoplankton and the eventual collapse of the cyanobacteria blooms can result in hypoxic conditions beneath the cyanobacteria bloom, which can lead to fish die-offs from oxygen depleted waters coupled with toxicity of cyanotoxins (Paerl et al. 2001, Mhlanga1 et al. 2006; Landsberg et al. 2020). Some of these bloom forming cyanobacteria can produce different toxins that are hazardous to wildlife, pets and human health. These toxins include: anatoxin-*a*(s) which can cause muscle tremors and respiratory failure, saxitoxins which can cause paralysis and respiratory failure, cylindrospermopsins which can cause organ damage, microcystins which is linked to liver and kidney damage, and β-Methylamino-l-alanine (BMAA) which causes muscle atrophy and is a possible contributor to neurodegenerative diseases (Table 1; Carmichael 1994; Paerl et al. 2001; O'Neil et al. 2012; Huisman et al. 2018). There are several species that have been attributed to Oregon cyanobacteria blooms, including *Dolichospermum flos- aquae, Microcystis aeruginosa*, *Aphanizomenon flos-aquae* and more (Jacoby and Kann 2007; OHA 2020). These cyanobacteria species are known to produce different cyanotoxins that can be detrimental to human health. The genus *Dolichospermum* has been reported to produce hepatotoxins, such as microcystin and cylindrospermopsin, as well as the neurotoxins anatoxin-*a* and saxitoxin, while cyanobacteria in the genus *Microcystis* can produce microcystin, anatoxin-*a* and BMAA (Table 1; Carmichael 1997; Chorus and Bartram 1999; Paerl et al. 2001; Funari and Testai 2008; OHA 2018).

2.2 Factors that Trigger Cyanobacteria Blooms

There are several different factors that can contribute to the formation of algal blooms, including nutrient loading, grazing by zooplankton, and temperature (Figure 1). These factors are impacted by changing climate, and indirectly increasing favorable conditions for cyanobacteria blooms. The combination of these factors can lead to blooms, but it is often hard to determine which factor is the biggest culprit for causing blooms as most blooms are lake dependent (Paerl et al. 2001).

Bloom-forming cyanobacteria reach the maximum growth potential at higher temperatures than most other phytoplankton (Konopka and Brock 1978; Robarts and Zohary 1987; Daivs et al. 2009; Paerl et al. 2011). This was highlighted by Canale and Vogel in their 1974 review of temperature and growth rate dynamics of diatoms, green algae, cyanobacteria, and flagellates. In their review, Canale and Vogel (1974) mainly looked at studies that involved laboratory experiments rather than *in-situ* observations. Canale and Vogel (1974) concluded that flagellates reached their peak growth rate at the lowest temperature, around 24^{o}C, followed by diatoms, green algae, and lastly cyanobacteria. In a 1978 study by Konopka and Brock the optimum temperature for photosynthesis of cyanobacteria was determined through *in- situ* and laboratory experiments. In this study, cyanobacteria cultures of three genera from Lake Mendota, WI were isolated and incubated for seven days at temperatures ranging from 2^{o}C to 37^{o}C. The optimum growth temperature for all three cultures was recorded at 25^{o}C, and both *Aphanizomenon* and *Anabaena* (now identified as *Dolichospermum*) had minimal growth under 15^{o}C and did not grow at the maximum temperature of 37^{o}C. In addition to the culture studies, Konopka and Brock (1978) also analyzed *in situ* cyanobacteria communities from Lake Mendota. In the *in-situ* portion of the study, photosynthetic rate of cyanobacteria was recorded from June to November and showed that the optimum temperature of cyanobacteria is often not reached in the natural environment. Therefore, it is thought that there is some adaptation to lower temperatures that allows cyanobacteria to grow without reaching their growth optima (Konopka and Brock 1978). The authors also noted that there are indirect influences in physical and biological variables that aid in the proliferation of cyanobacteria in Lake Mendota, which includes thermal stratifications, strong winds, and grazing by zooplankton.

In addition to higher temperature tolerances, cyanobacteria have also been shown to increase faster in growth rate when reaching their maximum growth potential/rate than other algal species (Figure 1; Carey et al. 2012; O’Neil et al. 2012; Huisman et al. 2018). Environmental conditions often aid cyanobacteria in successfully outcompeting other algae especially during the late summer months when temperatures are high (Paerl et al. 2001; Butterwick et al. 2005; Jöhnk et al. 2008). In a 2008 study by Jöhnk et al., a model was coupled with *in situ* lake monitoring to analyze how heatwaves/high air temperatures and water column stability influenced phytoplankton communities and supported late summer cyanobacteria blooms. The model showed that reduction in a few key meteorological variables, such as wind speed and cloud coverage, coupled with increases air temperature indirectly led to increases in cyanobacteria abundance by reducing water column mixing. This study found that artificial mixing suppressed cyanobacteria. When mixing stopped, cyanobacteria was found at concentrations 30-50 times higher at the surface. Jöhnk et al. (2008) concluded that the combination of increased temperatures, and increased water column stability in the later summer months allowed for cyanobacteria dominance. This study showed how these variables create a positive feedback loop that encourage cyanobacteria dominance (Jöhnk et al. 2008). Paerl et al. (2011) also refer to this positive feedback loop and add that the large green mats that often form on the lake surface, which increases light absorption and therefore increase water temperature and add to the loop.

During the late spring and early summer months, cyanobacteria use gas vesicles to stay at the water surface where they can access sunlight during the day and sink to the hypolimnion to access nutrients during the night, giving a competitive advantage over their competition (Kromkamp and Mur 1984; Reynolds et al. 1987; Walsby 1994; Jöhnk et al. 2008; Ho et al. 2019). These gas vesicles are comprised of proteins and are hollow, taking on a spindle- or cylinder-shape (Kromkamp and Mur 1984; Walsby 1994; O'Neil et al. 2012; Huisman et al. 2018; Pfeier 2021). The gas vesicles within the cells have a hydrophobic membrane, which allows for gas to pass through, but not water. Gas vesicles are formed at depth with low light intensities, allowing the cyanobacteria to move toward higher light intensities for photosynthesis (Pfeier 2021). There are two mechanisms that regulate buoyancy in cyanobacteria- carbohydrates and turgor pressure. Carbohydrates accumulate as a byproduct of photosynthesis, and due to its density can cause cyanobacteria to sink in the water column (Kromkamp and Mur 1984; Oliver and Walsby 1984; Reynolds et al. 1987; Walsby 1994; Havens et al. 2003). A 1984 study by Kromkamp and Mur highlighted the negative relationship between intracellular carbohydrates and buoyancy. Some cyanobacteria, such as *Microcystis sp.*, use intracellular carbohydrate content to vertically migrate within the water column

(Kromkamp and Mur 1984; Reynolds et al. 1987). Turgor pressure also plays a key role in buoyancy regulation of many cyanobacteria genera, such as *Aphanizomenon*, *Gloeotrichia*, *Nostoc*, *Dolichospermum* (formerly *Anabaena*). At high irradiances, turgor pressure builds up and causes the irreversible collapse of gas vesicles, causing cyanobacteria to sink and the process to begin again (Walsby 1994).

Nutrient dynamics also play a crucial role in cyanobacteria growth and bloom formation. When nitrogen: phosphorus (N:P) ratios are low, indicating a surplus of P, then N-fixing cyanobacteria have an advantage over other phytoplankton, as they can readily convert atmospheric nitrogen (N_2) to ammonia (NH_3) (Paerl et al. 2011; Paerl and Otten 2013). P can enter lakes in a variety of natural and anthropogenic pathways. P inputs to aquatic systems come primarily from livestock and agriculture, followed by human activities and waste products (Downing and McCauley 1992; Herath 1997; Sellner 2003). One study recorded agricultural inputs contributing to 43-57% of P loading into aquatic systems and human inputs and detergents contributing around 20% of P inputs into aquatic systems (Herath 1997). Since then, there has been increased in management of P and P has been removed from detergents in an effort to decrease P inputs to lakes and other aquatic systems. However, when P enters a lake as soluble reactive phosphorus (inorganic and organic phosphorus dissolved in water and ready for uptake by organisms; SRP) it often cycles through many processes or gets trapped in sediments, where it remains for quite some time (Kalff 2001). Even when little P is entering a lake, P can still be available through legacy P in lakes sediments. Some of the total P contained within a lake is contained within organisms as particulate organic P, as it is taken up and utilized by phytoplankton to aid in photosynthesis and growth. From there the phytoplankton may be grazed upon by zooplankton and move within the food web or the phytoplankton may die and decompose and may undergo the process of sedimentation. Orthophosphate (PO_4^{3-}) has a high affinity for iron (Fe^{3+}) and precipitates out into sediment under oxidizing condition (Gätcher et al 1988; Kalff 2001; Ding et al. 2016; Saeed et al. 2018). In stratified lakes P is often trapped beneath the thermocline, and therefore inaccessible to phytoplankton in the epilimnion. P can be made accessible again under reducing conditions where P experiences dissolution from compounds, such as iron, or be released via interactions with sediment microbes (Gätchter et al. 1988; Pettersson 1998; Kalff 2001; Saeed et al. 2018).

Low N:P ratios are only beneficial to these N-fixing cyanobacteria (Reynolds 1998; Paerl et al. 2011; Carey et al. 2012). Eutrophication of lakes and rivers has become an increasing driver of excessive algal growth and productivity. Human activities, such as livestock production and agriculture, have caused an increase in both P and N into aquatic systems through runoff (Sellner et al. 2003; Paerl and Otten 2013). While management practices have tried to reduce P runoff into water bodies, increased N levels are likely to cause a shift in cyanobacteria community composition from N-fixing cyanobacteria to non- N-fixing cyanobacteria like *Microcystis* (Huisman et al. 2018). This has been observed in Western Lake Erie (Allinger and Reavie 2013; Watson et al. 2016). For a while nutrient loading, particularly P loading was attributed as the cause of cyanobacteria blooms in Lake Erie. Since then, the reduction of P loading has caused a shift in the bloom taxa in Lake Erie. Blooms prior to reduction of P loading were dominated by diazotrophs (*Aphanizomenon* and *Dolichospermum*), whereas now cyanobacteria blooms are dominated by *Microcystis* (Newell et al. 2019). Newell et al. (2019) describe how the management plans in place do not account for the relative increase in N present and available for cyanobacteria. Specifically, the authors note that there has been a significant increase in the proportion of total Kjeldahl N (TKN) to nitrate over time present in inflowing Maumee River (Spearman's ρ=0.68, p=0.001), which brings more reduced forms of N into Western Lake Erie (Newell et al. 2019). The increase in TKN has also been significantly correlated to cyanobacteria biomass in Western Lake Erie (Spearman's ρ=0.64, p=0.003), however the importance of N, especially in reduced forms, on a system is often overlooked or too expensive to manage (Schindler 2012; Newell et al. 2019).

Another possible mechanism that favors cyanobacteria dominance is trophic interactions and predation, specifically whether a lake has a top- down or bottom- up control. Top-down interactions are controls over the populations in which the population density of the top predators inversely influences the population density of the organism one trophic level beneath them (Kalff 2001). In contrast, a bottom-up control occurs when resource limitations and the abundance of primary producers, or lack thereof, can increase or decrease the populations at trophic levels above them in the same direction (Kalff 2001). Carpenter et al. (1985) describe a top-down trophic interaction when the increase of piscivorous fish results in a decrease in planktivores, an increase in herbivores, and ultimately results in a decrease in phytoplankton due to the increase in grazing pressures. The opposite can be seen when nutrients control the interactions of populations and biomass of consumers. In this situation high availability of nutrients allows for increases in phytoplankton biomass, which increase zooplankton and herbivore biomass, which then increases planktivore biomass, and ultimately leads to an increase in piscivore biomass. One example of bottom-up control can be seen in a Finnish lake study (Horppila et al 1998). In this study, the mass removal of fish resulted in the collapse of the cyanobacteria bloom on Lake Vesijärvi. However, the authors determined that the removal of fish did not result in any changes in zooplankton community biomass, but rather that the removal of fish changed nutrient dynamics by causing a decrease in the amount of recycled P by the fish (such as though nutrient excretion by fish, bioturbation, and fish mortality). Therefore, Horppila et al. (1998) argue that the change in nutrient dynamics is what caused the cyanobacteria communities that were typically present in abundance in this lake to collapse.

Fish communities are also important to algal community structures and can indirectly promote cyanobacteria blooms. This can be seen in a study by Schindler et al. (2008). Schindler et al. (2008) noted that the addition of *Esox lucius* (northern pike), a piscivorous fish, to a eutrophic lake caused trophic cascades that resulted in cyanobacteria blooms. The pike eliminated planktivorous grazers from the forage fish present in the lake, which resulted in decreased zooplanktivory and higher abundances of large zooplankton. The zooplankton populations then grazed upon non-cyanobacteria phytoplankton communities, allowing cyanobacteria to increase in overall abundance and biomass during this time (Schindler et al. 2008). Schindler et al. (2008) noted that once all the pike fish were removed from the lake, rendering the lake fishless, there was a drastic drop in cyanobacteria and other algal taxa (chrysophytes, diatoms, cryptophytes, and dinoflagellates) measured by biomass (mg/m^3) and chlorophyll-a concentrations (µg/L).

Cyanobacteria can be unpalatable to most zooplankton and offer little nutritional value (Arnold 1971; Lampert 1987; Paerl et al. 2001; Huisman et al. 2018). Zooplankton that do not graze on cyanobacteria essentially remove other competing phytoplankton from the water column, allowing cyanobacteria to dominate the algal community. This was seen in Haney (1987), where grazer communities of *Daphnia* almost exclusively fed on small particulates and non-cyanobacterial phytoplankton. Haney (1987) also noted that cladocerans did not feed on cyanobacteria, as grazing on them impaired their ability to filter feed. Grazing on cyanobacteria can also be harmful to grazers due to the cyanotoxins produced by cyanobacteria (Lampert 1987; Work and Havens 2003; Ferraõ-Filho et al. 2009). While many zooplankton may avoid grazing upon cyanobacteria, cyanobacteria may still experience some grazing pressures. Burns and Hegarty (1994) used laboratory studies to determine the dietary preferences of the copepod *Boeckella*. In this study, *Boeckella* were fed different mixtures of cyanobacteria (*Dolichospermum flos-aquae (*previously *Anabaena flos-aquae), Nostoc*, *Oscillatoria tenuis*, and *Microcystis* *aeruginosa*), green algae (*Choricystis),* and a flagellate (*Cryptomonas).* The different phytoplankton were fed to the zooplankton at low concentrations alone, as well as in combinations of different mixtures. Burns and Hegarty (1994) used clearance rate, which was defined by the authors as the volume of water cleared of particles per unit time, in order to determine diet preference. When non-cyanobacteria were abundant, the zooplankton in the study preferred the non-cyanobacteria phytoplankton to cyanobacteria. However, when there were low concentrations of all phytoplankton *Boeckella* preferred *Anabaena* and *Nostoc* to other, non-cyanobacteria phytoplankton (Burns and Hegarty 1994). When presented mixtures of only containing cyanobacteria *Boeckella* shifted preference to *Anabaena* and *Oscillatoria*, avoiding *Microcystis* consistently throughout the study as it presented toxic effects to the zooplankton. There are species of zooplankton that have adapted to the cyanotoxins and low nutritional value of cyanobacteria and can feed on them (Arnold 1971; Lampert 1987; Epp 1996; Huisman et al. 2018). It is important that there is low grazing of cyanobacteria for bloom conditions to ensue (Figure 1; Paerl and Otten 2013).

Changing climate is projected to extend summer-like conditions in the Northern Hemisphere mid-latitudes to be longer and hotter, which is subsequently prolonging the cyanobacteria bloom season (Mote and Salathé 2010; Huisman et al. 2018). Dry summer conditions also pose a risk to low flow rates in watersheds, which decreases mixing in lakes, further perpetuating cyanobacteria dominance (Paerl and Paul 2012; Nwankwegu et al. 2019). Climate changes to winter conditions, such as snow droughts in the Pacific

Northwest, will also have adverse effects to lake communities and are also affecting summertime cyanobacteria bloom formation (Mote et al. 2005; Harpold et al. 2017). Greater precipitation could increase nutrient loading into lakes, which can create favorable condition for cyanobacteria blooms (Ho and Michalak 2019; Wheeling 2019). Mild winter snow and shorter winters will extend summer-time conditions, simultaneously extending the bloom season, giving cyanobacteria a longer time period to form blooms and outcompete other phytoplankton (Huisman et al. 2018; Ho and Michalak 2019). Increased temperatures throughout the summer will also allow the proliferation of cyanobacteria due to the high temperatures required for optimized growth rates (Paerl et al. 2001; Wheeling 2019). Warmer temperatures also have the potential to increase cyanotoxins, as Davis et al. (2009) found that *Microcystis aeruginosa* releases more cyanotoxins in higher water temperatures. These hotter, longer summers will also lead to longer durations of stratified water columns which also promotes cyanobacteria blooms, as cyanobacteria can control their buoyancy (Carey et al. 2012; Visser et al. 2016). This will also simultaneously shade out phytoplankton, further promoting cyanobacteria dominance (Wheeling 2019). As humans emit more greenhouse gases, especially CO_2, cyanobacteria and other phytoplankton will require more and more CO_2 from the atmosphere in order to perform photosynthesis, resulting in carbon limitation (Paerl et al. 2011). Cyanobacteria are already equipped with five different carbon uptake systems, two for CO_2 and three for bicarbonate. This is especially important for the success of cyanobacteria during bloom conditions, as dense cyanobacteria blooms shift the carbon equilibrium from inorganic carbon to bicarbonate and carbonate as blooms deplete CO_2 in the water column (Huisman et al. 2018). While more photosynthesis from algal communities is beneficial for turning lakes into carbon sinks, it promotes bloom formation as the cyanobacteria can interact with atmospheric CO_2 at the lake surface (Huisman et al. 2018; Ho et al. 2019).

2.3 Frequencies of Cyanobacteria Blooms

In recent years many scientists, lake managers, policy makers and members of the community have all had the same question: are algal blooms more common today, or are we more aware of them? A recent study by Ho et al. (2019) looked at the frequency of algal blooms occurring from 1984 to 2012 for 71 lakes in 33 countries. A time series of near surface bloom intensity, created using Landsat 5 satellite imagery, showed two-thirds of the study lakes increased in peak summertime algal bloom intensity from 1984 to 2012 (Ho et al. 2019). The authors also looked at precipitation, temperature and nutrient/fertilizer input to these lakes over the study period but found no consistent relationships between these factors and bloom intensity. Taranu et al. (2015) also examined how cyanobacteria has increased in dominance over the last 200 years. Myxoxanthophyll, an algal pigment produced by most bloom forming cyanobacteria taxa, was extracted from sediment cores in 108 northern, temperate- subarctic lakes. Cyanobacteria pigments were found to have increased by 58% in over 100 lakes during the Anthropocene (Taranu et al. 2015). Lakes that experienced management practices to reduce cyanobacteria or underwent restoration efforts did not experience an increase in cyanobacteria pigments. However, if left unmanaged Taranu et al. (2015) showed that cyanobacteria are likely to increase in both lowland and alpine lakes in the northern temperate region.

2.4 Cyanobacteria Bloom Monitoring and Management in Oregon

Oregon has recorded cyanobacteria blooms in over 60 lakes throughout the state (DEQ 2011; OHA 2023). The current approach to cyanobacteria blooms in Oregon is described in the cyanobacteria bloom surveillance program, which is led by OHA and the Oregon Public Health Division. The cyanobacteria bloom surveillance program relies on a collaborative effort between different organizations, such as lake associations, watershed groups, drinking water providers, state and government organizations (United States Forest Service, United States Army Corps of Engineers, United States Bureau of Reclamation), or any other organization that is willing to participate (DEQ 2011; OHA 2019). In situations where there is no defined organization or management agency for a lake, the Oregon Department of Environmental Quality (DEQ) will perform monitoring and sampling. Health and recreation advisories are posted when lake conditions meet one of the following guidelines (OHA 2019):

1. There is a visible scum on a water body, photos of the scum are taken and sent to the OHA and water samples will be taken for toxicity testing within one business day.

2. Toxin levels are greater than or equal to the recreational use values, which is 8 micrograms per liter of microcystin and saxitoxin and 15 micrograms per liter for anatoxin-a and cylindrospermopsins.

Health and recreational advisories are recorded and kept by the OHA and are easily accessible on the OHA website. While these requirements for posting advisories are effective, they are also extremely time consuming and very costly. The current advisory guidelines serve as a reactive mechanism for reporting cyanobacteria blooms, rather than a proactive approach.

3. Methods

3.1 Study Area

Oregon has a diverse landscape, from temperate forests in the West to arid deserts in the East. The annual precipitation for the western side of the state ranges from 400 to 3550 centimeters, based on a 30-year normal record (PRISM Climate Group 2015). The Pacific Ocean also helps to regulate temperatures along the Cascade Mountain Range, which extends from Northern California, USA to British Columbia, Canada. While Oregon has a diverse landscape, this study focuses on two lakes in the High Cascades of Central Oregon. The Oregon Cascades have been carved by alpine glaciation, which formed several lakes in the region. This area is classified as a Level IV ecoregion 4c, Cascade Crest Montane Forest (Thorson et al. 2003). This landscape is characterized by the mountainous ranges, snow-fed river, deep lakes, and heavily forested areas. Due to the location of these study lakes in the Cascade Mountain range, the surrounding area experiences heavy rainfall, strong winds move across the lake from the Northwest, and generally the air temperature remains cool. In 2019 the study area received 105 cm of rain and had an average daily temperature of 5.0^{o}C, an average daily maximum air temperature of 10.8^{o}C, and an average daily minimum temperature of -0.7^{o}C (PRISM Climate Group- New Crescent SNOTEL).

The two lakes in this study are Odell Lake (43.562262 N, -121.964550 W) and Crescent Lake (43.500832 N, -121.973205 W), located within the Deschutes River Basin (Hydrological Unit Code 8) in Central Oregon (Figure 2). The watersheds that encompass both Odell Lake and Crescent Lake can be characterized by the largely forested landscape (Table 2), which is comprised of *Tsuga mertensiana* (mountain hemlock), *Pinus contorta* (lodgepole pine), *Pinus monticola* (western white pine), *Abies amabilis* (pacific silver fir), *Abies procera* (noble fir), and others from the *Abies* genus (true firs) (Davis and Larson 1976; Johnson et al. 1985; Eliers et al. 2005). The Diamond Peak Wilderness area occupies nearly half of the southern end of Odell Lake’s watershed and nearly half of Crescent Lake’s northern portion of the watershed. Many people are drawn to these lakes, as well as other nature areas in Deschutes National Forest, due to the many recreational activities, such as hiking, skiing/snowboarding, site seeing, hunting, and fishing. These activities attract over 1.9 million recreation visits annually (Smith et al. 2011). While a popular location for recreation, less than 2% of the total watershed area of these two lakes is developed land (Table 2).

3.1.1 Lake Characteristics

Odell and Crescent lakes are similar in morphology, both are glacial scoured lakes that date back to the Pleistocene Epoch (Johnson et al. 1985; Eilers et al. 2005). Both lakes were scoured and formed behind a terminal moraine, which resulted in these single basin lakes (McArthur 1925; Johnson et al. 1985; Fies et al. 1996; Kalff 2001). Following the eruption of Mt. Mazama, volcanic ash was deposited over the landscape, which contributes to the volcanic nature of the area and consists of porous topsoil, comprised of volcanic ash, pumice, and glacial till, which allow for high infiltration rates, and ultimately results in low nutrient retention and high rates of throughflow (USFS n.d.; Davis and Larson 1976; Johnson et al. 1985; Hoblitt et al. 1987; Eilers et al. 2005). There are several inlets to Odell Lake and a single outlet to Odell Creek, which flows into Davis Lake and eventually the Deschutes River (via Wickiup Reservoir). The inlets into Odell are snow fed headwaters, and the watershed is characterized by the coniferous forest.

In addition to the similar morphologies and their proximity to each other, Odell Lake and Crescent Lake share many other similar lake characteristics, such as surface area, maximum depth, and depth of thermocline (Table 2). The watersheds of both Odell and Crescent border each other and are 9.5 kilometers apart from each other (Figure 2). Odell Lake spans 14.6 square-kilometers and lies at 1,459 meters of elevation. Odell has a maximum depth of 86 meters and an average depth of 40 meters (Table 2). The lake is dimictic, as it has been known to freeze over occasionally during the winter (Larson 1970; Johnson et al. 1985). The summer thermocline is typically recorded between 3 to 18 meters (Johnson et al. 1985; Fies et al. 1996). The depth of the thermocline is influenced by strong winds coming from the west and internal seiches (Larson 1970). The trophic status of Odell Lake is widely discussed, as the Secchi disk readings which ranged from 1 to 11.5 meters in 2004 and indicate oligotrophic conditions (Larson 1970;

Carlson and Simpson 1996; Eilers et al. 2005). Davis and Larson (1976) reported that developments along Odell have increased steadily since the 1920's with the building of the Southern Pacific Railroad, to the creation of Highway 58 in the 1940's, and lakeside campground, resorts and residences in the 1950's. From the development of the surrounding area, Odell has increased in productivity since the 1960's, which has been speculated to be a contributing factor in the classification of Odell as mesotrophic to eutrophic (Johnson et al. 1985).

Crescent Lake area is 16.2 square-kilometers at full pool and lies at an elevation of 1,475 meters (Johnson et al. 1985; Fies et al. 1996; USDA Forest Service n.d.). Crescent Lake has a maximum depth of 81 meters and an average depth of 37.8 meters (Table 2). There is a 12-meter concrete dam located on the lake that is used by the Bureau of Reclamation for summertime irrigation, which can cause the water level to drop about 4.5 meters (Johnson et al. 1985; Fies et al. 1996; Linenberger 1999). The lake is dimictic, and the thermocline in Crescent Lake has been reported to be between 9 to 18 meters by late June or early July (Fies et al.1996). The depth of the thermocline is attributed to the strong winds experienced by the lake. Crescent Lake has been described as having very low nutrient levels, however there are no historic records available to support this (Johnson et al. 1985). Fies et al. (1996) also defines Crescent Lake as oligotrophic due to the water transparency, around 6 meters year-round, and an average total dissolved solid of 15.5. The main inlet of Crescent Lake is Summit Creek, which brings snowmelt from the Eastern Cascade Mountain Range to Crescent Lake via Summit Lake and Summit

Creek. The outlet is Crescent Creek, which flows into the Deschutes River via the Little Deschutes River.

3.1.2 Land Use and Watershed Characteristics

During the summer months both lakes are used for recreation, such as boating, fishing, camping and hiking (USDA Forest Service 2020). Both lakes are easily accessible from Oregon Highway 58, with the Northeastern shoreline of Odell Lake neighboring the highway. The watersheds of both lakes are primarily forested, with very little of the land use designated as developed land (Table 2). There are two resorts located at the Northeast and Southwest ends of Odell Lake, along with a marina and five U.S. Forest Service campgrounds located along the shoreline, and about 70 private homes on the lake (ODFW 1996). Crescent Lake hosts seven U.S. Forest Service campgrounds and a private resort along its shoreline. Crescent Lake is also used by the Bureau of Reclamation as a supplemental source of irrigation water to approximately 8,000 acres of land in the Tumalo Irrigation District on the west side of the Deschutes River, about 115 Kilometers from Crescent Lake (Johnson et al. 1985, Linenberger 1999; Deschutes River Conservancy 2012).

3.1.3 Overview of Biological Communities

Due to the basin morphology of both Odell and Crescent lakes, the steep basins create a limited littoral zone, which leaves little room for macrophyte growth. Phytoplankton communities at Odell Lake are composed of different diatom taxa, such as *Tabellaria, Asterionella*, and *Fragilaria* (Johnson et al. 1985). Odell Lake has a history of cyanobacteria, such as *Dolichospermum flos-aquae* (formerly *Anabaena flos-aquae*), present in the form of cyanobacteria blooms. A study by Lindsay and Lewis (1978) found the zooplankton community was 73% *Cyclops* (28,000 individuals per cubic meter), and 23% *Daphnia* (10,000 individuals per cubic meter). Native fish communities in Odell consist of *Salvelinus confluentus* (bull trout), *Oncorhynchus mykiss gairdnerii* (redband rainbow trout), and *Prosopium williamsoni* (mountain whitefish) (Fies et al. 1996). Introduced fish species include *Salvelinus namaycush* (lake trout), *Siphateles bicolor* (tui chub), and *Oncorhynchus nerka* (kokanee salmon) (Johnson et al. 1985; Fies et al. 1996; Meeuwig et al, 2022; ODFW 2020). The USDA Forest Service reports that the lake is managed as a trophy lake and trout fishery (USDA Forest Service 2020). Similar to Odell Lake, Crescent Lake has limited littoral zones and subsequently little macrophyte growth. Some of the phytoplankton that have been documented in Crescent Lake include *Kephyrion*, *Dinobryon*, *Tabellaria*, and *Chromulina* (Johnson et al. 1985). Crescent Lake has communities of *Oncorhynchus mykiss (*rainbow trout), *Salmo trutta* (brown trout), *Salvelinus namaycush* (lake trout), *Prosopium williamsoni* (mountain whitefish) and *Oncorhynchus nerka* (kokanee salmon) (Johnson et al. 1985; USFS 2020).

3.2 Algal Bloom History

While these two lakes are very similar in terms of watershed characteristics and geomorphology of the basins, Odell has a history of cyanobacteria blooms and has had recreational advisories, while Crescent Lake has no recorded bloom history or recorded recreational advisories (Jacoby and Kann 2007; OHA 2023). The earliest bloom recorded in Odell Lake occurred in 2004 and was dominated by *Dolichospermum flos-aquae* (formally *Anabaena flos-aquae*) and had a recorded concentration of 598,000 cells per milliliter and 0.03 to 5.01 micrograms per Liter microcystin (Jacoby and Kann 2007), however the Oregon Health Authority began recording bloom events in 2007 (OHA 2007). Since 2007, there have been ten (10) recreational advisories issued on Odell Lake, with the latest algal bloom recorded by OHA in July 2020 (OHA 2020). The recorded cyanotoxin produced in Odell Lake is microcystin, with the latest advisory reaching 1710 ppb (OHA 2020).

3.3 Field Data Collection

The field data collection occurred from 19 June to 20 September 2019 and again from 23 April 2020 to 11 September 2020. Odell Lake samples were collected from the Sunset Cove boat dock, located at 43.562262 N, -121.964550 W (Figure 2). Crescent Lake samples were collected from the USDA Forest Service boat ramp at 43.500832 N, -121.973205 W, next to Crescent Lake Lodge and Resort (Figure 2). These locations were chosen due to the ease of access for sonde deployment, security of the equipment, and a representative location of the cyanobacteria bloom. For Odell Lake, a multiprobe sonde (Exo Multiparameter Sonde, YSI, USA) at Sunset Cove was placed at the Southeast end of the lake, which due to the orientation of the lake and the wind pattern, has been known to accumulate surface scum from algal blooms (Figure 3). The sonde location on Crescent Lake is near the outlet and dam located at the Northeast end of the lake. The sondes were placed no more than one meter from the surface.

3.3.1 Water Quality

Water quality was recorded by DEQ. The sonde recorded dissolved oxygen as percent saturation and concentration, water temperature in degrees Celsius, pH, phycocyanin as relative fluorescence units, and chlorophyll- *a* as relative fluorescence units at 15-minute intervals from 26 June 2019 through 20 September 2019 and again from 23 April 2020 to 11 September 2020. Sonde audits, including calibration, occurred on a bi-weekly basis. In 2019, DEQ collected other water chemistry and water quality measurements were taken, including chlorophyll-*a* concentrations (µg/L), pheophytin-*a* (µg/L), total P (mg/L), and total N (mg/L). In addition to the nutrients previously mentioned, DEQ added nitrate-nitrite (mg/L), ammonia as N (mg/L), orthophosphate (mg/L), and dissolved silica (mg/L) to the 2020 sampling guidance. These variables were collected as grab samples and taken on a bi-weekly basis during audits of the sondes. A list of the analytical methods and reporting limits are listed for each variable in Table 3. These data were downloaded through the DEQ’s Ambient Water Quality Monitoring System (AWQMS).

3.3.2 Phytoplankton Sampling

Phytoplankton samples were collected on a weekly basis from both Odell and Crescent lakes from June 2019 through September 2019 (n=26). Grab samples were taken next to the data sondes (Figure 2). Each sample was taken from half a meter below the water surface, following sampling guidelines published by the WHO and OHA (Chorus and Bartram 1999; OHA 2018). Approximately 200 milliliters of water were collected in Nalgene bottles and preserved with Lugol's Iodine solution. Lugol’s Iodine solution was made using standard protocol (Chorus and Bartram 1999). Samples were transported from the field in a cold, dark container to avoid photodegradation and then stored under the same conditions.

3.4 Laboratory Assessment

3.4.1 Algal Identifications

Initial samples were low in phytoplankton density and required concentration before identification and counts began. In order to concentrate samples, the initial volume from each sample was recorded. Grab samples were then placed into beakers and allowed 24 hours to settle phytoplankton to the bottom of the beaker. After 24 hours, the top layer of the water was siphoned off and the remaining volume was recorded. This process was repeated twice for all samples except for the two bloom samples. A 100-microliter sample was dispensed into a Hausser Scientific Palmer Nanoplankton counting chamber. For Odell Lake, at least 300 counting units of phytoplankton were counted in each sample (US EPA 2007). A counting unit is defined as a natural grouping of algae, either an individual filament, colony, or individual cell. Due to the oligotrophic nature of Crescent Lake, phytoplankton was counted in 200 field of views rather than 300 counting units. Phytoplankton was identified using a Leica DME microscope at 400x magnification and identified to at least the genus level. Prescott (1962), Prescott (1964), Patrick and Reimer (1966) and Round et al. (1990) were used as the primary references for identification. Phytoplankton abundance was calculated using the following equation:

$$\text{Cell density (cells/ mL)} = [\ \#\text{cells} \div (\ \text{FOV}_v \times \text{FOV}_n\ )\ ] \times (V_f \div V_{tot}) \qquad \text{(Equation 3)}$$

Where

FOV_{vol} is the volume counted per field of view, which was 9.12×10^{-5} milliliters.

FOV_n is the number of fields of views counted per slide.

V_f is the final condensed volume in milliliters and

V_{tot} is the total sample volume in milliliters.

3.5 Statistical Analysis

Summary statistics were calculated for the water quality variables. These statistics included average, standard deviation, minimum, and maximum (Table 4). The distribution of each water quality variable was determined by visually assessing the associated histogram and comparing the mean to the median. Ultimately, median was not included in this report due to the normal distribution of the variables.

3.5.1 Sequential Cluster Analysis

A cluster analysis is a type of analysis that places objects or observations into groups based on similarities, such as species abundances (Edwards and Cavalli-Sforza 1965; Gotelli and Ellison 2012). A sequential cluster analysis is especially useful to this study because it allows for the creation of groups without interfering with the natural order in which the communities occurred in over time. This analysis was chosen in order to divide the phytoplankton communities in each lake into distinct groupings that would allow for a characterization of the phytoplankton traits and over targeted periods of the study season. This analysis was performed in R version 3.6.2 (R Core Team 2019) using the packages rioja 0.9.21 (Juggins 2017) and vegan 2.5.6 (Oksanen et al. 2019).

The first step in a sequential cluster analysis was to calculate a distance matrix, in which the Bray-Curtis index was used. The Bray- Curtis index is a dissimilarity or distance matrix that is used to describe differences in community composition. The ultimate number of groups chosen was based on the results of a broken stick model. A broken stick model chooses groupings that explain more variance than would be expected by randomly dividing the variance into x groupings, which in this case was three groups.

3.5.2 Indicator Taxa Analysis

An indicator species, or taxa, analysis was performed in order to identify the unique phytoplankton taxa in each of the groupings determined by the sequential cluster analysis. This analysis was chosen in order to use phytoplankton characterization to better understand the water quality dynamics from the pre-bloom to bloom to post-bloom phases. An indicator species, or in this case an indicator taxon, is a genus that can be used as an ecological indicator of the surrounding environment based on the specific preferences of that genus (McGeoch and Chown 1998; De Cáceres et al. 2010). Using the groupings from the cluster analysis, the indicator taxa tell us which genera are commonly found in a given group and present in the majority of sites within the group (Dufrêne and Legendre 1997). Because the taxa are common and abundant in the group, it is often considered the most characteristic of the group and therefor useful for describing the conditions that are representative of the sites or grouping. For example, if the indicator taxa are known to be found in eutrophic lakes, then these indicator taxa can be used to make inferences about the conditions present in the environment that allow for these taxa to flourish.

The Dufrene- Legendre indicator analysis was performed in R version 3.6.2 (R Core Team 2019) using the package labdsv version 2.0-1 (Roberts 2019). The indicator taxa were calculated for three groups in each lake. For Odell Lake, the indicator taxa were determined for the pre-bloom (19 June – 11 July 2019), bloom (24 – 30 July 2019), and post-bloom groups (7 August – 19 September 2019). In Crescent Lake, the indicator taxa were determined using Group 1 (19 June – 11 July 2019), Group 2 (24 July – 29 August 2019), and Group 3 (5 – 19 September 2019). The indicator value generated in this analysis considers the relative abundance of the taxa while also factoring in how frequently or in frequently a given taxon occurs throughout the sample season (Dufrêne and Legendre 1997; McGeoch and Chown 1998; De Cáceres et al. 2010).

3.5.3 Non-Metric Multidimensional Scaling

Non-metric multidimensional scaling (NMDS) is a dimension reduction analysis that rearranges similar objects to be positioned more closely together and put a greater amount of distance between dissimilar objects or samples. In this project these objects represented phytoplankton communities by genera at specific points in time. The objects were arranged within an ordination plot based on how similar or dissimilar the objects are to each other. To do so, this analysis preserved the rank order of the objects, which allows the original distance between the objects to be rearranged and changed. NMDS analysis does not require normality or linearity, which was beneficial for analyzing the phytoplankton data (Gotelli and Ellison 2012). NMDS analysis was chosen to analyze the phytoplankton dynamics- specifically to better characterize the difference in phytoplankton communities as well as to understand the temporal shifts in phytoplankton that occur within Odell and Crescent lakes on their own. This analysis highlighted how the phytoplankton communities differ between the two lakes, despite having similar watershed characteristics, morphology and land use. This analysis was performed in R version 3.6.2 (R Core Team 2019) and used packages tidyverse 1.3.0 (Wickham et al. 2019), vegan 2.5.6 (Oksanen et al. 2019), MASS 7.3.50 (Venables and Ripley 2002), and zoo 1.8.7 (Zeileis and Grothendieck 2005). Before performing the analysis, the community data were transformed using a square root transformation in order to minimize the impact of highly abundant taxa. NMDS creates a distance or dissimilarity matrix index based on a chosen index (Gotelli and Ellison 2012). The Bray- Curtis Index is often used for continuous numerical data and was chosen because it is often used to show differences in species composition between different sites, with 0 being the most similar and 1 being completely different. When used in an NMDS, it represents a community similarity index by subtracting the calculated similarity index from one. A Shepard diagram was created to show the goodness-of-fit between the distances created using the Bray- Curtis Index and the map distance within the NMDS plot. The goodness-of-fit is represented by a stress value, which is the minimum number of dimensions in which a given dataset can be visualized without inducing unacceptable levels of distortion (Kruskal 1964). Ultimately, the NMDS analysis was run 20 times with a different random ordination each time. The final NMDS dimensions and ordination plot chosen was based off the lowest stress value, or best fit.

3.5.4 Generalized Additive Mixed Models

A generalized additive model (GAM) is a statistical model that uses regression-based methods in order to estimate trends (Simpson 2018). These models are useful in analyzing time series data that are non-linear and uses smooth functions to create a function for the shape of the data rather than forcing onto the data, as seen in linear regressions and polynomial regressions (Simpson 2018). A smooth function is a non-linear function that is used to describe the data and unique to the data. This differs from other approaches, such as linear and polynomial regression which use predetermined shapes that most closely describe the trend in the data. A generalized additive mixed model (GAMM) is a GAM that incorporates autocorrelation into the model. Autocorrelation is the relationship between one observation and a separate observation at a prior time step, which results in observations being dependent on those prior to it. Since the data in this project were time series, and therefore not independent from each other, a GAMM was used for this study. This analysis was chosen to analyze temperature data and identify the periods of significant temperature change in the study lakes. This analysis helped identify if and how temperature influences cyanobacteria bloom formation in Odell Lake, and how temperature affects phytoplankton community dynamics.

The GAMM was performed in R version 3.6.2 (R Core Team 2019), along with the use of the following packages for analysis: mgcv 1.8.24 (Wood 2011), nlme 3.1.137 (Pinheiro et al. 2019). The figures were made using the following packages: ggpubr 0.4.0 (Kassambara 2020) and tidyverse 1.3.0 (Wickham et al. 2019). A partial autocorrelation function was used to test for autocorrelation for each variable. Partial autocorrelation is used instead of autocorrelation because partial autocorrelation controls for any correlation between observations of shorter lags. If the data were autocorrelated, multiple GAMMs were generated using four different smoothness selections (k=1-4). An ANOVA was then used to compare the different GAMMs to determine which smoothness selection (k) would be used for the final model. Choosing an optimal k is important for the analysis to ensure the model does not overfit or underfit the data. The ANOVA generated Bayesian Information Criterion, and the GAMM that was ultimately chosen for the analysis was that which had the lowest Bayesian Information Criterion. Once the model was fit to account for autocorrelation, the model can be examined to find points of significant change in the given water quality variable over time. To do so, I must identify whether the first derivative of the fitted spline or trend at a given time differs from the null hypothesis of zero, or no change in slope, in order to identify significant changes in the variable over time.

This analysis was performed in order to identify significant changes in temperature over the sample season. Temperature was recorded at 15-minute intervals using a sonde. For this analysis, the daily average, daily minimum, and daily maximum of each variable was taken and used to produce the results of GAMM. Summary statistics for temperature were used for GAMM analysis because temperature thresholds are often reported as temperature maximum and minimum thresholds (Konopka and Brock 1978; Robarts and Zohary 1987). The temperature difference between Odell Lake and Crescent Lake were calculated for daily average, daily minimum, and daily maximums and were used to generate GAMMs.

4. Results

4.1 Phytoplankton Dynamics

4.1.1 Community Composition in Odell and Crescent Lakes

NMDS ordination plot separated the algal communities of Odell Lake and Crescent Lake (Figure 4), with little overlap of the data points. The stress value for the NMDS was 10.16, which indicates that the distance matrix was a good fit for the data. The gradient in community composition along NMDS axis I was most strongly associated with the phyla cyanobacteria and Bacillariophyta. NMDS axis II was a gradient of dinoflagellates and Ochrophyta (Figure 5). The difference in phytoplankton communities in each lake was quantified by looking at genera richness, where a total of 35 algal taxa were identified in both lake samples, with 31 different taxa found in Odell Lake and 26 different taxa identified in Crescent Lake. In addition, Odell was dominated by the phylum Cyanobacteria, with an average relative abundance of 59.8 ± 30.3% (n=13; average ± standard deviation), and a range from 7.50% to 99.9% (relative abundance of total density). Crescent Lake was co-dominated by the phyla Bacillariophyta and Ochrophyta, which had an average relative abundance of 28.6 ± 14.0% and 20.9 ± 14.8% and ranged from 10.0% to 48.3% and 0.00% to 39.0%, respectively.

The sequential cluster analysis identified three distinct groups in both Odell and Crescent lakes, respectively (Figure 6; Figure 7). In Odell Lake the first group consisted of the first four sampling dates, from 19 June to 11 July 2019, and is considered the "pre-bloom phase". The second group, or the "bloom phase", in Odell Lake consisted of the two sampling periods during the visible bloom period on 24 July and 30 July 2019 (Figure 8). The remainder of the sampling period is considered the "post-bloom phase", went from 7 August to 19 September 2019. In Crescent Lake, Group 1 encompassed communities from 19 June to 11 July 2019. Crescent Lake's Group 2 consisted of samplings between 24 July to 29 August 2019. The final group ran from 5 to 19 September 2019.

An indicator taxa analysis suggested that Group 1 or the Pre-Bloom Phase in Odell Lake had five indicator taxa (Table 5). The significant indicator taxa for Odell's Pre-Bloom Phase were *Dinobryon* (indicator value= 0.998, p=0.001), *Asterionella* (indicator value= 0.990, p=0.002), *Tabellaria* (indicator value= 0.966, p=0.003), *Cocconeis* (indicator value= 0.66, p=0.035), and centric diatoms (indicator value= 0.545, p=0.020), which in total represent 13.9% of the total abundance in this group (Table 5). Group 2, or the Bloom Phase, had a single significant indicator taxon of *Dolichospermum sp.1* which represents 98.8% of the total Bloom Phase abundance (indicator value = 0. 974, p=0.04; Table 5). The most abundant taxa in the Pre-Bloom Phase in Odell Lake were *Dolichospermum sp.1* (41.5%), *Microcystis* (40.7%), and *Dinobryon* (5.81%) (Figure 10). The most abundant taxon in the Bloom phase was *Dolichospermum sp.* 1 (98.8%) (Figure 10). The four most abundant taxa in the Post-Bloom phase were *Tribonema* (39.9%), *Microcystis* (10.1%), *Dolichospermum sp. 2* (9.87%), and *Fragilaria* (8.96%) (Figure 10).

There were no significant indicator taxa for the first group in Crescent Lake. The second group had a single indicator taxon of centric diatoms (indicator value = 0.714, p= 0.002; Table 5), which represented 7.23% of the total relative abundance in this group. In Group 3, *Asterionella* (indicator value=0.714, p=0.002) was the single indicator taxon and represented 15.9% of total relative abundance in this final grouping (Table 5). The three most abundant taxa in Group 1 were *Dinobryon* (26.5%), *Microcystis* (10.7%), and *Cosmarium* (9.81%). The most dominant taxa in Group 2 were *Dolichospermum sp.1* (25.9%) and *Dinobryon* (21.1%), and *Dolichospermum sp.2* (21.1%). Group 3 was dominated by *Microcystis* (36.4%), *Asterionella* (15.9%), and *Dinobryon* (5.96%; Figure 11).

4.1.2 Bloom Conditions

A visible cyanobacteria bloom was noted on 24 July and 30 July 2019 during sample collection (Figure 8). These dates coincide with the maximum cell counts captured via microscopy, which were enumerated as 8,154,432.5 cells per milliliter on 24 July 2019 and 1,256,876.8 cells per milliliter on 30 July 2019 (Figure 9). The Cyanobacteria Assessment Network (CyAN) data recorded the maximum cyanobacteria abundance on

24 July and 30 July 2019 as 1,106,624 cells per milliliter and 602,560 cells per milliliter, respectively (Figure 3, Figure 9; USEPA 2019). There was a total of 7 days throughout the sample season in which cyanobacteria detections were recorded by CyAN, which occurred between 16 July and 31 July 2019 (Figure 9; USEPA 2019). While phytoplankton samples were not taken in 2020, the satellite data recorded a cyanobacteria bloom from 15 July to 31 July 2020.

4.2 Water Quality Conditions

Water quality conditions are representative of the epilimnion of both Odell and Crescent lakes. In 2019, the overall mean water temperature and mean dissolved oxygen percent saturation were higher at Crescent Lake while mean conductivity, dissolved oxygen concentration, pH, and chlorophyll fluorescence were higher in Odell Lake (Table 4). However, the range for all environmental variables were greater in Odell Lake. The overall temperature patterns in both Odell and Crescent lakes were very similar (Figure 12, Figure 13). While the pattern was similar, a generalized additive mixed model identified periods of significant increase and decrease in the temperature between the two lakes (Figure 14). The concentration of nutrients in both lakes were very low (Table 4), and the general pattern of nutrient dynamics in Odell Lake mimicked the surge in cyanobacteria abundance (Figure 15, Figure 16).

4.2.1 Surface Temperature Dynamics in Odell and Crescent Lakes

The overall daily average temperature at the surface of Crescent Lake was slightly warmer than that of Odell Lake (Table 4, Figure 12). The daily average temperature in Crescent Lake was 19.4 ± 1.56°C (mean ± SD) and 18.8 ± 1.74°C in Odell Lake (Table 4). Surface temperature in Odell and Crescent lakes ranged from 13.7 °C to 23.5°C and 14.9 °C to 22.1°C, respectively (Table 4). Visually, the temperature between the two lakes also mimicked each other. This is true when looking at the raw data collected by the sondes as well as the temperature summaries for daily average, maximum, and minimum (Figure 12). The GAMM for the temperature summaries also showed that both lakes experienced significant increases and decreases in water temperature simultaneously (Figure 13).

The difference in daily temperature between Odell and Crescent lakes was summarized. The mean difference in daily temperature average was 0.29 ± 0.49°C (mean ± SD), while the mean difference in maximum daily temperature was 1.06 ± 0.95°C, and lastly the mean difference in minimum daily temperature was -0.26 ± 0.45°C (Figure 14). While the overall mean water temperature in 2019 would indicate that Crescent Lake was warmer than Odell Lake, the GAMM for the difference in average daily water temperature between two lakes showed Odell Lake became significantly warmer than Crescent Lake from 30 June to 15 July 2019 (Figure 14). This period of significant increased temperature coincided with the cyanobacteria bloom in Odell Lake. From 30

June to 15 July 2019, the maximum daily temperature difference between Odell and Crescent also indicated that Odell was getting significantly warmer than Crescent at this time (Figure 14). The GAMM also indicated that there is a significant increase in the minimum daily water temperature difference between Odell Lake and Crescent Lake from 2 July to 21 July 2019 (Figure 14). The GAMM for the 2020 differences in water temperature showed that there was no significant increase or decrease for daily averages, however the difference in daily maximum indicated Odell was increasingly warmer than Crescent Lake water temperature from 17 June to 7 July 2020 (Figure 14).

4.2.2 Nutrient Dynamics in Odell and Crescent Lakes

The nutrient data collected in 2019 (total nutrients only) showed that Odell Lake had higher nutrient concentrations than Crescent Lake though this was not statistically significant (for TN, p =0.07; for TP, p = 0.11). TN and TP were higher in Odell Lake than Crescent Lake for all nutrient sample dates (Figure 15). This is true for the 2020 total nutrient and dissolved inorganic N and P data as well (Figure 16). However, In Crescent Lake dissolved silica concentrations were on average 6.3 times greater than the those in Odell Lake (Figure 16).

In 2019 TN and TP peaked in Odell Lake during the CyAN detected bloom period, at 1.75 mg/L and 0.08 mg/L, respectively (Figure 15). During this time chlorophyll-*a* concentrations peaked at 52.4 µg/L (Table 4). TN in Crescent Lake peaked at the start of the sample season, at 0.096 mg/L, and decreased throughout the study season (Figure 15). This contrasts with chlorophyll-*a* concentrations, which showed the highest concentration at the end of July, 0.50 µg/L, and again at the end of the study period in mid-September. TP concentrations in Crescent Lake were below detection limits during the entirety of the 2019 sample season (Table 3; Figure 15).

The 2020 nutrient analysis for Odell Lake showed similar patterns to the 2019 results. The 2020 nutrient sampling included dissolved inorganics, as opposed to the 2019 sampling which only accounted for total nutrients. Nitrate and ammonia recorded non-detects for Odell at all sample dates except for the samples taken during the CyAN recorded bloom (Figure 16). TN and TP also peaked during the time period of cyanobacteria detections via CyAN (Figure 16). Orthophosphate, on the other hand, was highest at the start of the sample season, and quickly declined before CyAN detected a bloom (Figure 16). Dissolved silica concentrations were highest at the start and end of the sample period and decreased to its lowest points from May 2020 to the end of June 2020, after which it increased for the remainder of the sample season. Crescent Lake reported non-detects for ammonia, nitrate, orthophosphate, and TP for the entirety of the 2020 sample period (Figure 16). TN peaked at 0.22 mg/L in late-July during the CyAN recorded bloom period. Pheophytin-*a* and chlorophyll-*a* concentrations in Crescent Lake peaked at 0.3 µg/L and 1.7 µg/L at the end of the sample season in late-October.

Dissolved silica remained relatively constant in Crescent Lake, with an average concentration of 6.8 ± 0.20 mg/L (Figure 16).

5. Discussion

5.1 Shifts in Phytoplankton Community Dynamics

Results from this study supported the hypothesis that the phytoplankton communities in Odell and Crescent lakes differed from each other, with eutrophic phytoplankton prevalent in Odell Lake and mesotrophic phytoplankton prevalent in Crescent Lake. The dominant phylum in Odell Lake was cyanobacteria which primarily consisted of the taxa *Dolichospermum sp.1*. This genus is a common freshwater cyanobacteria that can produce cyanotoxins such as microcystin, cylindrospermopsins, saxitoxin and anatoxin-*a* (Carmichael 1994; Chorus and Bartram 1999; Paerl et al. 2001; Pelaez et al. 2009; OHA 2019). The OHA bloom advisory archive reported that Odell Lake has reported microcystin toxins during previous bloom events (Jacoby and Kann 2007; OHA 2023), and in 2019 OHA issued a recreational advisory for Odell Lake from 2 August to 14 August (OHA 2019). *Dolichospermum* in Odell Lake is known for producing microcystin as well as other cyanotoxins (Table 1; Carmichael 1994; Funari and Testai 2008; Sivonen 2009; OHA 2019a). *Dolichospermum* species are typically phosphorus limited, as they can fix atmospheric nitrogen (N_2) into biologically available ammonium (NH_3) and become dominant in warm, stratified waters (Fay 1992; Böhme 1998; Adams 2000; Paerl et al. 2001; Berman- Frank et al. 2003; Wang et al. 2018). Odell Lake appeared to experience potential nitrogen limitation (TN:TP < 7) at the start of the sampling season in both 2019 and 2020, but this changed following the collapse of the bloom in both years.

After the cyanobacteria bloom dissipated, Odell Lake experienced potential phosphorus limitation (TN:TP > 14; Downing and McCauley 1992; Hellström, 1996; Kalff 2001).

Another common cyanobacteria genus in Odell Lake is *Microcystis* which is often found to dominate after the abundance of nitrogen fixing cyanobacteria wanes, as *Microcystis* cannot fix nitrogen (McDonald and Lehman 2013; Paerl and Otten 2016; Wu et al. 2016). This pattern is exhibited in a study on *Aphanizomenon* and *Microcystis* succession in Dianchi Lake, China (Wu et al. 2016). Of the cyanobacteria present in Dianchi Lake, 95% of the total biomass consisted of *Aphanizomenon flos- aquae* and *Microcystis*. *A. flos-aquae* began growing as early as February and reached its peak abundance in April, while *Microcystis* did not begin to experience significant growth until March and did not form blooms until May (Wu et al. 2016). A similar pattern has been recorded in Upper Klamath Lake, Oregon where the collapse of spring diatom blooms resulted in excess nutrient supplies for cyanobacteria blooms, dominated by *A. flos- aquae,* to flourish (Essaid et al. 2021; Tanvir et al. 2021). Research has noted that *Aphanizomenon* and *Microcystis* are anticorrelated (McDonald and Lehman 2013; Miller et al. 2013), and this idea can be carried across to other diazotrophic cyanobacteria, such as *Dolichospermum* (Paerl and Otten 2013; Wan et al 2019). *Microcystis aeruginosa* is known to produce the cyanotoxin microcystin (Carmichael 1994; Spoof 2005; Funari and Testai 2008; Harada and Tsuji 2009) and can generally be found in lakes that experience nutrient loading (especially high N:P ratios), raised pH, decreased CO_2, low grazing rates of cyanobacteria (Visser et al. 2005). Perhaps the most notable bloom of *Microcystis* occurs along the western shore of Lake Erie. Lake Erie experiences high nutrient loading from the surrounding watershed, consisting of low TP (0.2 µmol/L), high nitrate and nitrite (13.2 µmol/L), and low ammonium concentrations (0.37 µmol/L) (Charlton and Milne 2004; North et al. 2007). Studies on the Lake Erie bloom have shown that phytoplankton are co-limited by nitrogen, phosphorus, and iron, as iron is needed to facilitate the uptake of nitrogen through the reduction of nitrate to ammonium (North et al. 2007).

The indicator taxa identified in each lake are important for understanding the lake dynamics at different time periods throughout the study period. The pre-bloom indicator taxa identified in Odell Lake are *Dinobryon*, *Asterionella*, *Tabellaria*., *Cocconeis*, and centric diatoms (Figure 10). *Tabellaria* are the most abundant diatom of the indicator taxa in Odell Lake, and one of the most common genera found in freshwater environments (Koppen 1978). *Tabellaria* are commonly found in mixed environments within oligotrophic to mesotrophic lakes (Koppen 1978; Reynolds et al. 2002; Padisák et al. 2009). *Tabellaria* are sensitive to stratification but can be found in stratified waters if mixing is occurring within the top 2-3 meters of the water column (Reynolds et al. 2002; Padisák et al. 2009). The presence of *Tabellaria* was consistent with the sampling location in Odell Lake, which was a shallow bay no more than two meters deep. *Asterionella*, which accounts for 2.00% of the pre-bloom relative abundance (Table 5), are often found in mesotrophic to eutrophic waters, typically in mixed water columns as *Asterionella* are sensitive to stratification (Lund 1950; Reynolds 2018; Krivtsov et al. 2000; Reynolds 2002), and has been reported as a common diatom taxa in Odell Lake

(Johnson et al. 1985; Eilers et al. 2005). *Asterionella* can grow in waters ranging from 1.5^{o}C to 24.0^{o}C and reaches its growth maximum around 20.0^{o}C (Lund 1950; Hughes and Lund 1962; Butterwick et al. 2005). *Dinobryon* was the most abundant of the indicator taxa in this group (Table 5) and are a common freshwater chrysophyte that are typically found in ultra-oligotrophic and oligotrophic lakes (Reynolds et al. 2002). Due to the oligotrophic nature of the lakes that *Dinobryon* reside in, this genus is known to use mixotrophy to supplement nutrient uptake (Caron et al. 1993; Kamjunke et al. 2007) as well as to use bacterivory to supplement growth, as *Dinobryon* is an obligate phototroph and cannot rely on bacterivorous behavior and mixotrophy alone (Dokulil and Skolaut 1991; Caron et al. 1993; Rottenberger et al. 2013). *Cocconeis* and centric diatoms were also identified as indicator taxa. The last indicator taxa, the centric diatoms, is an overarching category and therefore difficult to classify the characteristics of this grouping. The bloom-phase in Odell Lake had a single indicator taxon of *Dolichospermum*. This genus is found in eutrophic, stratified water bodies (Visser et al. 2016; Wheeling 2019; Lehman et al. 2020). Unlike the first grouping, where the indicator taxa were not representative of the most abundant taxa, the indicator *Dolichospermum* also represented 98.80% of the total abundance during this phase (Table 5).

Overall, the first group of indicator taxa in Odell Lake is indicative of mesotrophic to oligotrophic conditions with an unstratified water column. While the diatom indicator taxa in the pre-bloom phase are typically sensitive to stratification (Reynolds et al. 2002), the water column during this time was stratified (Appendix). A depth profile taken at the deepest point of the lake on 28 June 2019 showed that the depth of the epilimnion was 13.1 meters (Appendix). However, it is important to remember that the phytoplankton sampling was taken from a single point at the Southeast end of the lake (Figure 2). The sampling location is in a shallow bay, no more than two meters deep, and the due to the bay's location and orientation the sample area is exposed to winds and there is likely mixing occurring within this bay. This is supported by the fact that maximum depth near the sampling location was two meters, yet the thermocline was recorded between 11 and 18 meters throughout the summer (Appendix). The second group, or the bloom phase, clearly displays the eutrophic, bloom conditions on Odell, which were captured by the visible change in water quality (Figure 8) and high abundance of cyanobacteria (Figure 9). The post-bloom phase did not have any indicator taxa. This can be attributed to the fact that this time period spans over half the sample season and therefore there is not a representative taxon to appropriately represent the changing algal community over this time span (Figure 6). The post-bloom communities are positioned far apart from each other on the NMDS ordination plot (Figure 10), indicating that there is variability between the community samples in this group.

Crescent Lake exhibited a different community structure than Odell Lake. Crescent Lake did not have any indicator taxa in Group 1. The lack of indicators for this group indicated that the individual sampling events that comprised this group had community structures that varied from each other substantially and therefore there was not a taxa in this grouping that was uniquely representative of this phase (De Cáceres 2020), which was not unexpected given that the NMDS for Crescent Lake showed that communities in this first grouping were positioned closely between Group 2 and 3 (Figure 11). In other words, there was likely some overlap between previous groupings that left no distinct taxa to represent Group 1 in Crescent Lake. Group 2 had a single indicator taxon, represented by centric diatoms that comprised 7.23% of the total relative abundance of this grouping (Table 1). Similar to the analysis of Odell's centric diatom communities, it was difficult to make assumptions about which centrics were present in Crescent Lake, as there was limited previous research on the phytoplankton in this lake. However, the lake has been characterized as an oligotrophic system, so it is likely that the centrics were also representative of these conditions (Johnson et al. 1985; Fies et al. 1996). Lastly, Group 3's indicator taxon was *Asterionella*, representing 15.9% of the total abundance in the phase (Table 5). As stated above, *Asterionella* is found in mesotrophic to eutrophic waters (Lund 1950; Reynolds 2018; Krivtsov et al. 2000; Reynolds 2002). While Crescent Lake has not been considered a eutrophic system historically, the presence of *Asterionella* indicated that there could be an unknown source of nutrient enrichment that was present in Crescent Lake.

Due to the lack of indicator taxa for every group in these two lakes, it was important to also understand the most abundant taxa in each lake. In Odell Lake, the dominant taxa by relative abundance in the pre-bloom phase included *Dolichospermum* (41.71%), *Microcystis* (40.67%), and *Dinobryon* (5.81%), indicating that the lake was dominated by filamentous algae that are representative of the eutrophic conditions (Figure 10).

Cyanobacteria was dominant from the start of the sample season, but there seems to be environmental conditions that impeded the start of visible cyanobacteria bloom formation in the early summer months (Figure 10). The bloom phase is almost exclusively comprised of cyanobacteria, which was expected based on the bloom history reported by OHA (Eilers et al. 2005; Jacoby and Kann 2007; OHA 2020). Following the collapse of the bloom, the post-bloom phase still had cyanobacteria present in high relative abundances. However, two taxa were also highly abundant- *Tribonema* (39.90%) and *Fragilaria* (8.96%) (Figure 10). *Tribonema* and *Fragilaria* are commonly found in mixed, eutrophic lakes (Reynolds et al. 2002). It is likely that there is some mixing occurring that disrupted the cyanobacteria bloom while simultaneously bringing up nutrients from the hypolimnion (Kalff 2001).

In Crescent Lake, the most abundant taxa in Group 1 were *Dinobryon*, *Microcystis*, and *Cosmarium* (Figure 11). While *Dinobryon* and *Microcystis* are found in lakes with opposite trophic environments, *Cosmarium* are typically found in mesotrophic habitats (Reynolds et al. 2002; Padisák et al. 2009). *Cosmarium* can sustain growth at temperatures from 4^{o}C to 32^{o}C and reaches optimum growth at 20^{o}C (Duthie 1965; Butterwick et al. 2005; Stamenković and Hanelt 2013). *Cosmarium* is also sensitive to stratification but can be found in the top few meters of the epilimnion so long as there is regular mixing within the top layer (Padisák et al. 2009). The dominant taxa of Group 2 were *Dolichospermum sp. 1, Dinobryon,* and *Dolichospermum sp. 2*, which on the surface appear to represent contrasting trophic conditions, however, both

Dolichospermum and *Dinobryon* have alternative nutrient uptake abilities, such as through nitrogen fixation and mixotrophy, respectively, which could have aided their growth and abundance in the oligotrophic waters of Crescent Lake (Dokulil and Skolaut 1991; Veen 1991; Caron et al. 1993; Kamjunke et al. 2007).

Phytoplankton are found in various shapes and sizes, which is exemplified when looking at the following taxa- *Staurastrum planctonicum, Asterionella formosa,* and *Dolichospermum flos-aquae*. The size of these three algal species varies, with *S. planctonicum* ranging from 40-59 micrometers long (Prescott 1962; Prescott 1964; Kusber and Scharf 2009), *A. formosa* ranging from 45 to 68 micrometers long by 1.1 to 4.5 micrometers wide (Prescott 1962; Round et al. 1990), and a single cell of *D. flos-aquae* can range from 5 to 20 micrometers in diameter (Prescott 1964; Rosen and St. Amand 2015). Due to their size and abundance, each individual cell will contribute differently to the overall biomass of phytoplankton in the study lakes. Cell counts performed in this study likely biased high the impact of cyanobacteria in terms of biomass. This is because the cell counts did not factor in biovolume of algal taxa and because cell counts were derived using counting units. Recall from section 3.3 that a counting unit is independent cells, colonies or filaments. Using counting units without correcting for biovolume can potentially cause for conclusions to be misled. This can occur when there are high abundance of a small species and low abundance of large species. The small species might be contributing less than the large species to the overall biomass, but cell counts and abundance does not account for this (Hillerbrand et al.

1999). Biovolume can help correct this and can serve as a proxy for biomass. While phytoplankton are very diverse in shapes, studies have made immense efforts to find the balance between and accuracy and practicality while still being a comprehensive resource (Hillerbrand et al. 1999). There are several resources available, such a paper by Sun and Liu (2003), which list out phytoplankton by genera, the shape applicable to the genus, and the appropriate equations to calculate volume.

In summary, the indicator taxa and the most abundant taxa told us opposing stories of the algal communities in Odell and Crescent lakes, however both were important metrics and can be useful in understanding these communities. In this study, the indicator taxa told of the intricacies of the non-dominant taxa, while the most abundant taxa provided insight on the lake conditions. It is known that the indicator taxa are not always the most abundant taxa (De Cáceres 2020), which is evident given the results in Table 5, but can instead tell a story about the environment they are in (De Cáceres et al. 2010). The algal communities in each lake can be used to better understand how the changes in environmental conditions within the lake led to a visible cyanobacteria bloom in Odell Lake, but not in Crescent Lake.

5.2 Water Quality Dynamics

5.2.1 Temperature and Cyanobacteria Bloom Formation

The average daily temperature recorded via sondes in the epilimnion of Odell Lake was on average 0.29 ± 0.49^{o}C warmer than that of Crescent Lake, which supports the second hypothesis that if temperature is a contributing factor to cyanobacteria blooms in these lakes, then I expect warmer temperatures in Odell Lake. This trend was also seen with the daily maximum, where the difference was on average 1.1 ± 0.95^{o}C warmer in Odell than Crescent. The depth profiles of Odell and Crescent lakes also showed the hypolimnion of Odell Lake to be warmer than Crescent Lake (Appendix). The temperature trends between Odell and Crescent Lake were very similar (Figure 12; Figure 13) and due to the high frequency of the data collection it was difficult to visually decipher the temperature difference between the two lakes (Figure 12). The difference between water temperature daily average, daily maximum, and daily minimum at Odell and Crescent lakes show that most of the time Odell Lake is warmer than Crescent Lake (Figure 14), which supports my second hypothesis. However, it is important to also determine if the warmer temperatures in Odell give any indication to supporting or potentially regulating the bloom formation in Odell Lake.

The GAMM analyses identified significant changes in temperature that could potentially influence the cyanobacteria bloom. By looking at the temperature trends defined in the GAMM, the temperature trends for difference in daily average and difference in daily maximum showed Odell became increasingly warmer than Crescent as the bloom approached (Figure 14). During the periods of significant temperature change the average difference in daily average temperature between Odell and Crescent lakes was small at 0.25 ± 0.34^{o}C. However, the average difference in maximum temperature between the two lakes was very large, at 5.73 ± 1.15^{o}C (Figure 14). It is also possible that the temperature recorded by the sondes was affected by their location within the lake. While each sonde was incased in tubing that protected them from direct exposure to the elements, the sonde in Crescent Lake was located underneath a floating dock, therefore the surrounding area was always shaded and likely cooler than Odell Lake, where the sonde was more exposed to the sun and therefore possibly experienced localized heating within the docking area that could have resulted in this temperature difference.

The minimum temperature threshold for cyanobacteria was reached in both lakes, indicating that temperature alone was not the only factor influencing cyanobacteria bloom formation. When looking at the temperature trends of each lake on its own, the water temperature maximum never reached the optimum temperature for *Dolichospermum* growth of 25^{o}C (Robarts and Zohary 1987; Konopka and Brock 1978; Chonudomkul et al. 2004; Butterwick et al. 2005; Figure 12). However, the ambient temperature at Odell Lake during the 2019 bloom had an average daily maximum temperature of 26.0^{o}C (NOAA’s National Center for Environmental Information, 2019). This maximum water temperature is an important influence in cyanobacteria bloom formation, as the temperature threshold of cyanobacteria is often higher than the competing phytoplankton (Butterwick et al. 2005; Jöhnk et al. 2008). This ability allows cyanobacteria to outcompete other phytoplankton due to the inability of other algal species to grow in high temperatures. While this is true for many lakes, this is not the case for the cyanobacteria bloom formation in Odell Lake. However, despite maximum and optimum temperature thresholds not being met in Odell or Crescent Lake, the minimum temperature in these lakes is consistently above 15^{o}C starting in July of both sample season. This is important to note because it has been recorded that cyanobacteria need a minimum temperature of 15^{o}C in order to support growth (Konopka and Brock 1978; Chonudomkul et al. 2004; Butterwick et al. 2005).

5.2.2 Impact of Nutrient Dynamics on Cyanobacteria Bloom Formation

Nutrient dynamics between Odell and Crescent lakes showed that nutrient conditions were not only more favorable to cyanobacteria in Odell Lake, but also less desirable to diatoms. The third hypothesis, which stated that if nutrients are a likely driver of blooms in Odell Lake, then there would be higher nutrient concentrations in Odell Lake and not Crescent Lake, was supported but results should be taken with caution. Since 2019 was a pilot study for DEQ, dissolved nutrients were not collected from Odell and Crescent lakes. Limited nutrient analysis in 2019 coupled with lack of phytoplankton community data in 2020 resulted in conclusions to be made based of the assumption that the lake dynamics did not differ from 2019 to 2020. While it is likely that the general behaviors of the lake were consistent, having a better understanding of the intricacies between nutrient dynamics and phytoplankton populations could offer deeper insight and stronger conclusions. Inferences can be made about the dynamics of dissolved nutrients in these lakes by examining and comparing the trends in total and dissolved nutrients in 2020. This is extremely valuable to this study because the 2019 sample season showed clearly defined peaks in both TN and TP during the bloom period in Odell Lake, while nutrients in Crescent Lake remain below detection limits (Figure 15). While the peaks coincide with the cyanobacteria bloom, they are also representative of an increase in algal biomass which was captured when looking at total nutrients in Odell Lake (Kalff 2001). This pattern of peak TN and TP during the cyanobacteria bloom were seen in the 2020 data as well, however the dissolved nutrients did not behave in the same way (Figure 15). The dissolved inorganic nitrogen dynamics in Odell Lake mirrored that of TN, all demonstrating a peak concentration during the bloom (Figure 16). The nitrogen in the water column can be attributed to the production of NH_3 by *Dolichospermum*, which is a biologically usable form of dissolved nitrogen. This was expected as the bloom was dominated by *Dolichospermum*, a nitrogen fixing cyanobacteria that is commonly found in waters with low N:P ratios (Smith 1983; Schindler 1985; Smith 1990; Reynolds 1998; Havens et al. 2003). The TN:TP ratios in both lakes indicated that the lakes were N limited (Downing and McCauley 1992). These low N:P ratios have been documented as favorable conditions to bloom formation (Smith 1983; Schindler 1997; Havens et al. 2003; Wagner and Adrian 2009). Most notably, Schindler (1977) showed how fertilization experiments with N:P mass ratios below 14 allowed for nitrogen-fixing cyanobacteria to become dominant, as well as increase the amount of nitrogen fixation that occurred within the study lake. However, this still does not fully explain why bloom conditions only existed in Odell Lake, indicating that there were a multitude of factors that can explain bloom formations.

Since N in Odell was likely a result of nitrogen fixation by the algal communities, it was important to also understand the role of P in these lakes. Prior to the bloom, the concentration of orthophosphate was relatively high in Odell Lake (Figure 16), this was important to note because orthophosphate is a dissolved inorganic phosphate (PO_4^{3-}) that is biologically available for organisms to uptake (Kalff 2001). Orthophosphate depleted to undetectable levels from late spring to the bloom period. The rapid depletion of orthophosphate in late spring/early summer indicated that there was likely some kind of spring algal bloom, which likely consisted of diatoms, that depleted the water column of key nutrients in Odell Lake (Figure 16). This is consistent with Phytoplankton Ecology Group (PEG) Model by Sommer et al. (1986). In the PEG model, Sommer et al. describe how environmental controls influence the successional patterns of phytoplankton and zooplankton in lakes. According to the PEG model, algal communities experience two peaks in algal abundance- once in the springtime and once in the summertime (Sommer et al. 1986; Smayda 1997; Sommer et al. 2012; Figure 17). The spring bloom is often dominated by fast growing algae and short lived due to grazing activities by emerging zooplankton and depletion of nutrients during this spring bloom (Sommer et al. 1986; Lampert et al. 1986; Balvey et al. 1990; Kalff 2001). In 2020, the nutrient data collected at Odell Lake showed the tail end of this spring bloom as SRP concentration depleted to non-detectable levels at the beginning of the sample season (Figure 16). This, in combination with increased temperatures and the establishment of stratification (Balvay et al. 1990), could have led to a spring bloom crash, known as the clear water phase. During the clear water phase nutrients began to build back up and zooplankton became food limited (Sommer et al. 1986; Lampert et al. 1986; Kalff 2001; Sommer et al. 2012). Dissolved forms of N, TN, and TP increased in 2020, which was likely related to the increase in nitrogen- fixing cyanobacteria abundance and increased biomass from the cyanobacteria bloom (Figure 16). The PEG model suggests that the flux in nutrients and the reduced grazing pressure allows for cyanobacteria and other inedible phytoplankton to increase, which results in cyanobacteria blooms (Sommer et al. 1986; Sommer et al. 2012). The bloom conditions in Odell Lake likely experienced this reduction in grazing pressure, and despite the lack of increased SRP during the clear water phase, the nitrogen fixing abilities of *Dolichospermum* allowed for bloom conditions to take off in 2019 and 2020.

5.3 Future Research: Other Contributing Factors to Cyanobacteria Bloom Formation

It is well researched that nutrients and temperature are not the only contributing factors to cyanobacteria bloom formation, and that grazer communities are influential to cyanobacteria blooms as well. Sommer et al. (1986) reported that grazing is an important biological control to algal communities in eutrophic lakes in the summer. While this study did not identify nor examine community dynamics beyond the phytoplankton communities, previous studies and documentation of zooplankton and fish communities can allow for hypotheses and predictions.

There is a crucial need for understanding the trophic structure in Odell and Crescent lakes. The general food web of both Odell and Crescent lakes can be inferred based upon the information known about the fish, zooplankton, and phytoplankton communities (Figure 18). Primary producers, consisting of algae and macrophytes, rely upon nutrients essential to phytoplankton success, such as ammonium (NH_4^+), orthophosphate (PO_4^{3-}), silica, etc. Phytoplankton are preyed upon by zooplankton, such as *Daphnia* and chironomids which have been documented in Odell Lake in previous studies (Fies et al. 1996; Eilers et al. 2005). Many of the planktivorous fish documented in Odell and Crescent lakes are planktivorous only during their early years, such as kokanee. Past research has indicated that larger, adult kokanee shift from planktivorous diet in their youth, consuming primarily macroinvertebrates and zooplankton, to a more piscivorous diet (Shedd et al. 2015). From what is known of Crescent Lake and Odell Lake, the organisms that comprise the lake communities are very similar. However, the phytoplankton communities summarized in this paper indicate that the interactions among higher trophic level organisms differ. These gaps in our understanding further stresses the need for in depth understanding of the lake community dynamics in Odell and Crescent lakes and how they differ.

The food web in Figure 18 is meant to serve as a simplified version of the community structure and ecosystem found in Odell and Crescent lakes. Of course, there are more in-depth interactions between these organisms, such as redistribution of nutrients into the system from excretion, etc. Another example would be the interactions between zooplankton, including predation of small zooplankton by larger zooplankton. It is also important to note this food web does not include macrophytes, as there is limited macrophytes in each of the lakes, but this is still an important component of the ecosystem. Top-down controls, such as those mentioned in Section 2.2 of this paper, may impact phytoplankton communities in Odell and Crescent lakes. Top-down control of planktivorous fish on phytoplankton communities has been documented in many lakes, including in Diamond Lake, Oregon. Diamond Lake is a naturally fishless lake but has experienced fish stocking since the early 1900s. The introduction of tui chub, an omnivorous cyprinid fish that was introduced to the lake as discarded live bait, has largely impacted phytoplankton communities and cyanobacteria blooms (Eilers et al. 2007). The presence of tui chub in Diamond Lake greatly altered the community structure, and ultimately led to the proliferation of cyanobacteria. Tui chub fed primarily on benthic macroinvertebrates and large zooplankton, which decreased grazing pressures on all phytoplankton communities (Eilers et al. 2007). Eilers et al. argue that reduced grazing pressure and P additions enrichment from fish carcasses, which resulted from rotenone treatments, is likely responsible for the overall increase in phytoplankton abundance especially regarding N-fixing cyanobacteria (Eilers et al. 2008).

Sommer et al. (2012) describe how controls and limiting factors of phytoplankton differ, depending on the trophic status of the lake (Figure 17). Sommer et al. (2012) explain that phytoplankton in eutrophic lakes, such as Odell Lake, are more influenced by grazing communities and nutrient limitation during summer months, whereas physical lake controls (light availability, mixing, etc.) play a more significant role in phytoplankton dynamics in the spring and winter months. These influences are similar in oligotrophic systems, such as Crescent Lake, although nutrient limitations have a stronger influence in low nutrient lakes (Figure 17). Sommer et al. continue to explain that during this time, eutrophic systems typically experience reduced biomass of zooplankton, and subsequently lower grazing levels, as a result of die offs and/or population reductions following collapse of spring diatom blooms. In oligotrophic lakes, however, the zooplankton communities reach peak biomass levels and thus higher grazing rates occur in these systems. Future research should examine the findings in the Plankton Ecology Group model and determine how Odell and Crescent Lakes compare (Sommer et al. 1986; Sommer et al. 2012)

Another mechanism that could have largely impacted cyanobacteria blooms in Odell Lake is stratification. In 2019, depth profiles in Odell and Crescent lakes collected via data sondes recorded that Odell Lake was stratified as early as 28 June 2019 (Appendix), which was consistent with historical records of late June stratification (Larson 1970). As previously mentioned, the samples for Odell and Crescent lakes were taken at the surface and in areas with shallow depths. The shallow depths of the cove combined with the orientation of the lake made the sampling location very susceptible to mixing. The wind patterns experienced on Odell Lake are also known to create surface and internal seiches at Odell Lake, which may be responsible for release of nutrients from the hypolimnion. The depth profiling, data sondes recorded peak phycocyanin RFU in the hypolimnion and peak chlorophyll RFU in the metalimnion (Appendix). While mixing is not normally a favorable condition for cyanobacteria bloom development, it could be an important dynamic for nutrient cycling that can aid in the proliferation of cyanobacteria. Carpenter (1989) describes the importance of understanding the three different scales at which cyanobacteria blooms form- at the watershed level, the lake level, and the different stratified layers. The hypolimnion is especially important, as cyanobacteria resting cells often precede any surface bloom by 1 to 16 weeks (Carpenter 1989). In the hypolimnion, P can be available to cyanobacteria due to the reducing environment often found in deep hypolimnion, as explained in Section 2.2 of this paper. Future research should aim to better understand how the wind patterns and internal mixing interact with nutrient cycling in order to better understand what, if any, influence this has on cyanobacteria blooms in Odell Lake.

6. Conclusions and Management Implications

The results of this study imply that temperature and nutrients play a key role in cyanobacteria bloom formation Odell Lake. Temperatures between Odell and Crescent lakes showed significant warming in Odell Lake compared to Crescent Lake directly prior to the 2019 cyanobacteria bloom. The orientation of Odell Lake also likely aids in the formation of cyanobacteria blooms. Northwest winds move across the lake and push water towards the eastern shoreline where many coves, such as Odell Lake's sampling location at Sunset Cove, provide optimal shelter and localized warming for cyanobacteria blooms to flourish. When looking at the 2020 temperature data between the two lakes, Odell Lake does not exhibit consistent warmer temperatures than Crescent Lake as observed in 2019 (Figure 14). Phycocyanin relative fluorescence was also higher in 2020 than 2019 (Figure 15). It is likely that temperature aids in cyanobacteria bloom intensity, but other factors are likely more important in terms of bloom formation.

The temporal pattern of TP and TN in 2019 and 2020 were very similar, with peak nutrient concentrations at Odell Lake that occurred during the cyanobacteria blooms (Figure 15). Due to the similarities in total nutrients between the two years, I operated under the assumption that the dissolved nutrients behaved similarly in 2019 and 2020. Orthophosphate in Odell Lake was highest prior to the bloom in late spring 2020, which created favorable conditions to the nitrogen fixing *Dolichospermum* population and ultimately contributed to cyanobacteria bloom development in Odell Lake. One of the key differences between Odell and Crescent lake’s nutrient dynamics is the difference in dissolved silica concentrations (Figure 15). Throughout the 2020 study period dissolved silica in Crescent Lake was on average 6.26 times greater than that in Odell Lake. Diatoms are silica limited organisms, as their cell walls are composed of silica (in the form of silica dioxide). The low levels of dissolved silica in Odell Lake were a hinderance on diatom abundance which also likely aided in the difference of the phytoplankton communities in the two lakes. Understanding the source of the nutrients will be a crucial next step in understanding and ultimately managing cyanobacteria blooms in these lakes.

While this study gave context to potential factors that influence cyanobacteria blooms in Oregon Lakes, which is advantageous for cyanobacteria bloom management, there is still much that can be done to better understand cyanobacteria blooms across Oregon. In recent years there has been an increase in ongoing research and advances in the understanding of cyanobacteria blooms across the State of Oregon, including genetic identification of gene toxins in cyanobacteria through quantitative polymerase chain reaction analysis (Darling and Wirtis 2022, 21:00). I recommend that state agencies also invest in understanding phytoplankton community dynamics, similar to the analysis performed in this study. DEQ reported that there are 132 waterbodies of concern for cyanobacteria bloom formation in Oregon (DEQ 2011). While characterizing phytoplankton communities in each of these Oregon waterbodies is likely not logistically or financially possible, I would recommend this be done for any lake listed as a concern that also serves as a drinking water source. I would also recommend that future management strategies adjust their sampling frequency, especially in comparison to this study. Due to the possible influence thermal stratification may have on cyanobacteria blooms and the fact that there are likely spatial differences in phytoplankton communities, I would recommend that future sampling occur on a less frequent basis at more locations across each lake. Depth integrated samples should also be collected in order to identify and characterize phytoplankton communities in the epilimnion, metalimnion, and hypolimnion. Characterizing how algal communities shift on a temporal and spatial scales across these lakes of concern can allow for better management and mitigation of cyanobacteria blooms across Oregon.

Tables

Table 1. Cyanotoxins and their impacts to human health. The Oregon Recreational Use Value is the concentration of toxin that must be present in a water body for the State of Oregon to declare a recreational advisory.

Toxin	**Oregon Recreational Use Value[1]**	**Common genera**	**Toxic impact**
Microcystin	8 µg/L	*Microcystis, Anabeana, Dolichospermum, Leptolyngbya, Nostoc, Phormidium, Plantothrixm, Synechococcus*	Liver and kidney damage, gastroenteritis, tumour promotion, reduced DNA repair and reproductive toxicity
Saxitoxins	8 µg/L	*Aphanizomenon, Cuspidothrix, Cylindrospermopsis, Dolichospermum*	Paraesthesia, numbness, paralysis, and respiratory failure
Anatoxin- a	15 µg/L	*Anabaena, Aphanizomenon, Cuspidothrix, Dolichospermum, Oscillatoria, Phormidium*	Loss of coordination, muscle tremors and respiratory failure
Anatoxin- a (s)	15 µg/L	*Dolichospermum*	Salivation, incontinence, muscle tremors and respiratory failure
Cylindrospermopsins	15 µg/L	*Cylindrospermopsis, Anabaena,Aphanizomenon, Chrysosporum, Raphidiopsis*	Damage to multiple organs, gastroenteritis and genotoxicity
Nodularins	n/a	Nodularia	Same effects as microcystins plus weak carcinogenicity

Continued next page

Table 1. Cyanotoxins and their impacts to human health. The Oregon Recreational Use Value is the concentration of toxin that must be present in a water body for the State of Oregon to declare a recreational advisory (continued).

Toxin	**Oregon Recreational Use Value[1]**	**Common genera**	**Toxic impact**
Beta- N-methylamino- l-alanine (BMAA)	n/a	Microcystis and Nostoc; possibly widespread among cyanobacteria, but no consensus yet (Sources)	Loss of coordination, muscle atrophy and possible contributions to neurodegenerative diseases (for example, amyotrophic lateral sclerosis and Alzheimer disease)
Lipopolysaccharides		All cyanobacteria	Skin irritation, fever and gastrointestinal upset

[1] Oregon Health Authority (2019); Carmichael (1994); Sivonen (2009)

Table 2. Morphometry and watershed characteristics of Odell Lake and Crescent Lake.

	Odell Lake	**Crescent Lake**
Lake Characteristics		
Elevation (m)	1459	1475
Surface Area (sq. km)	14.6	16.2
Maximum Depth (m)	86	81
Mean Depth (m)	40	38
Thermocline Depth (m)	3.0 -10.0	15.0 -18.0
Trophic Status	Mesotrophic	Ultraoligotrophic/ oligotrophic
Watershed Characteristics		
Evergreen Forest (%)	80.4	83.0
Developed Land (%)	1.0	0.08

[1] Johnson et al. (1985); Eilers et al. (2005); USDA Forest Service (n.d.)

Table 3. List of variables collected by Oregon Department of Environmental Quality and their respective methods.

Variables	**CAS**	**Method context**	**Method ID**	**MDL**
Total Nitrogen	7727-37-9	APHA	4500-N-C	0.05 mg/L
Chlorophyll *a*	479-61-8	APHA	10200-H	0.1 µg/L
Total Phosphorus	7723-14-0	APHA	4500-P-E	0.01 mg/L

Table 4. Summary of water quality variables in Odell and Crescent lakes during the 2019 sample season. Data were recorded via sondes at a single point in each lake. The data were recorded at 15- minute intervals from 26 June 2019 to 20 September 2019.

	Average (± SD)		Maximum		Minimum	
	Crescent	Odell	Crescent	Odell	Crescent	Odell
Temperature (°C)	19.41 ± 1.56	18.83 ± 1.74	22.14	23.54	14.86	13.67
Dissolved Oxygen (%)	107.06 ± 1.91	105.69 ± 4.75	110.1	138.5	99.4	85.3
Dissolved Oxygen (mg/L)	8.21 ± 0.27	8.25 ± 0.58	8.95	10.37	7.75	6.54
pH	7.79 ± 0.07	8.71 ± 0.41	8.04	9.92	7.49	7.29
Conductivity (µS/cm)	25.76 ± 0.44	35.40 ± 1.06	27.2	45.00	24.80	32.9
Chlorophyll (RFU)	0.15 ± 0.02	0.71 ± 0.36	0.21	4.87	0.09	0.06
	0.12 ± 0.03	0.77 ± 1.81	0.37	22.06	-0.03	-0.03
Total Nitrogen (mg/L)	0.08 ± 0.01	0.44 ± 0.58	0.10	1.75	0.06	0.15
Total Phosphorus (mg/L)	<0.01	0.03 ± 0.03	<0.01	0.08	<0.01	<0.01
Chlorophyll-*a* (µg/L)	0.40 ± 0.10	8.99 ± 19.17	0.50	52.4	0.30	0.50

Table 5. Indicator taxa of Odell Lake and Crescent Lake, along with the relative abundance of each taxon in their given group. Groupings were taken from the sequential cluster analysis. Indicator taxa determined using the labdsv package in R (Roberts 2019).

	Relative Abundance (%)	**Indicator Value**	**P- Value**
Odell Lake			
Group 1			
Dinobryon	5.810	0.998	0.001
Asterionella	2.000	0.990	0.002
Tabellaria	4.980	0.966	0.003
Cocconeis	0.210	0.660	0.035
Centric diatoms	0.940	0.545	0.020
Group 2			
Dolichospermum sp.1	98.80	0.974	0.04
Crescent Lake			
Group 2			
Centric diatoms	7.230	0.714	0.002
Group 3			
Asterionella	15.890	0.665	0.0200

Figures

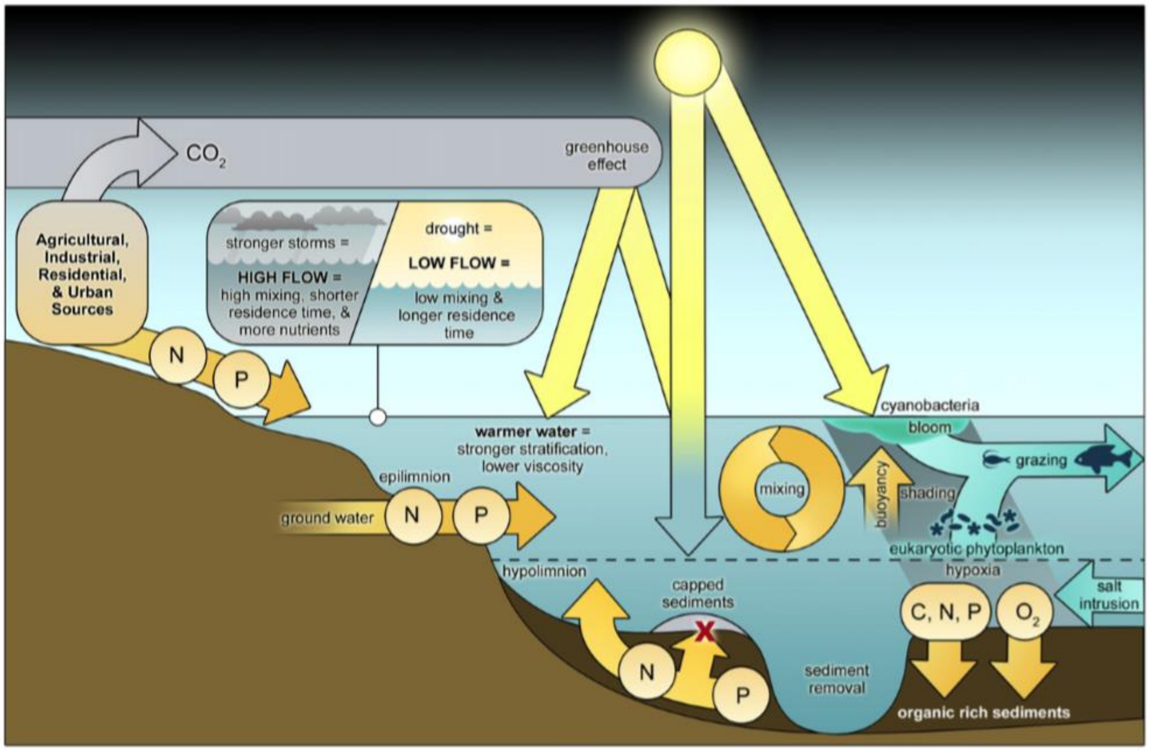

Figure 1. Conceptual diagram of the factors that influence and trigger cyanobacteria harmful algal blooms in freshwater systems (Paerl et al. 2011).

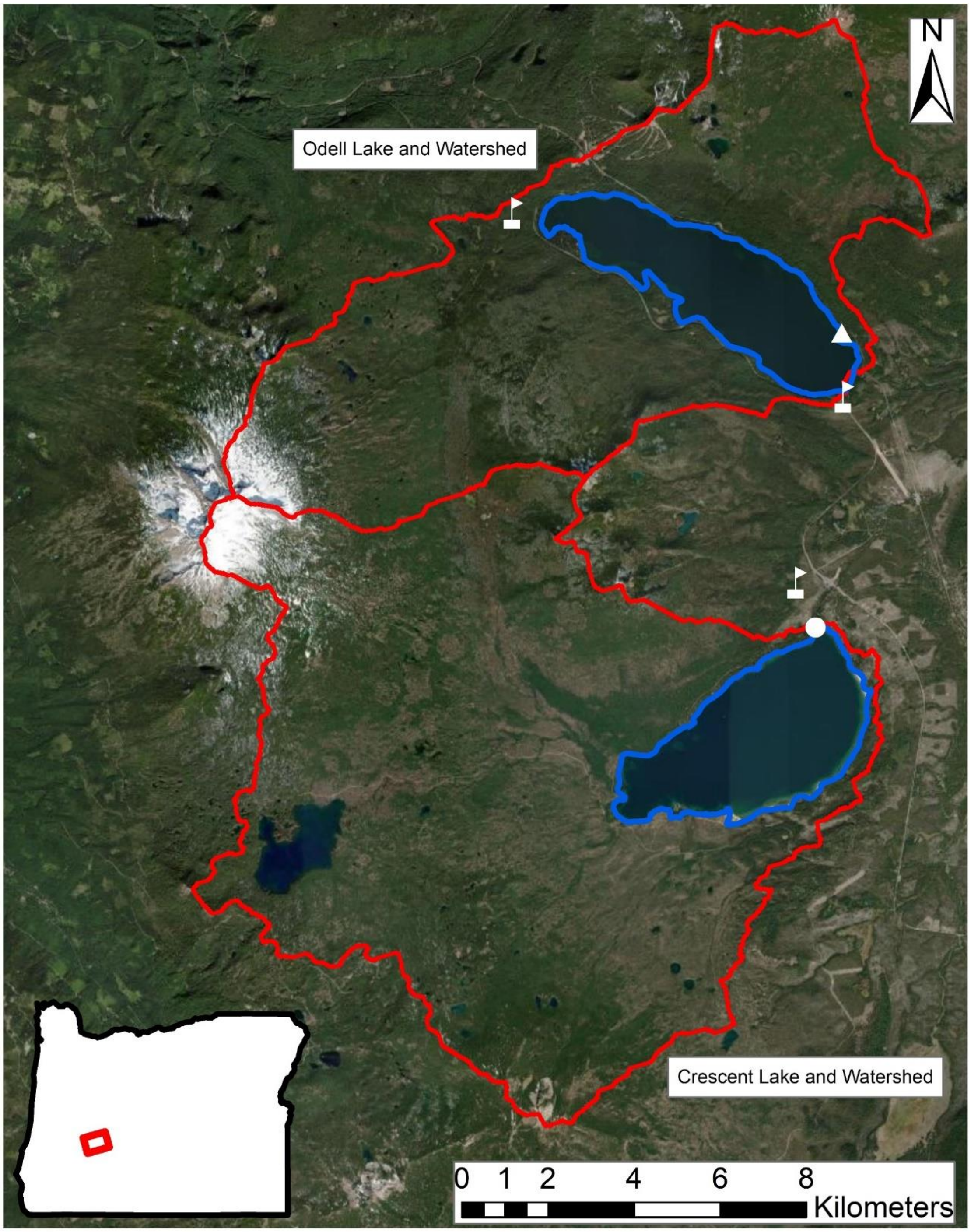

Figure 2. A map of the study area in the High Cascades, Oregon, USA. Both lakes are outlined in blue, with their watersheds in red. The sonde location on Odell Lake is represented by a triangle (Δ**)** and Crescent Lake is represented by a circle (○). Weather stations are also shown as flags on the map.

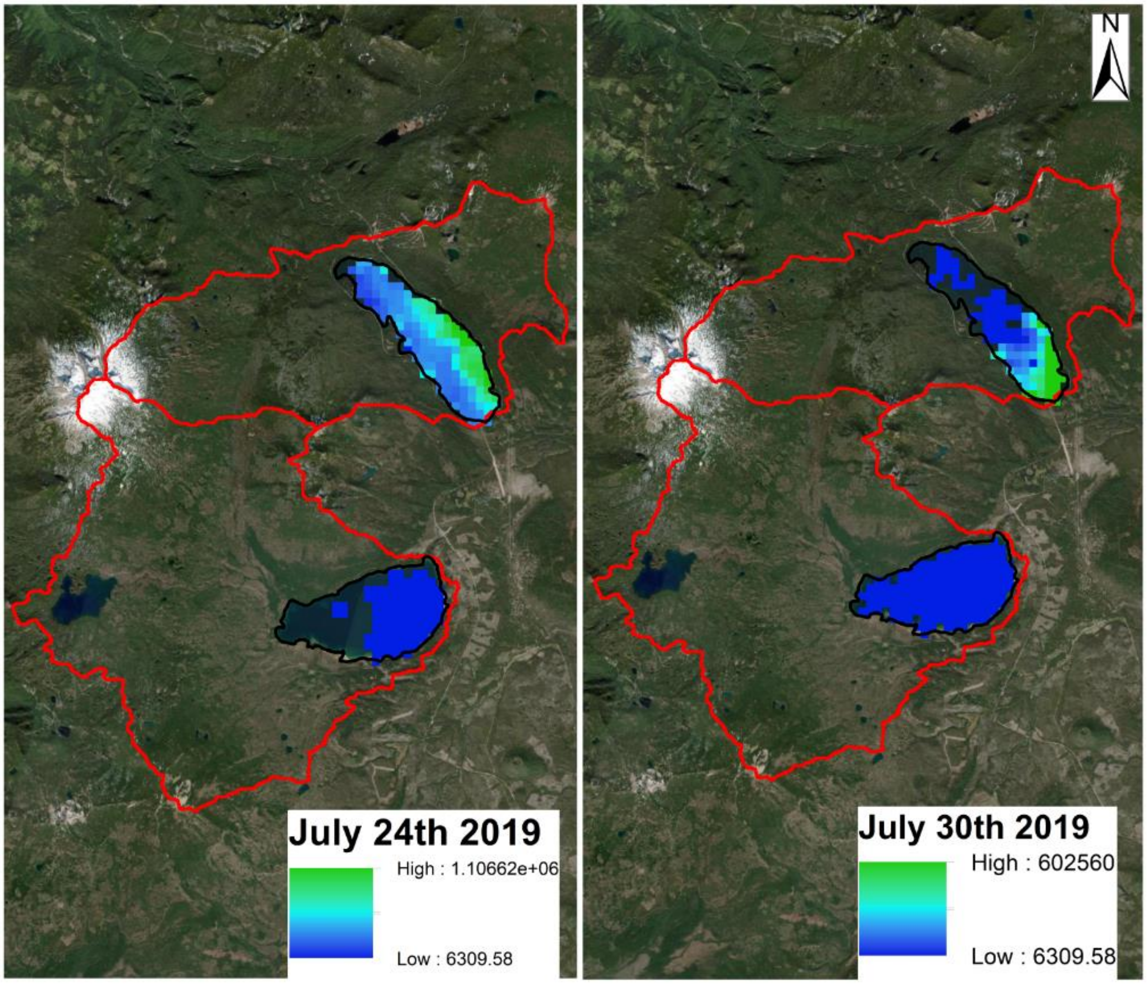

Figure 3. Map of the study area, Odell and Crescent lakes, during the bloom period on 24 July 2019 and 30 July 2019. The color gradient indicates cyanobacteria abundance in cells per milliliter recorded by the EPA's Cyanobacteria Assessment Network. The low value of 6309.58 cells per milliliter is considered a non-detect. The satellite data shows that the cyanobacteria cells aggregate along the eastern shoreline of Odell and move from the northeast to the southeast end which is near the sonde and grab sample location.

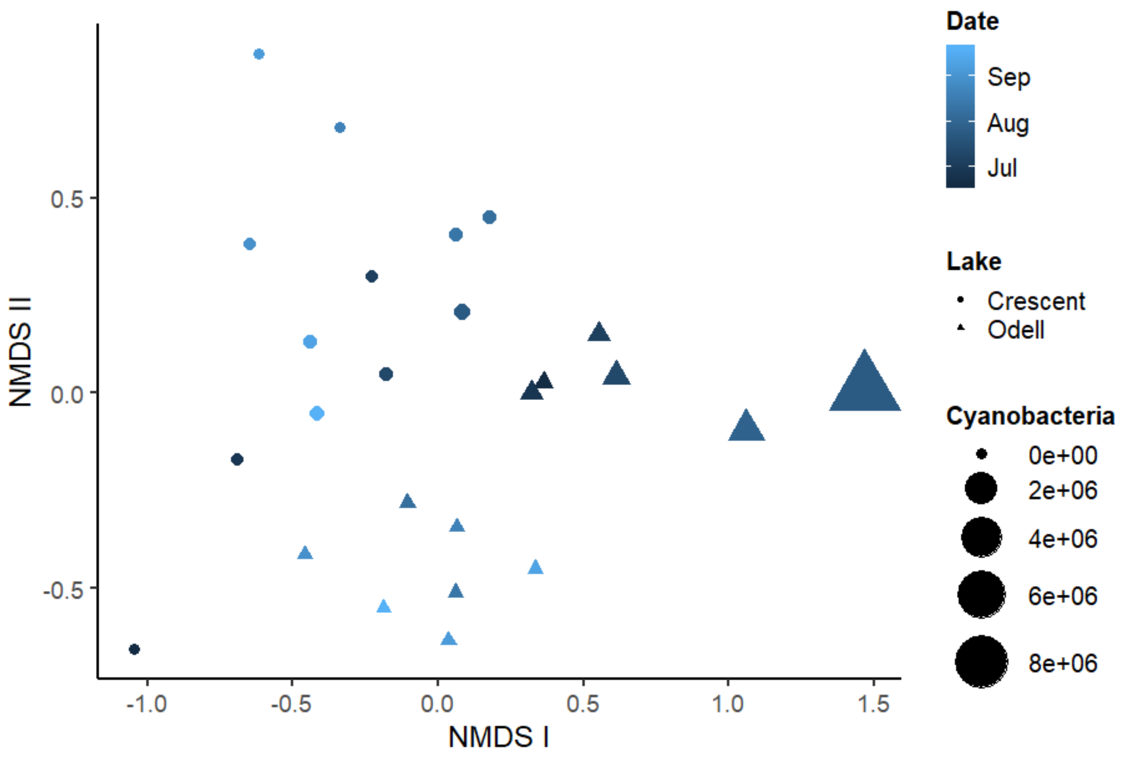

Figure 4. Two-dimensional ordination plot using a non-metric Multidimensional Scaling of both Odell Lake (triangles) and Crescent Lake (circles) represents algal communities based on genus level identifications from each sampling date. The stress value for this NMDS is 10.16. Color gradient shows temporal scale, while size scaling that represents cyanobacteria cell abundance (cells/mL).

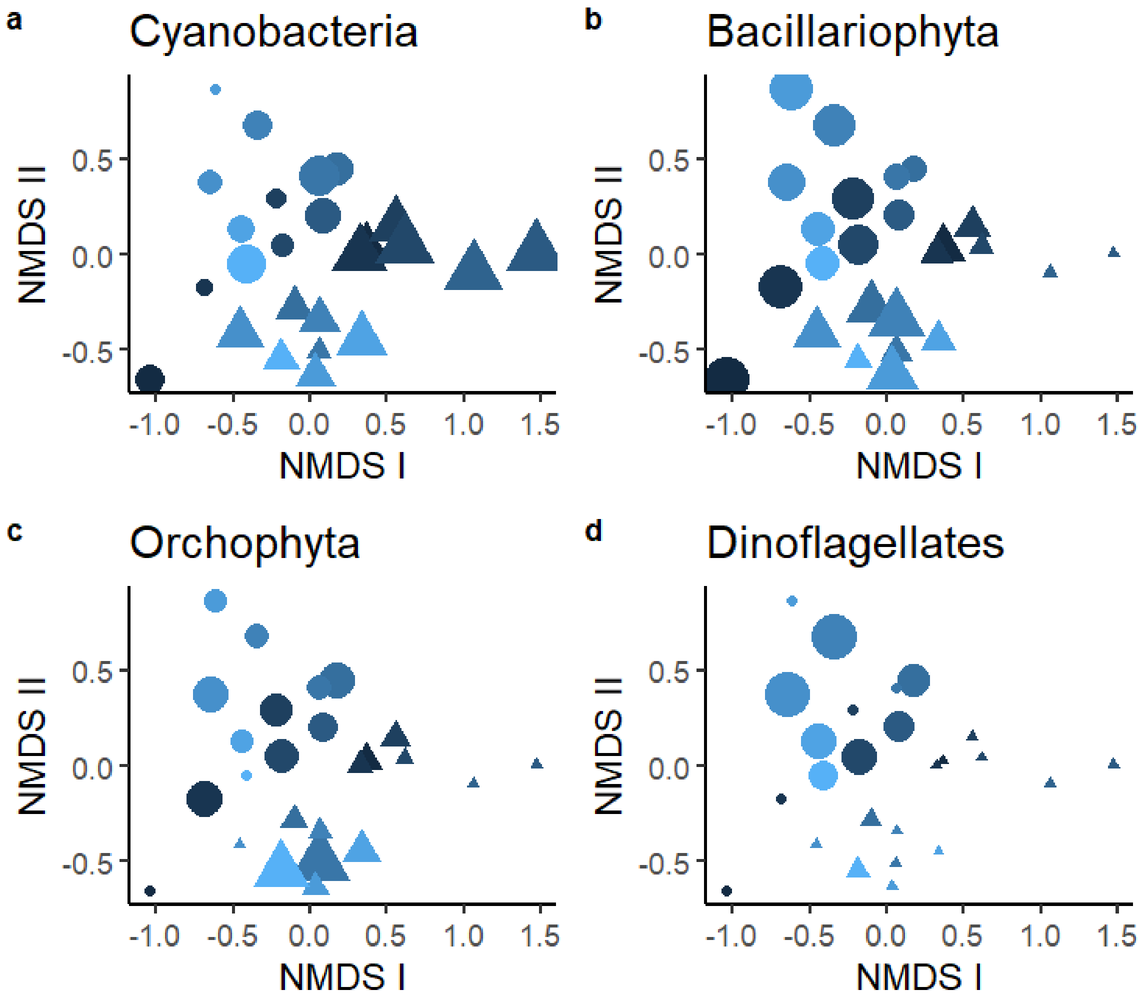

Figure 5. Two-dimensional ordination plot using a non-metric Multidimensional Scaling of both Odell Lake (triangles) and Crescent Lake (circles) represents algal communities based on genus level identifications from each sampling date. The stress value for this NMDS is 10.16. Color gradient shows temporal scale, while size scaling that represents the relative abundance of (a) Cyanobacteria, (b) Bacillariophyta, (c) Orchophyta, and (d) Dinoflagellates.

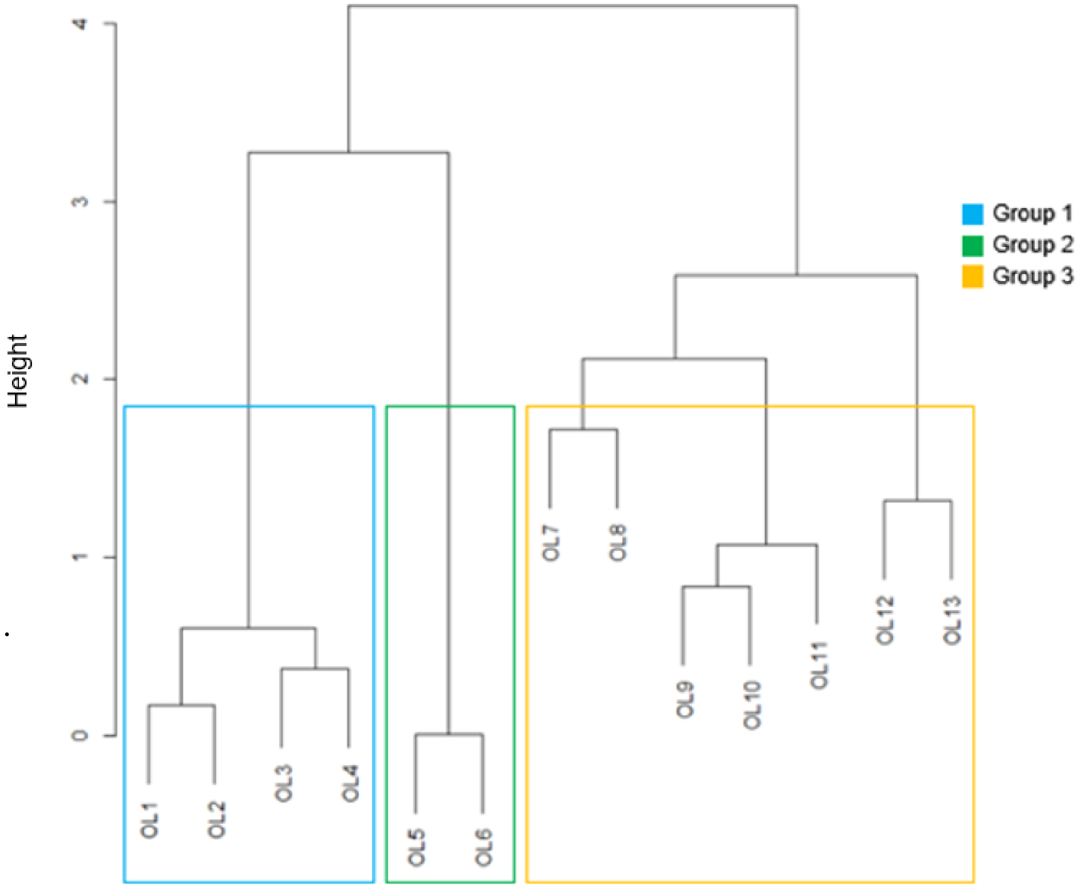

Figure 6. The dendrograms with the groupings for Odell Lake (OL) determined by the sequential cluster analysis shows Group 1 (Pre-bloom), Group 2 (Bloom), and Group 3 (Post- Bloom). Each branch labeled OL1-OL13 represents the number sampling event for the 2019 season, with OL1 being the first sampling event on 19 June 2019 and so on.

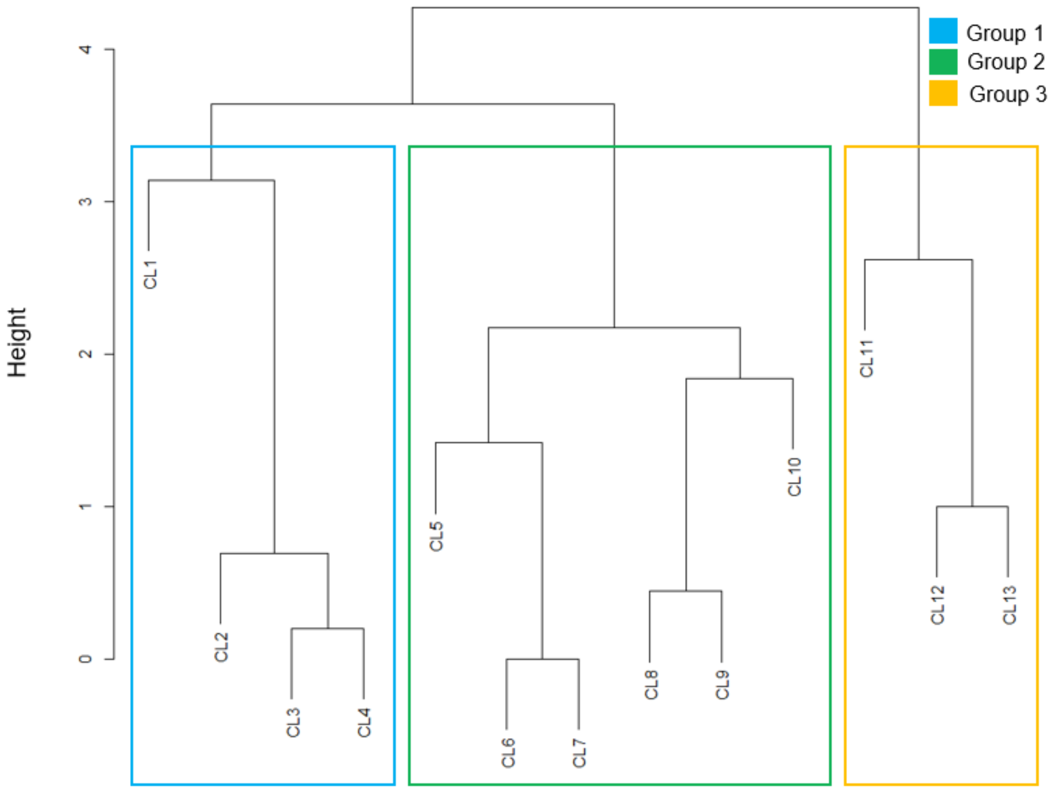

Figure 7. The dendrograms with the groupings for Crescent Lake (CL) determined by the sequential cluster analysis shows Group, Group 2, and Group 3. Each branch labeled CL1-CL13 represents the number sampling event for the 2019 season, with CL1 being the first sampling event on 19 June 2019 and so on.

Figure 8. Visual change in water quality from cyanobacteria harmful algal Bloom taken at Sunset Cove sampling location (43.562262 N, -121.964550 W) on Odell Lake on July 5, 2019 (left) before the onset of a cyanobacteria bloom and on July 23, 2019 (right) at the peak of the cyanobacteria bloom.

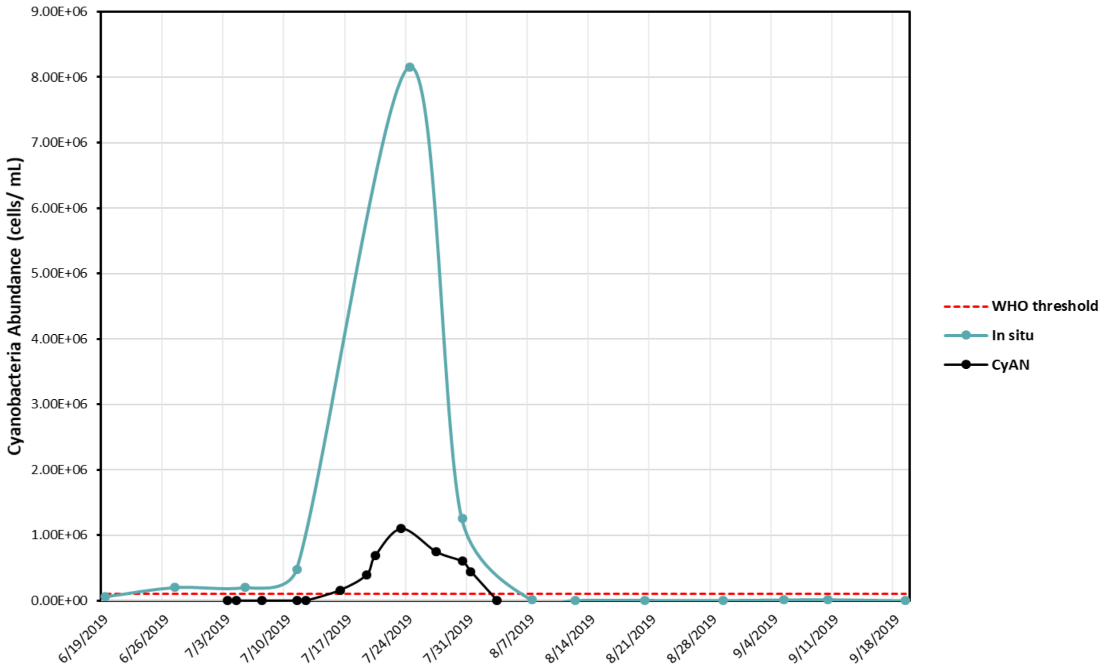

Figure 9. Cyanobacteria absolute abundance (cells/mL) recorded via microscopy and the cell counts determined via satellite data using CyAN’s algorithms during the 2019 sample season. The World Health Authority (WHO) definition or threshold for classification of a Cyanobacteria bloom is 100,000 cells/ mL (Chorus and Bartram 1999).

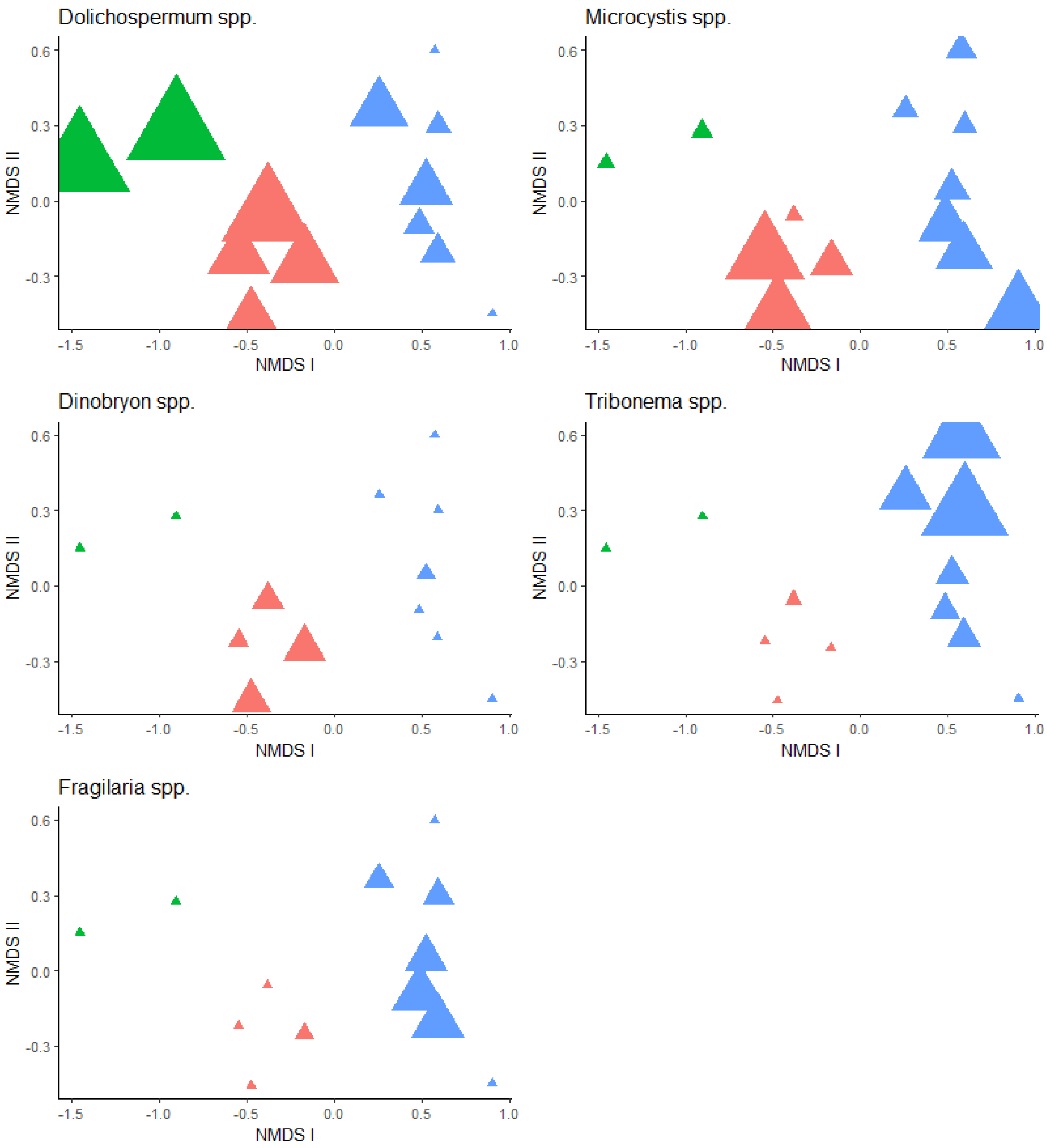

Figure 10. Nonmetric multidimensional scaling ordination plot for Odell Lake, showing the relative abundance of the most dominate taxa in each grouping. The dominate taxa in the Pre-Bloom phase include *Dolichospermum sp.1* (41.71%), *Microcystis* (40.67%), *Dinobryon* (5.81%). The dominant taxon in the Bloom phase is *Dolichospermum sp.1* (98.80%). The Post-Bloom phase consists of *Tribonema* (39.90%), *Microcystis* (10.14%), *Dolichospermum sp.1* (9.87%), and *Fragilaria* (8.96%).

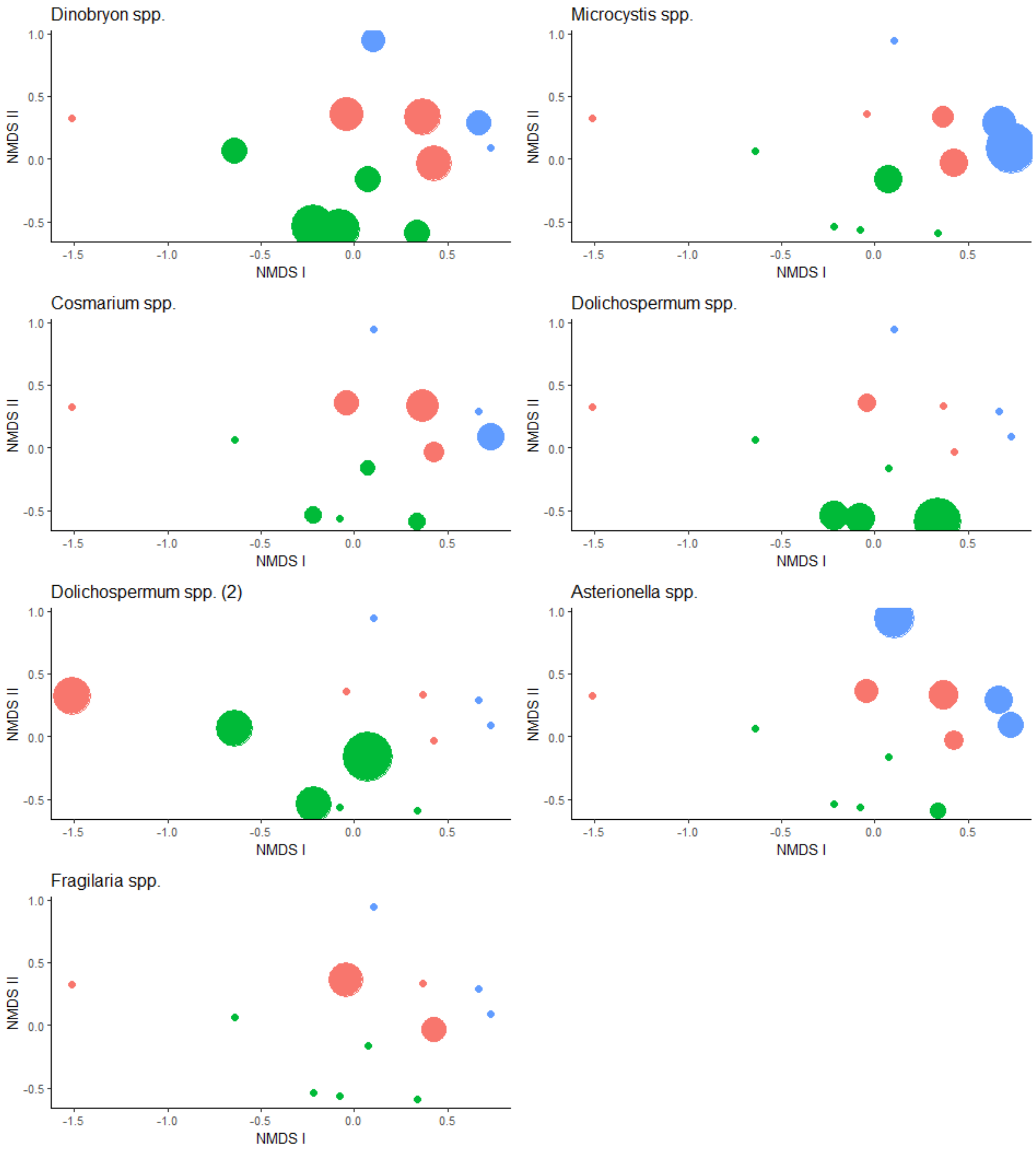

Figure 11. Nonmetric multidimensional scaling ordination plot for Crescent Lake, showing the relative abundance of the most dominate taxa in each grouping. The dominate taxa in the Pre-Bloom phase include *Dinobryon* (26.5%), *Microcystis* (10.7%), *Cosmarium* (9.81%). The dominant taxa in the second phase were *Dolichospermum sp.1* (25.9%), *Dinobryon* (24.1%), *Dolichospermum sp.2* (21.1%). The last phase consisted of *Microcystis* (36.4%), *Asterionella* (15.9%), and *Dinobryon* (5.96%).

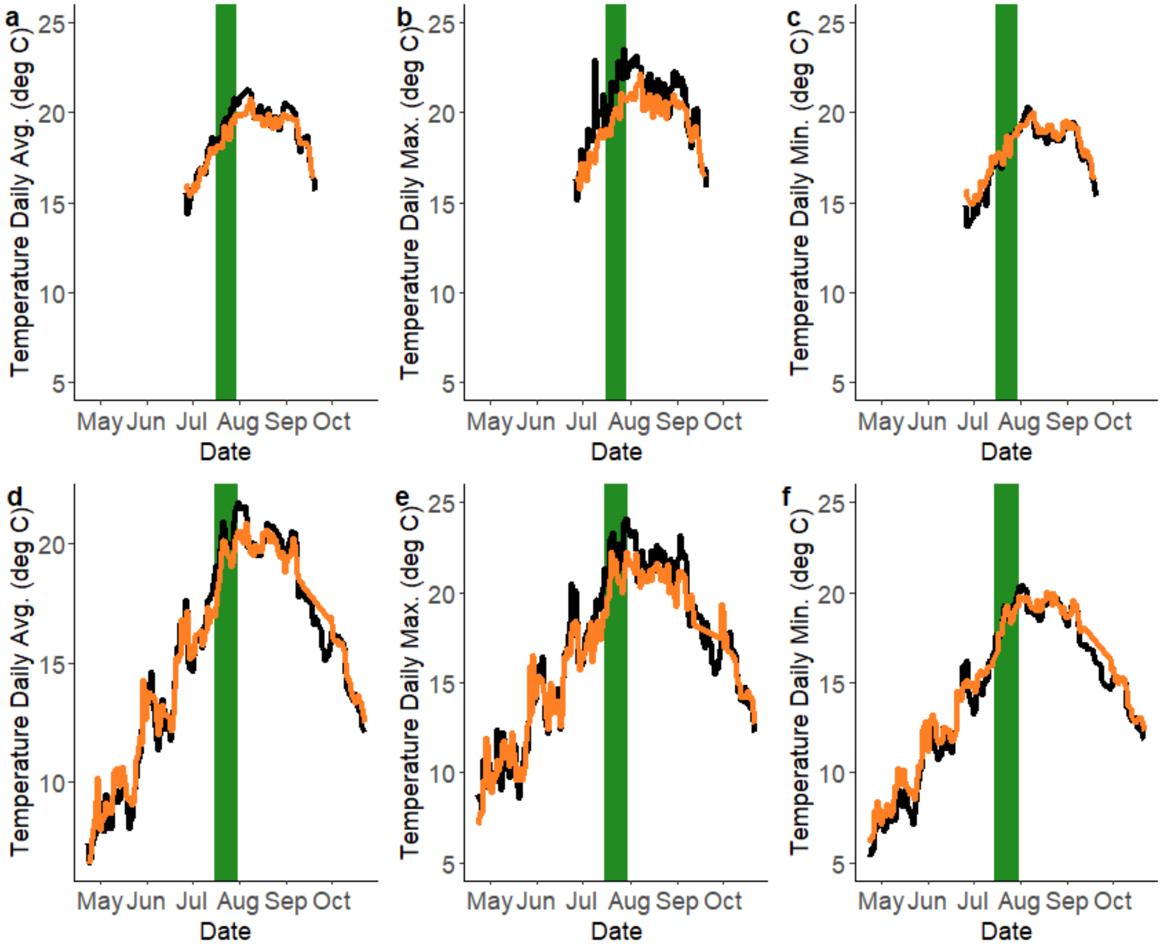

Figure 12. Water temperature in degrees Celsius for Odell Lake (black) and Crescent Lake (orange). Plots from left to right show raw temperature data in degrees Celsius (deg C) recorded by the sonde at each lake, along with daily average (avg.), daily maximum (max.), and daily minimum (min.) for both 2019 (a-c) and 2020 (d-f) sample season. The green shaded area shows the cyanobacteria bloom defined in this study using satellite detection of cyanobacteria.

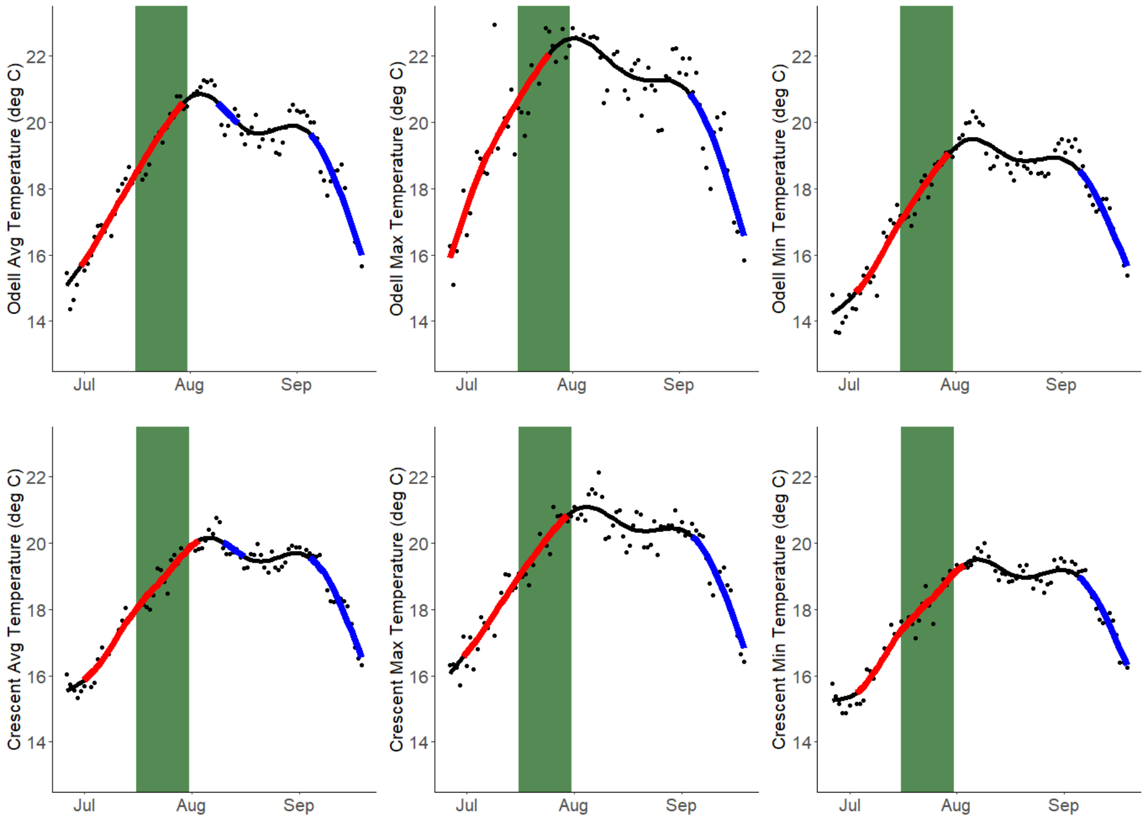

Figure 13. Generalized additive mixed model results indicating the model (black line) the 2019 water temperature in degrees Celsius (deg C) trends at Odell Lake (a-c) and Crescent Lake (d-f). The temperature daily average (avg), daily maximum (max), and daily minimum (min) in lake are shown above as black dots, with blue lines indicating periods of significant ($p<0.05$) increase along the model and red lines as significant ($p<0.05$) declines along the model.

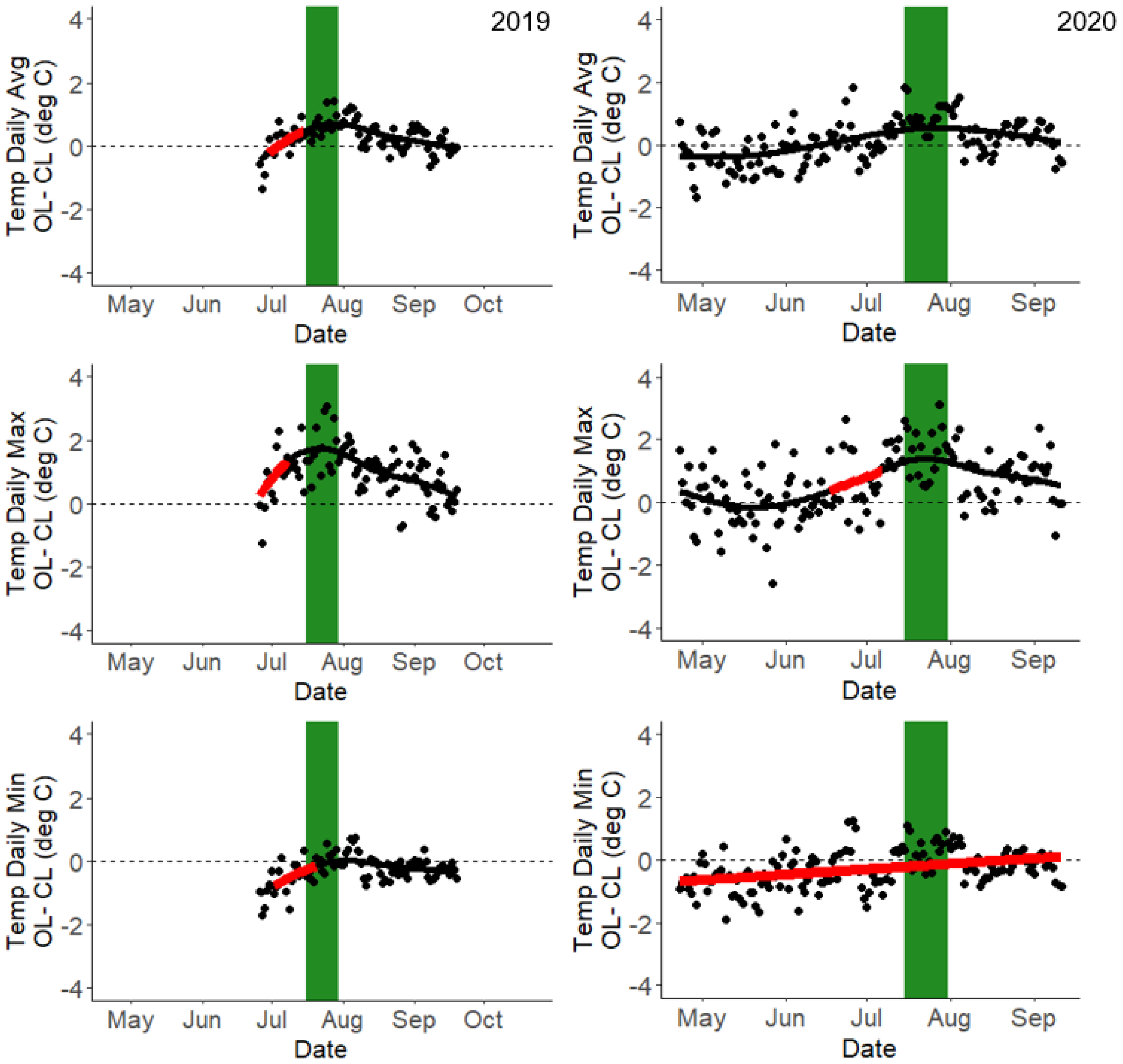

Figure 14.Generalized additive mixed model results indicating the model (solid black like) of temperature differences between Odell Lake (OL) and Crescent Lake (CL). The temperature (temp) summary statistics used for the differences were daily average (avg), daily maximum (max), and daily minimum (min). When points are above the dashed line (y=0), the temperature is greater in Odell Lake and when points are below, the temperature is greater in Crescent Lake. The red line indicates periods of significant (p<0.05) increase along the model for each temperature summary statistic, and there are no periods of significant decrease in temperature. The green shaded area shows the cyanobacteria bloom defined in this study using satellite detection of cyanobacteria.

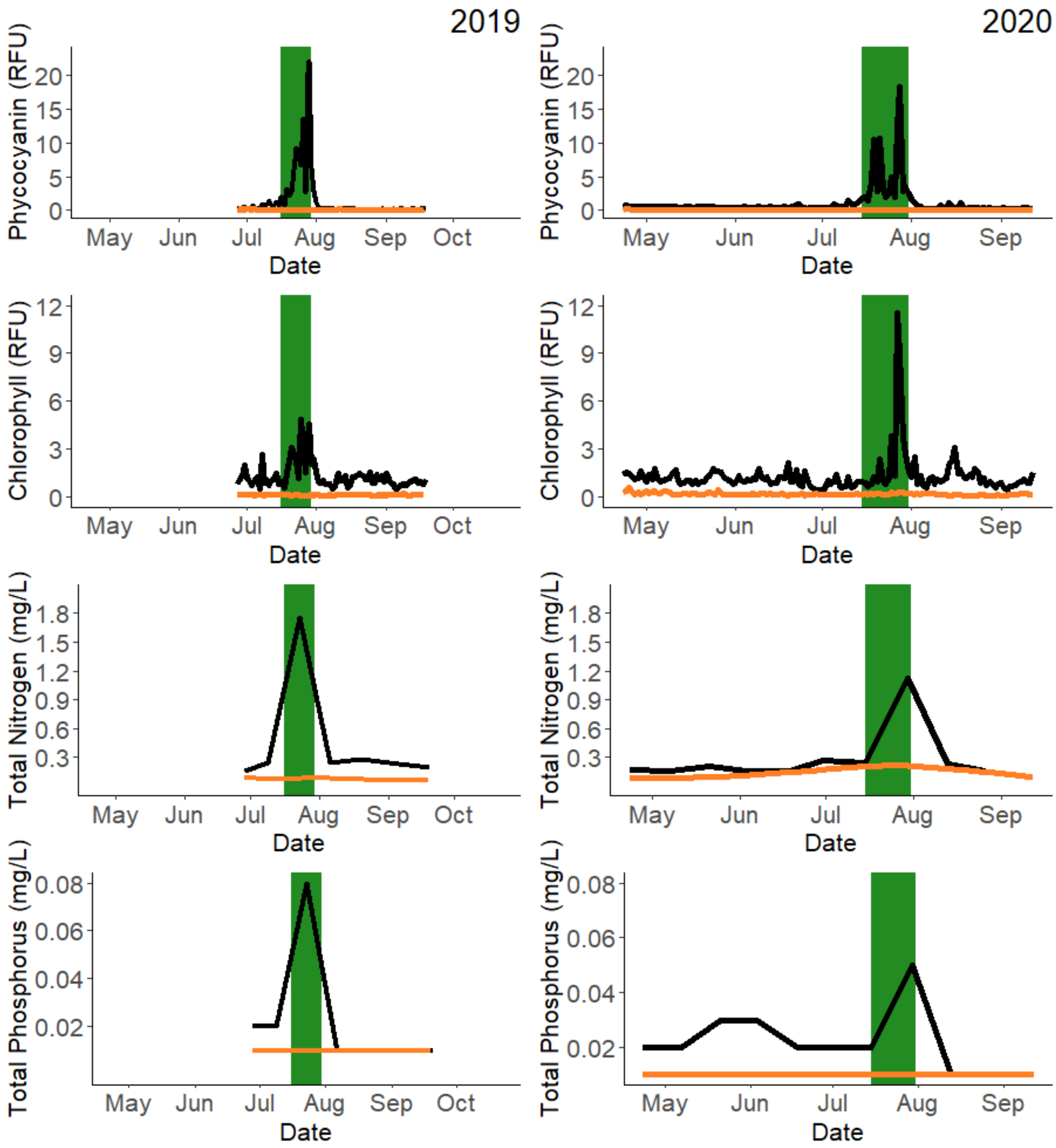

Figure 15. Temporal pattern of total nitrogen (TN) and total phosphorus (TP) during the 2019 in Odell Lake and Crescent Lake. Phycocyanin (RFU) is an algal pigment associated with cyanobacteria, and chlorophyll (RFU) is an algal pigment that encompasses all photosynthetic organisms. The green shaded areas, refers to the time period where cyanobacteria were detected in Odell Lake by satellites and recorded by the EPA's Cyanobacteria Assessment Network.

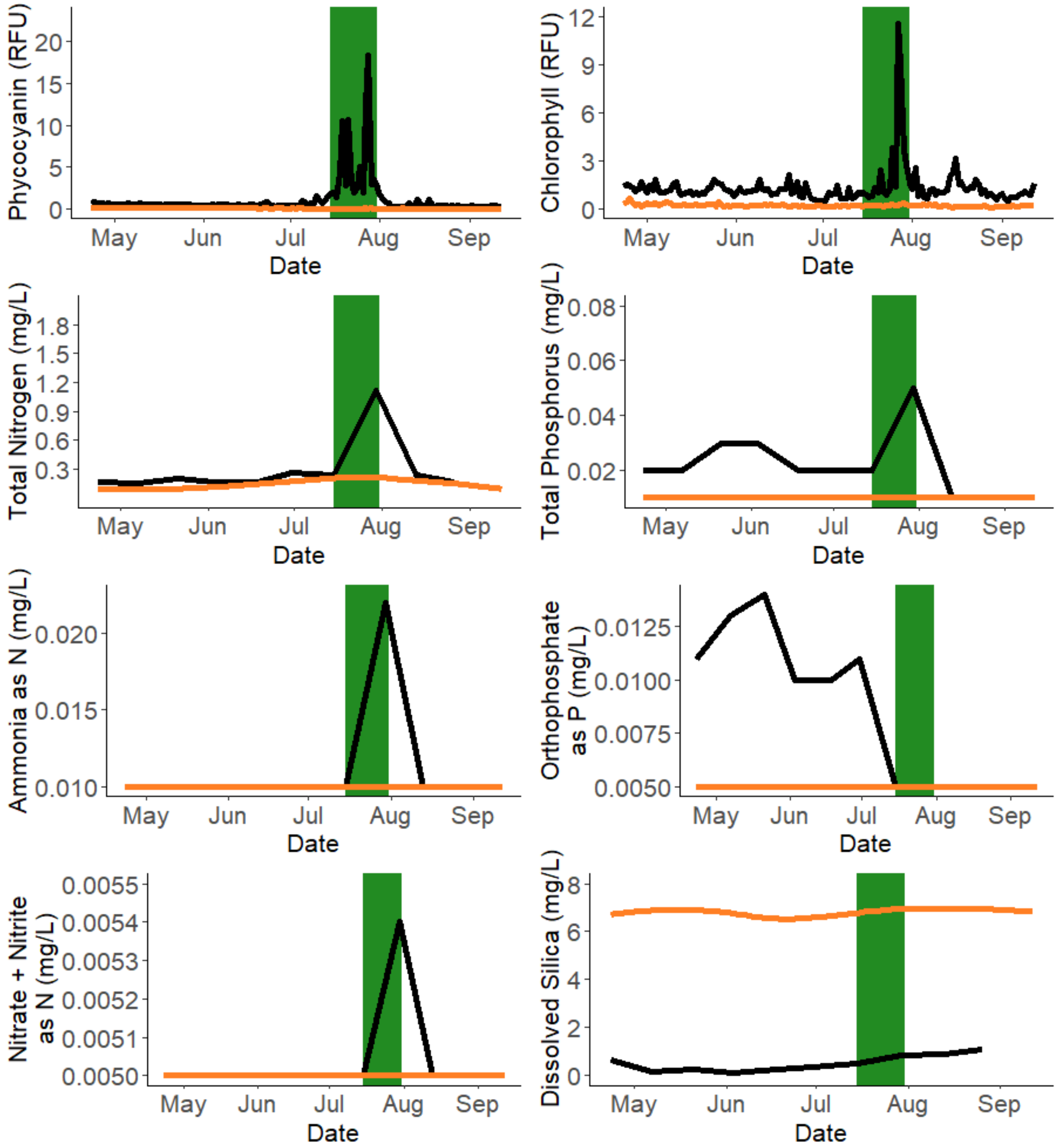

Figure 16. The 2020 temporal pattern of total nitrogen, ammonia, nitrate and nitrite, total phosphorus, orthophosphate, and dissolved silica in Odell Lake and Crescent Lake. Phycocyanin (cyanobacteria algal pigment) and chlorophyll (algal pigment) are also shown to give reference to how algal biomass and nutrients respond to one another. The green shaded areas, or CyAN HAB, refers to the time period where cyanobacteria were detected in Odell Lake by satellites and recorded by the EPA’s Cyanobacteria Assessment Network.

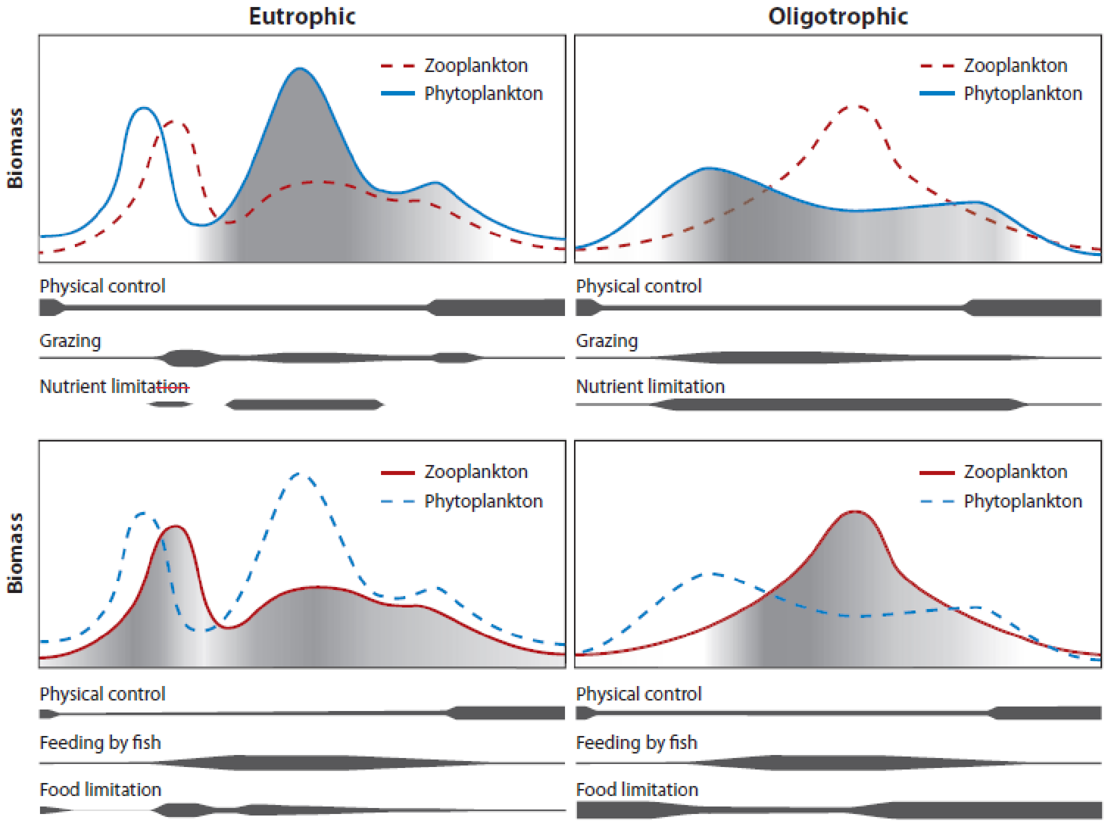

Figure 17. “Seasonal (winter through autumn) biomass patterns in eutrophic (left) and oligotrophic (right) water bodies. (Top) Focus on phytoplankton (blue solid line) (dark shading, inedible for zooplankton; light shading, edible for zooplankton). (Bottom) Focus on zooplankton (red solid line) (dark shading, small herbivores; light shading, large herbivores). The thickness of the horizontal bars indicates the seasonal change in relative importance of physical factors, grazing, nutrient limitation, fish predation, and food limitation (with kind permission of E. Schweizerbart publishers).” (Sommer et al. 2012).

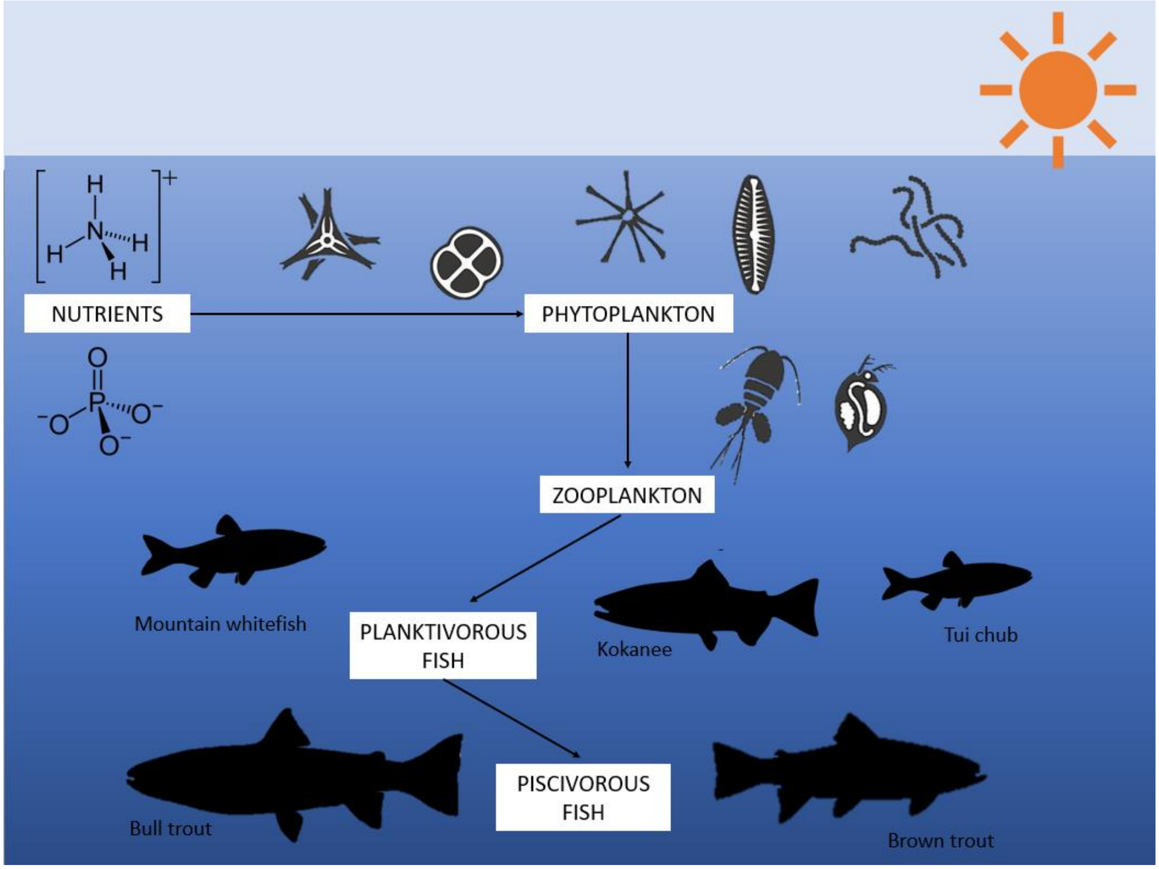

Figure 18. Conceptualized food web of Odell and Crescent lakes. (Organisms are not shown to scale).

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Appendix Odell Lake and Crescent Lake Depth Profiles

Depth profiles of Odell (a-c) and Crescent lakes (d-f) during the 2019 sample season. The depth profiles are from the deepest point at Odell Lake (43.56578282 N, -121.9864759 W) and the deepest point at Crescent Lake (43.47948436 N, -121.9927598 W). The depth profiles used sondes to record water quality variables such as temperature in degrees Celsius (red line), phycocyanin as relative fluorescence (blue line) and chlorophyll as relative fluorescence (green line). The June depth profile on Crescent Lake is incomplete due to strong winds that interfered with boat sampling.