THE RESPONSE OF UTAH LAKE'S PLANT AND ALGAL COMMUNITY

STRUCTURE TO CULTURAL EUTROPHICATION

by

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ABSTRACT

The Response of Utah Lake's Plant and Algal Community

Structure to Cultural Eutrophication

by

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Anthropogenic activities can lead to increased nutrient availability in water bodies, which can lead to increased harmful algal blooms, reduced visibility, and reduced macrophyte cover. In turn, these ecological impacts can have considerable local economic impacts. Understanding the ecosystem dynamics and anthropogenic drivers that lead to and maintain such eutrophic conditions is essential for effective lake management and restoration efforts. In order to examine the historical ecological conditions of Utah Lake and potential drivers of eutrophication, I used a combination of retrospective analyses and predictive primary production models.

I used a multi-proxy paleolimnological approach to reconstruct shifts in community composition, as well as to differentiate between pre- and post- industrial lake conditions. Our data show a marked transition at 30 cm, associated with ~1869 ± 25 years, from historically greater macrophyte representation to an increase in phytoplankton production, including an increase of cyanobacteria associated with

harmful algal blooms. Isotope geochemistry indicates the continued input of wastewater treatment plant effluent into the lake as a driver of increased nutrient loading. My data indicate that the current eutrophic state of Utah Lake, and the timing of the shift, is the result of anthropogenic forcing, through the introduction of common carp and continued external nutrient loading.

Additionally, I modeled and measured benthic and planktonic primary productivity along a gradient of water clarity and recent surface water levels to provide insight into the necessary light conditions that would allow for a dominant benthic primary producer community. I show that a transition to benthic dominance would be possible with water clarity increases of 0.9 m (at 2018 water levels), though recognize that wind-driven sediment resuspension may make this difficult to attain at a full-lake scale. Within areas that offer greater protection from wind-driven resuspension, water clarity would need to increase by 0.3 m (from 2018 means) for benthic dominance, which is likely an attainable target via reduced nutrient loading efforts. Increasing water clarity within these areas could have far-reaching positive repercussions on the water quality and ecosystem functioning of this lake.

(97 pages)

PUBLIC ABSTRACT

The Response of Utah Lake's Plant and Algal Community

Structure to Cultural Eutrophication

Leighton R. King

Human activities have long had a negative impact on the water quality of freshwater lakes around the world. Utah Lake, located in north-central Utah, has been a subject of such impacts, as the lake experiences recurrent harmful algal blooms during the summer months. Lake warnings and closures have made the public increasingly aware of the ecological and economic impact of these blooms. The objectives of this study were to: 1) compare historical and present-day water quality and ecosystem conditions using environmental data contained in sediment cores, 2) identify whether, and when, Utah Lake transitioned from clearwater to turbid conditions, and 3) incorporate historically-validated lake plant community structure models into establishing forward-thinking lake management targets. The first two objectives will guide lake remediation efforts by providing insight into where lake managers should set our water quality goals and help identify the main driver(s) of eutrophication in Utah Lake. Environmental data from sediment cores indicate a transition in the lake's recent history, marking a shift to greater phytoplankton dominance, which I attribute to the introduction of invasive common carp around 1881. The third objective provides management and restoration efforts with the water clarity requirements for returning the lake to its historical ecological state.

ACKNOWLEDGMENTS

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CHAPTER 1

INTRODUCTION

In freshwater lakes, excessive anthropogenic phosphorus loading is the most common cause of eutrophication and poor water quality (as reviewed by Correll 1998). Poor water quality conditions can have considerable economic and ecological impacts, including a loss of local recreation revenue and harmful impacts on fish and other aquatic life by reducing food and habitat supplies (Søndergaard et al. 2003; Dodds et al. 2008), and can result in the loss of ecosystem functions and services (Hilt et al. 2017). To make matters worse, returning lakes from eutrophic to oligotrophic or mesotrophic conditions can be difficult and costly (Jeppesen et al. 2005). Shallow lakes often do not respond gradually to increasing nutrient concentrations, but rather exhibit self-stabilizing regimes: a clear water, macrophyte dominated regime or a turbid, phytoplankton dominated regime (Scheffer et al. 1993). Once a lake is established in a phytoplankton-dominated, turbid state, even drastic reductions in nutrient loading may only lead to improvements in water quality after 10-15 years (Jeppesen et al. 2005). One prominent feature of turbid, eutrophic lake conditions is harmful algal blooms (HABs), which can have both direct and indirect harmful effects on an ecosystem (Landsberg 2002). However, for lakes which may have been naturally eutrophic, distinguishing natural from anthropogenic ecological conditions may be more complicated (Räsänen et al., 2006), and conservation or management targets for such lakes may thus require a greater understanding of lake-specific historical conditions.

Utah Lake, located in north-central Utah, is a prime example of a large (surface area= 385 km²), shallow (mean depth = 3.2 m) lake featuring poor water quality

conditions, as it experiences recurrent HABs and high turbidity. The increasing frequency of HABs has drawn increased public attention and research into lake dynamics due to repeated closures during the summer months. Judging from early anecdotal reports of abundant submerged macrophyte communities in the lake (which are now largely absent), Utah Lake may have undergone a regime shift from a relatively clear, macrophyte dominated regime to a turbid, phytoplankton dominated regime, though it has also been argued that it was a historically turbid, eutrophic lake prior to European settlement in its watershed (Bushman 1980 and references therein). Current anthropogenic influences on the lake include agriculture and storm water runoff, logging and grazing, and wastewater discharges (PSOMAS and SWCA 2007). The current state of Utah Lake is thought to be heavily affected by both historical non-native fish introductions and ongoing effluent loading from multiple wastewater treatment plants discharging directly into the lake. External nutrient loading from the watershed, as well as the effects of invasive benthic-feeding common carp, have received much of the attention as the primary drivers of the lake's ongoing water quality concerns (Miller and Crowl 2006). Despite local debate regarding the natural condition of the lake and therefore the cause of eutrophication, there is no empirical record as to whether this lake's waters were historically clearer, and if so, when the transition occurred.

Utah Lake is a culturally and environmentally critical ecosystem that provides abundant wildlife habitat and a multitude of recreational opportunities. Each year approximately 150,000-200,000 people visit Utah Lake; however, the number of visitors in recent years has declined due to negative water quality perceptions and low water levels (Horns 2005). It is also a major source of water for irrigation for the nearly

250,000 people who live in the watershed as the outlet river, the Jordan River, flows through greater Salt Lake City and is used for commercial, agricultural, and household irrigation. Utah Lake was once home to thirteen native fish species; however, only three currently remain: the Utah chub, Utah sucker, and the endemic June sucker.

The data sets contained in sediment cores provide a valuable method to determine lake-specific historical conditions. Paleolimnological analyses of lake sediment cores can provide detailed, long-term information on historical conditions and ecological changes using the geochemical and biological indicators stored in lake sediments. Lakes are influenced by multiple, interacting factors and therefore the use of multiple proxies provides a more comprehensive indication of lake dynamics (Davidson et al. 2018). It is especially useful in providing the historical context for present conditions, such as the timing of environmental changes that define the initial onset and development of eutrophication. This information can also be used to establish lake reference conditions and guide current management decisions in the absence of long-term monitoring data.

I have established the historical context for Utah Lake's present water quality conditions allowing lake managers to be better equipped to manage the current poor water quality concerns. Despite major advances in identifying the primary drivers of eutrophication (Schindler et al. 1978; Elser et al. 1990), and ways to remediate lakes via reduced nutrient loading (Jeppesen et al. 2005), it remains a critical concern, especially in shallow lakes within agricultural catchments. A simple reduction in nutrients is often insufficient, and a combination of nutrient reduction and food web management is often required (Scheffer et al. 2001). Ecological modeling provides a valuable approach to determine lake responses to changing environmental conditions driven by anthropogenic

activities. As benthic primary production (including submerged macrophytes and periphyton) is primarily limited by light availability at the sediment surface, predictive models of benthic periphyton production and phytoplankton production can be useful to determine the necessary light requirements for benthic primary production dominance. This is significant, as benthic primary production can potentially play an important role in controlling both internal nutrient loading and resuspension in shallow lakes (Madsen et al. 2001; James et al. 2004; Brothers et al. 2014).

Benthic production can play an important functional role in shallow lake nutrient cycling, energy flow, and food webs (Vadeboncoeur et al. 2002). Periphyton stabilize lake sediments (Vignaga et al. 2012), which decreases sediment resuspension by fish, an important mechanism affecting nutrient release from sediments in shallow lakes (Søndergaard et al. 2003). Additionally, periphyton reduce nutrient fluxes, such as phosphate, from the sediments by oxygenating the sediment-water interface (Carlton and Wetzel 1988). They also have a competitive advantage over phytoplankton when it comes to taking up nutrients released from the sediments, which helps regulate the availability of nutrients to phytoplankton (Hansson 1990). Periphyton is strongly light limited (Vadeboncoeur et al. 2014), and thus an increasing phytoplankton biomass, driven by external nutrient loading (Karlsson et al. 2009), suppresses periphyton growth by attenuating light between the lake surface and its sediments (Genkai-Kato et al. 2012; Anderson et al. 2002; Vadeboncoeur et al. 2002). Due to the high turbidity (associated with wind-driven sediment resuspension) and excess nutrient levels, some suggest that light is the most important limiting factor to total algal biomass, including phytoplankton, in Utah Lake (Fuhriman et al. 1981). Increased transparency in Utah Lake could thus

increase periphyton production, as well as historically-present submerged macrophytes (Brotherson 1981), with broad implications for the water quality and ecosystem services to be provided by Utah Lake (Hilt et al. 2017).

Altogether, this study has provided an improved understanding of the mechanisms and controls of eutrophication in shallow, eutrophic lakes. It has provided a clear historical framework and description of the timing of environmental shifts as they may relate to natural variability or anthropogenic forcing in the catchment and lake. These data will also provide insights into the potential interactions between regime shifts, plant community structure, and full-lake primary production. This project produces a timeline for the history of eutrophication in Utah Lake, as well as the necessary information for establishing baseline environmental conditions for Utah Lake management agencies and restoration efforts. Ultimately, these data will be used to determine whether the lake was historically clearer, and if so, identify the time period during which the lake transitioned to turbid conditions. Finally, this study will provide insight into the necessary water clarity increases that would allow for benthic primary production dominance and a return to historic clearwater conditions. This will provide valuable information for Utah Lake management agencies (e.g., the Utah Dept. of Environmental Quality) by providing them with detailed baseline conditions for water quality and plant community composition, which could be an essential component in the remediation of Utah Lake.

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CHAPTER 2

USING A MULTI-PROXY PALEOLIMNOLOGICAL APPROACH TO

DISTINGUISH BETWEEN NATURAL AND ANTRHROPOGENIC

DRIVERS OF ECOLOGICAL CONDITIONS IN UTAH LAKE

Abstract

Anthropogenic disturbance can have negative impacts on lake ecosystems that lead to increased harmful algal blooms and habitat changes such as reduced macrophyte cover. Utah Lake is a large shallow lake located in north-central Utah that is currently a turbid, eutrophic lake but may have historically been mesotrophic with substantial macrophyte cover. Despite local debate regarding the natural condition of the lake, there is no empirical record as to whether this lake's waters were historically clearer and if so, when the transition occurred. I used a multi-proxy paleolimnological approach to identify and reconstruct shifts in macrophyte production and community composition, as well as to differentiate between natural and anthropogenic ecological conditions. All proxies indicate a transition around 30 cm depth (~1869 ± 25 years). At this time, loss-on-ignition, plant material and gastropod shells, and C:N ratios indicate a transition in the lake's recent history marking a shift from macrophyte to phytoplankton dominance. Algal pigments, representative of all algae, increase above this horizon, as well as pigments associated specifically with cyanobacteria. Furthermore, eDNA of phytoplankton and macrophyte communities indicate a transition at roughly the same time. $\delta^{15}N$ data indicate a shift to higher values associated with wastewater treatment plant effluent. Algal pigments also indicate a substantial change in preservation, likely due to increased

mixing and associated aeration from a loss of macrophytes. BACON modeling of ^{137}Cs

dates associate this critical transition depth with ~1869 ± 25 years. Due to the abrupt

transition in all the proxies, I attribute this regime shift largely to the introduction of

common carp in 1883, with subsequent eutrophication occurring as the population and

associated effluent increased in the lake's catchment. Overall, this study suggests that the

current eutrophic state of Utah Lake, and the timing of the shift, can be attributed to

anthropogenic forcing rather than natural conditions.

Introduction

A major challenge to lake managers is identifying whether impacts to lake

ecosystems are driven by anthropogenic activities or natural climate changes (Battarbee

and Bennion 2011). Distinguishing natural from anthropogenic ecological conditions may

be particularly difficult in naturally mesotrophic or eutrophic lakes (Räsänen et al. 2006).

Thus, conservation efforts for such lakes requires a greater understanding of lake-specific

historical conditions and processes. In the absence of long-term monitoring, case histories

of individual lakes are the only evidence available to guide management policies

(Schindler 2012). Multi-proxy paleolimnological sediment records can provide insight

into differentiating between natural and anthropogenic variation in regionally unique and

potentially highly altered lake ecosystems.

Anthropogenic activities have introduced new challenges and threats to lake

ecosystems. Nutrient enrichment is the most common cause of eutrophication in

freshwater lakes (as reviewed by Correll 1998; Conley et al. 2009), which can have

considerable economic and ecological consequences (Søndergaard et al. 2003; Dodds et

al. 2008). Through excessive algal growth, increased nutrient concentrations can have a

significant negative impact on water clarity, which can result in the loss of ecosystem functions and services (Likens 1972; Hilt et al. 2017). Likewise, the introduction of invasive, non-native fish species to lakes can have catastrophic impacts on food-web structure (David et al. 2017). Shallow lakes are particularly susceptible to anthropogenic impacts and often do not respond gradually, but rather exhibit one of two self-stabilizing regimes: a clear water, macrophyte-dominated regime or a turbid, phytoplankton-dominated regime (Scheffer et al. 1993). Shifts can occur cyclically as a result of natural regime shifts and/or can be driven by either sudden or gradual impacts on the ecosystem (Scheffer and Jeppesen 2007).

Utah Lake is a prime example of a shallow, naturally mesotrophic lake with no empirical record of whether this lake's waters were historically clearer, and if so, when the transition occurred. Judging from early anecdotal reports of abundant macrophyte communities in the lake (which are now very sparse or absent; Janetski 1990; Miller and Crowl 2006), Utah Lake may have undergone a regime shift from a relatively clear, macrophyte-dominated regime to a turbid, phytoplankton-dominated regime. Some early settlers described the lake as having clear waters and abundant macrophytes in their journals (Bushman 1980) and initial paleolimnological analyses indicated a recent increase in diatom taxa indicative of shallow, eutrophic waters (Bolland 1974). However, other early reports described the lake as being naturally turbid (Bushman 1980 and references therein). Specifically, the lake's relatively large catchment area (~10,000 km^2), surface area, and shallow mean depth could together lead to naturally elevated nutrient concentrations and low water clarity, with frequent wind-driven resuspension events potentially precluding the growth of submerged macrophytes in much of the lake.

My research examines the history of eutrophication in Utah Lake using a multi-proxy paleolimnological approach. I use well-tested, independent biological and geochemical proxy data sets contained in lake sediment cores. The purpose of this study is twofold: (1) to identify the biological and geochemical baseline historic conditions and (2) to identify the transitional time period from clear-water to turbid conditions.

Study Site Description

Utah Lake is a shallow (mean depth = 3.2 m), turbid, eutrophic (mean annual TP = 80 μg L^{-1}) lake located in north-central Utah (Fig. 2-1). It is one of the largest (surface area= 385 km²) freshwater lakes in the western United States and has experienced harmful algal blooms (HABs) regularly since at least the 1970s (Strong 1974). The increasing severity and frequency of blooms has spurred increased public interest and research into lake dynamics surrounding the HABs. Due to public health concerns, it has become increasingly common for the lake to experience closures during the summer months. Each year approximately 150,000-200,000 people visit Utah Lake; however, the numbers of visitors in recent years has declined due to negative perceptions and low water levels (Horns 2005). The outlet river, the Jordan River, flows through the greater Salt Lake City region and is used for commercial, agricultural, and household irrigation. It is also a major source of irrigation water, delivering 154,583 acre-feet per year of water via canals and direct withdrawals from the lake (PSOMAS and SWCA 2007). Anthropogenic influences on the lake, and potential drivers of a regime shift, include European settlement, the introduction of non-native fish species, the increase in water fluctuations due to the lakes use as a reservoir, and the construction of wastewater treatment plants (Bushman 1980; PSOMAS and SWCA 2007). Pre-European inhabitants

of the region included the Timpanogos band of the Ute people who relied heavily on the lake for its plentiful food supply. European settlement of the valley began in the late 1840s, when pioneers first arrived in the valley and almost immediately began modifying the environment by cultivating the land and manipulating the drainage basin (White et al. 1969; Janetski 1990). Settlers marveled at the lake's size, water clarity, and abundance of macrophytes in their journals (Bushman 1980).

In 1883, common carp were introduced to the lake as a commercial food source, quickly becoming the dominant fish species and contributing to the decline of many native fish species (Heckmann et al. 1981). Utah Lake was once home to thirteen native fish species; however, only three currently remain: the Utah chub, Utah sucker, and the endemic June sucker. Once abundant, the June sucker is now listed as an endangered species. The 1883 introduction of invasive bottom-feeding common carp is widely believed to have severely reduced the abundance of macrophytes and has been supported by macrophyte recovery following carp exclusion experiments to limit sediment resuspension (Miller and Crowl 2006; Miller and Provenza 2007). Carp not only consume but also uproot macrophytes while feeding, which in turn increases sediment resuspension in the water column and limits light attenuation to benthic algae and submergent macrophytes (Rivera et al. 2013). Efforts have been underway since 2009 to significantly reduce the abundance and biomass of the carp population by removing carp on a full-time basis to reestablish submerged macrophytes to benefit native fish species dominance in the lake (Gaeta et al. 2018).
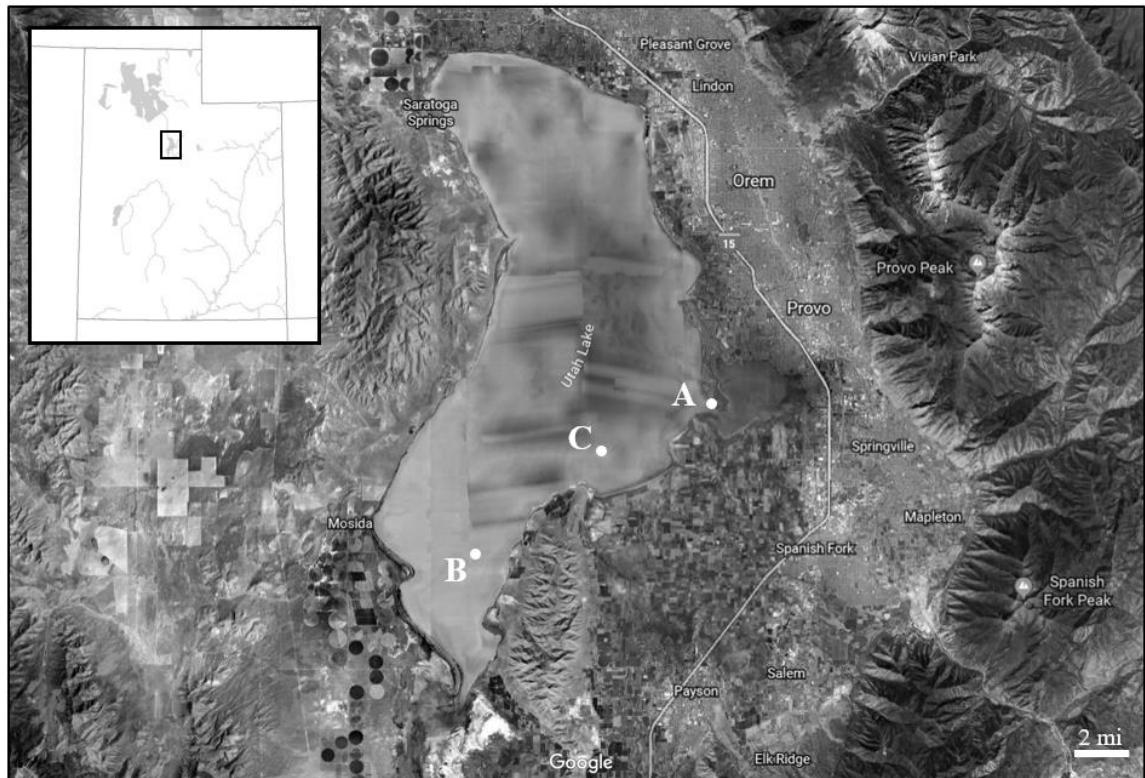
Although carp have received much of the attention as a driver of phytoplankton dominance in Utah Lake, multiple anthropogenic stressors may be involved in the

eutrophication of Utah Lake. Due to its proximity to the Provo metropolitan area, Utah

Lake has been largely manipulated and managed. Drought during the 1930s was the

impetus for many water diversions in the Wasatch Front after water levels were too low

in the Utah Lake to be used for irrigation (Hooton 2003). Construction on the Geneva

Steel mill was completed in 1944 at the eastern-shore of the lake, which produced a

considerable amount of wastewater and other pollutants that were discharged into the

lake. Most surrounding cities constructed wastewater treatment plants (WWTP) by 1954,

but raw sewage continued to enter the lake until 1967. Thirteen WWTPs located along

the lake's eastern shore discharge directly into the lake and its associated tributaries, after

undergoing only secondary treatment, which does not remove dissolved nutrients.

Approximately 230 tons/year of phosphorus loading is associated with the discharge from

WWTPs (PSOMAS and SWCA, 2007).

Methods

Analyses

A multi-proxy paleolimnological approach was used to investigate the role of

natural versus anthropogenic forcing of eutrophication in Utah Lake. Four sediment cores

(~1m long) were collected from Utah Lake during the summer of 2018 in three regions,

representing different habitats (the two areas in which historical reports indicated

macrophyte abundance, as well as an open-water site at the lake's deepest point). Cores

were collected using a Livingstone/Bolivia piston coring system in clear polycarbonate

tubes. Coring locations included near Provo Bay, Goshen Bay, and near Bird Island (Fig.

2-1). The upper, water-logged portion of the core was sectioned on shore in 0.5 cm

Fig. 2-1 Map of coring locations in Utah Lake. The stars indicate the three coring locations, including: Provo Bay (A; 40.1817°, -111.7181°), Goshen Bay (B; 40.1086°, -111.8751°), and near Bird Island (C; 40.1712°, -111.7998°).

increments using an extruder to prevent mixing during transport. Subsections were sealed in Whirl-Pak™ bags.

The Provo Bay and Bird Island cores were shipped directly to the National Lacustrine Core (LacCore) Facility at the University of Minnesota for splitting and initial core descriptions (ICD). The two cores were split into an archive and working half, with the archive half being stored at LacCore. ICD included high-resolution imagery and multi-sensor logging (Geotek sensors) for variations in density and magnetic susceptibility. X-ray fluorescence and digital x-radiography were carried out at the Large Lakes Observatory at the University of Minnesota-Duluth for non-destructive analysis of

element concentrations and density variations, respectively. The working halves were sub-sampled in 0.5 cm increments from the center of each core to maintain stratigraphy and avoid cross contamination that can occur during sampling and from the core tube, sealed in Whirl-Pak[TM] bags, and transported back to Utah State University (USU).

To define sediment facies, moisture content, percent of organic matter, and the percent of carbonates were determined through standard loss-on-ignition (LOI) methods (Dean 1974; Fig. A1). Homogenized samples of 1-3 grams were dried at 100°C overnight (for a minimum of 12 hours). Organic material was then ignited and burned off at 550°C for 4 hours. Finally, carbonates were ignited and burned off at 1000°C for 2 hours.

The Goshen Bay core was used for eDNA analysis and was thus transported back to USU for immediate sampling. The core was sectioned in 0.5 cm increments and 1-4 grams were taken from the center of the core, placed in 20mL plastic scintillation vials (all equipment pre-sterilized with UV light), and placed in the freezer. Sterile gloves and ethanol were used to prevent contamination between samples. The presence or absence of fossilized macrophyte vegetation was noted during sub-sampling of each core. Direct counts of macrophytes can provide insight into ecological changes as they relate to natural and anthropogenic variability (Birks 2000; Karst and Smol 2000).

Concentrations of ^{210}Pb were not high enough to support incremental sediment layer dating; therefore, sediment layers were dated using gamma spectroscopy to measure ^{137}Cs in order to establish the depth-time profile, which was present in high enough concentrations with a clear onset and peak. This chronological method is based on atmospheric fallout of ^{137}Cs from nuclear weapons testing, with the onset occurring in 1954 and the peak in 1963. Homogenized sub-samples from 0.5 cm increments of 2-3

grams were shipped frozen in Whirl-Pak^{TM} bags to the University of Regina

(Saskatchewan, Canada) for dating purposes. The ^{137}Cs associated dates were calibrated

to years before present (1950) for the age-depth models which were produced, with

uncertainty, using Bayesian statistics (BACON) (Blaauw and Christen 2011). The

method divides the sediment core into thin sections (thick = 0.5 cm) and then runs

millions of Markov Chain Monte Carlo (MCMC) iterations to estimate the accumulation

rates for each section. Combining the accumulation rates with the known start date (top

of the core represents the present) forms the age-depth model with uncertainty. It is

possible that counting ^{210}Po, rather than ^{210}Pb, may have had greater success due to better

counting efficiencies for alpha decays. All data associated with the age-model will be

reported and archived as suggested in Mustaphi et al. (2019).

Carbon and nitrogen concentrations and isotopes were used to provide insight into

the dominant sources of organic matter and assess shifts in nutrient sources to Utah Lake.

Clear-water regimes dominated by benthic taxa tend to have high total carbon (TC) to

total nitrogen (TN) ratios compared to turbid, planktonic-dominated regimes. Macrophyte

dominance is characterized by C:N ratios typically around 20 or greater due to the high

cellulose content and relatively low protein content. Algal C:N ratios are usually 4-10 due

to their high protein content resulting in a larger N content (Meyers 1994). Natural

nitrogen isotope values typically range between 0-5‰, while wastewater is typically

between 10-15‰ due to bacterial processing of the lighter δ^{14}N isotope during the

denitrification process, which leads to an increase in abundance of the heavier δ^{15}N

isotope (Heaton 1986; Anderson and Cabana 2006; Finlay and Kendall 2007). Prior to

analyses, carbonates were removed from freeze-dried sediment samples using acid

fumigation. Organic carbon and nitrogen isotopes, and the percentage of organic carbon and nitrogen, were determined using a Costech 4010 elemental analyzer in the Geology Department at USU.

All algal taxa produce pigments, such as chlorophylls and carotenoids, which are retained in sediments as biogeochemical markers. While some pigments are common to all algae, other pigments are species-specific (Leavitt and Hodgson 2001). Pigment concentrations in sediment were used to determine shifts in algal production and community composition. Homogenized sediments (~2-3 grams) were placed in Whirl-Pak^{TM} bags and kept frozen prior to, and during, shipping. Care was taken to minimize exposure to light to prevent pigment degradation. Samples were shipped to the University of Regina (Saskatchewan, Canada) for pigment analyses using methods outlined in Leavitt and Hodgson (2001). Pheophytin-a is the product of Chlorophyll-a decomposition and was used as an index of pigment decomposition.

Complementary to fossil and biomarker remains, environmental DNA (eDNA) is an emerging tool that detects taxa that are not present in the fossil record. It has been used to successfully reconstruct algal, zooplankton, and fish community shifts that have occurred parallel to anthropogenic activities within catchments (Capo et al. 2016; Monchamp et al. 2017). Frozen eDNA sediment samples (sampling description above) were shipped to Jonah Ventures (Boulder, CO) for analysis, which included next-generation sequencing (NGS) of fish, macrophyte, and phytoplankton assemblages. Primers were used to amplify DNA sequences preserved in the sediments, and then sequences were matched to a reference database for identification. The phytoplankton

primer used was 23S and the macrophyte primer used was trnL. Only samples that were

identified with >97% certainty were used for analysis.

Statistical Analyses

The Sequential Regime Shift Detection (SRSD) method, developed by Rodionov

(2004), was used to determine significant changes through time in the proxy records. This

method is based on a sequential student t-test (two-tailed, unequal variances) analysis to

detect significant shifts in the mean. The two parameters used to detect regime shifts are

the target significant level, p-value=0.05, and the cutoff length, l=20 or 40 depending on

the proxy, which determine the magnitude and scale of the shifts to be detected. The

lower the significance level, the larger the magnitude of the shift must be to be detected.

The direction of the shift, increase vs. decrease, is indicated by a positive or negative

number. For each time series input, the SRSD calculates the regime shift index (RSI), the

mean values of each regime, the length of the regime, the p-value associated with the

shift, and the weights of the outliers.

Results
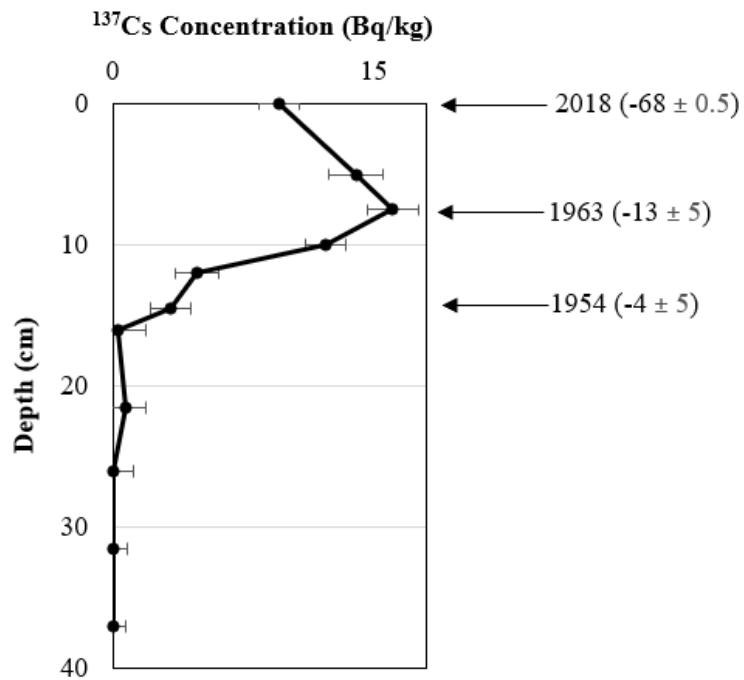
The cores collected from Provo Bay, Goshen Bay, and near Bird Island were 74.5

cm, 60.5 cm, and 94 cm, respectively. High-resolution imagery, multi-sensor logger data,

and XRF indicate good stratigraphy throughout the cores and clear shifts in sediment

character. Preserved remains of plant matter and gastropod shells were found in all three

cores. In the Provo Bay core, five pieces of plant remains were found in the core, with

four of the five occurring between 30 cm and 60 cm. All gastropod shells found in this

core were also between 30-60 cm. No plant remains were found above 30 cm in the

Goshen Bay core, while plant remains and gastropod shells were found in every few samples below 30 cm. The Bird Island core contained seven gastropod shells throughout the entire 94 cm core.

Concentrations of ^{137}Cs increased up-core from 15 cm to 8 cm, where they peaked (Fig. 2-2). The onset and peak of global nuclear testing can be correlated with the initial increase of ^{137}Cs representing ~1954 and the peak in ^{137}Cs corresponding with the peak of nuclear testing in 1963. The non-zero concentrations below this horizon may result from sediment mixing or from a lesser degree of nuclear testing from 1944-1954. Extrapolating this model (Fig. A2) to the remainder of the core produces an estimate that the Goshen Bay core represents about 300 years of history, ~1715-2018, and the Provo Bay core represents about 370 years, ~1641-2018. Pending radiocarbon dates, I assigned the arrival date of European settlers (late 1840s) to correspond with ~35 cm. I can attribute the 30 cm mark, where most shifts are observed, to ~1869 ± 25 years.
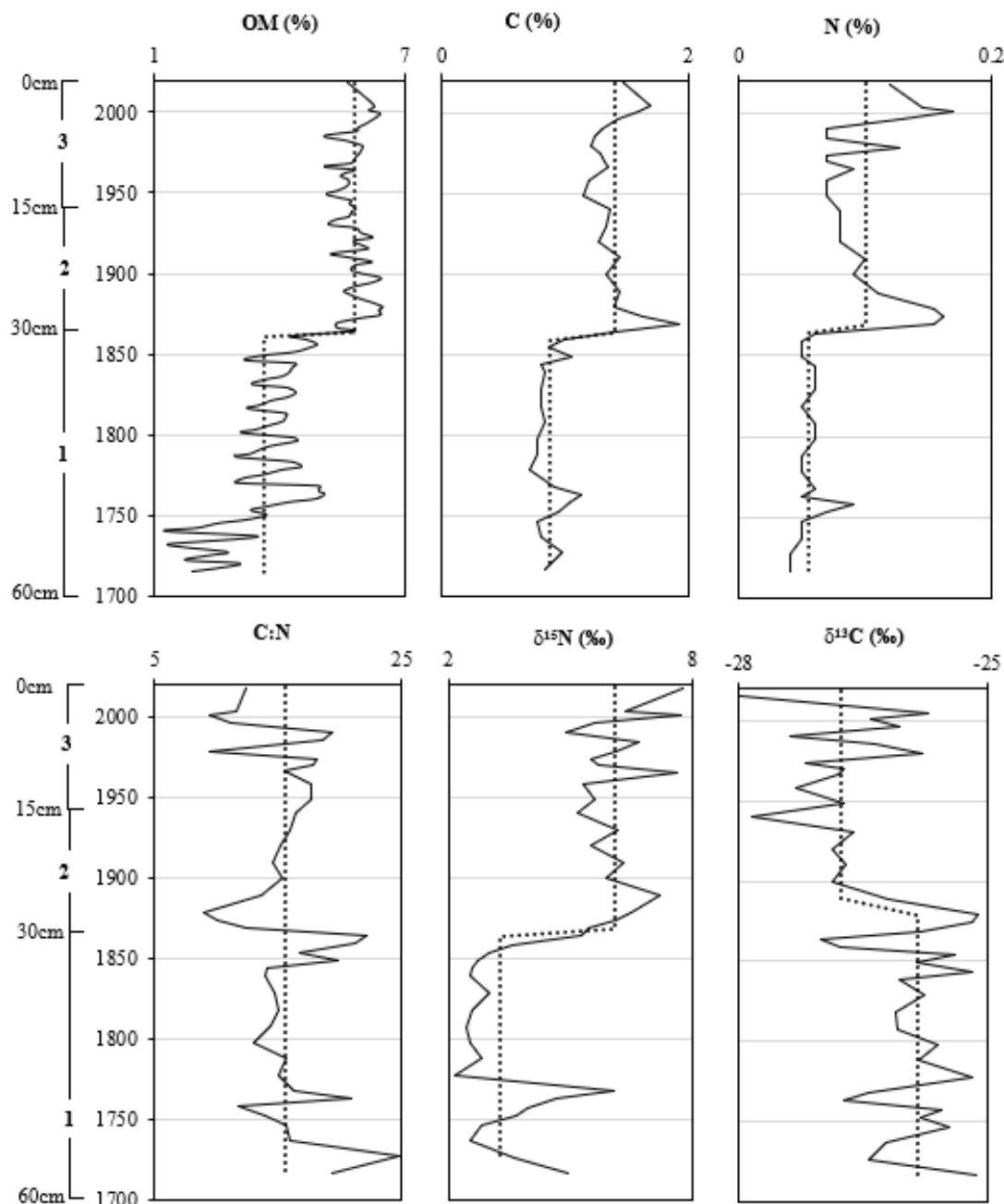
I attempted ^{210}Pb radioisotope dating techniques, but the ^{210}Pb activity was generally too low and consistent throughout the core to make any inferences from, which is typical of desert lakes with low atmospheric ^{210}Pb fallout (Appleby 2008). Pending radiocarbon dating, the depth-time profile favors more recent conditions as the ^{137}Cs dates are correlated with the top portion of the core and therefore may not accurately reflect sedimentation rates at the bottom of the core. Radiocarbon dates will provide more accurate estimates of the depth-time profile by incorporating date estimates for older sediments. This is particularly important for interpreting differences in the sedimentation rate of the lake prior to the 30 cm horizon, where algal pigments suggest a substantial shift in lake conditions.
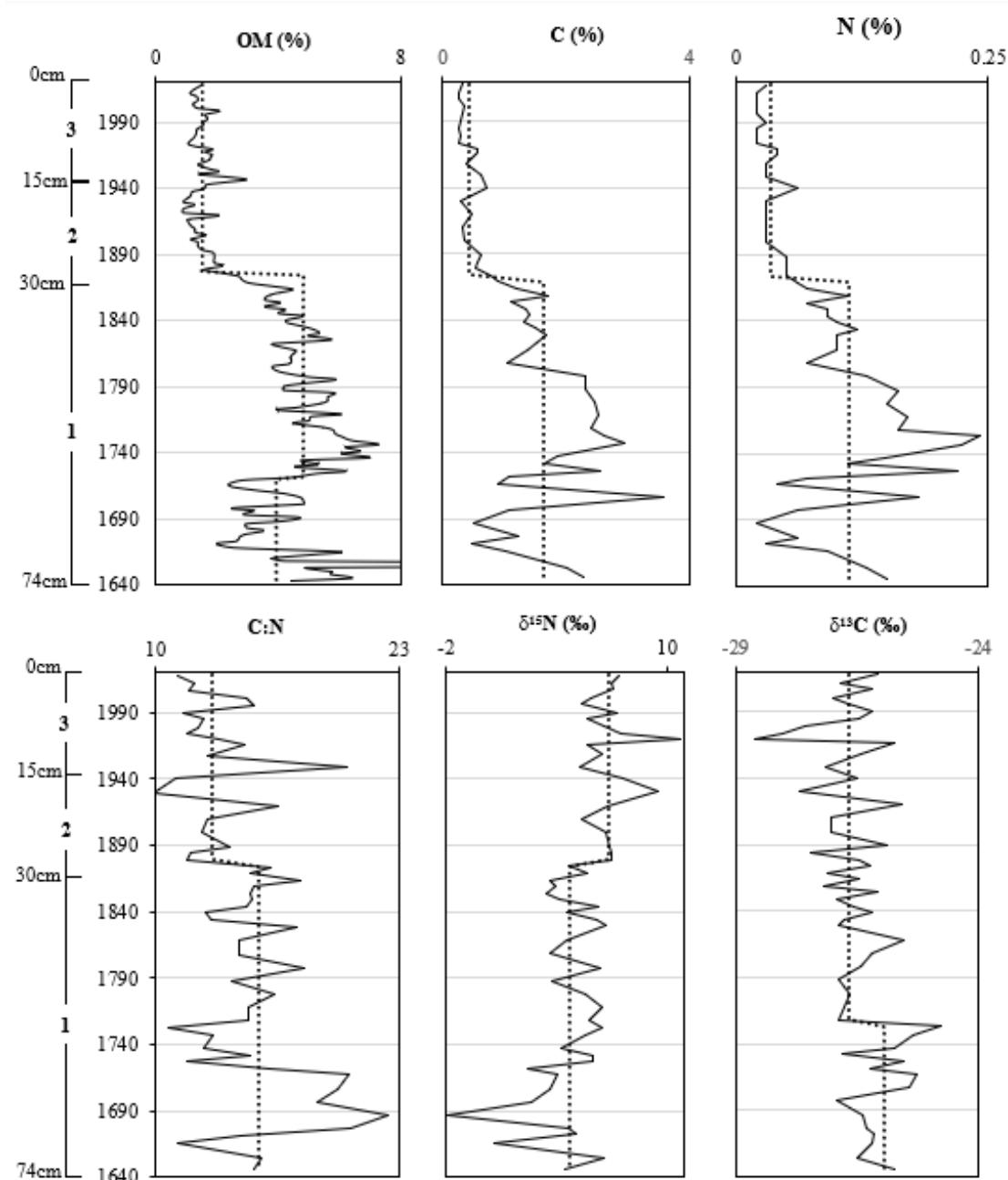
Fig. 2-2 Concentrations of [137]Cs (with error bars) measured throughout the Goshen Bay core. Arrows indicate known dates due to nuclear testing (calibrated to radiocarbon years in parentheses).

I subdivided the cores into three distinct units based on the shifts and transitions I observed in the physical core properties and proxy sets: from the base of the core to ~30 cm (Unit 1), from ~30 cm to ~15 cm (Unit 2), and from ~15 cm to the top of the core (Unit 3). Organic matter, C:N ratios, $\delta^{15}N$ values, and most of the algal pigments underwent the largest regime shift around this ~30 cm, corresponding to ~1869 ± 25 years. Fig. 2-3 shows the significant regime shifts detected in the Goshen Bay core. Organic matter, carbon, nitrogen, and $\delta^{15}N$ all exhibited significant increases by 2.2% (RSI=-1.87), 0.52% (RSI=-1.14), 0.04% (RSI=-0.45), and 2.19‰ (RSI=-1.35), respectively. The C:N ratios in the Goshen Bay core had no significant shift. A significant decrease by 0.91‰ (RSI=0.47) was observed in the mean $\delta^{13}C$ (‰). Fig. 2-4 shows the significant regime shifts detected in the Provo Bay core. At a similar depth,

Fig. 2-3 Organic matter, carbon, nitrogen, C:N ratios, δ^{15}N, and δ^{13}C throughout the Goshen Bay core. The dashed lines indicate significant regime shifts (Rodionov, 2004) using a target p-value=0.05, cutoff length=20 or 40, and tuning constant=2.
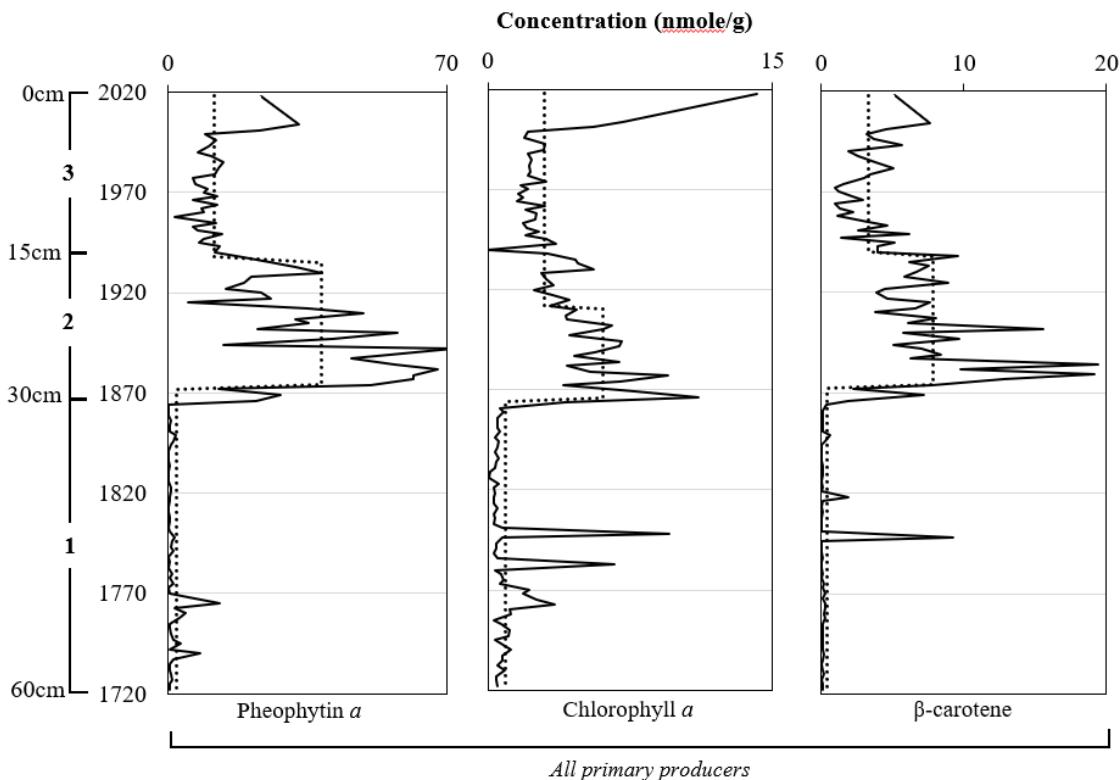
Fig. 2-4 Organic matter, carbon, nitrogen, C:N ratios, $\delta^{15}N$, and $\delta^{13}C$ throughout the Provo Bay core. The dashed lines indicate significant regime shifts (Rodionov, 2004) using a target p-value=0.05, cutoff length=20 or 40, and tuning constant=2.

significant decreases in the mean were observed in organic matter, carbon, nitrogen, and the C:N ratio. Organic matter decreased 3.3% (RSI=1.72), carbon decreased 1.21% (RSI=1.52) nitrogen decreased 0.08% (RSI=1.36), and the C:N ratio decreased 2.52 (RSI=0.12). The regime shift increased the mean δ^{15}N value by 2.84‰ in the Provo Bay core (RSI = -0.48). The small shift observed in the organic matter of Provo Bay prior to ~1740 was not significant.

All algal pigments detected in the Goshen Bay core experienced large, significant increases in concentration at approximately the same ~30 cm horizon. Algal pigments identified included fucoxanthin, diadinoxanthin, alloxanthin, diatoxanthin, lutein, canthaxanthin, chlorophyll-*a*, echinone, pheophytin *a* & *b*, and β-carotene. Pheophytin *a*, a decomposition product of chlorophyll-*a*, abruptly increased 57.09 nmole/g (RSI=-2.05) (Fig. 2-5). Chlorophyll-*a* and β-carotene, representative of all algal species, increased 5.47 nmole/g (RSI=-1.93) and 7.35 nmole/g (RSI=-1.81), respectively. Concentrations of these three pigments did experience a subsequent decrease to lower concentrations, but not to pre-impact conditions (RSI= 0.9: pheophytin; 0.68: chlorophyll *a*; 0.53 β-carotene).
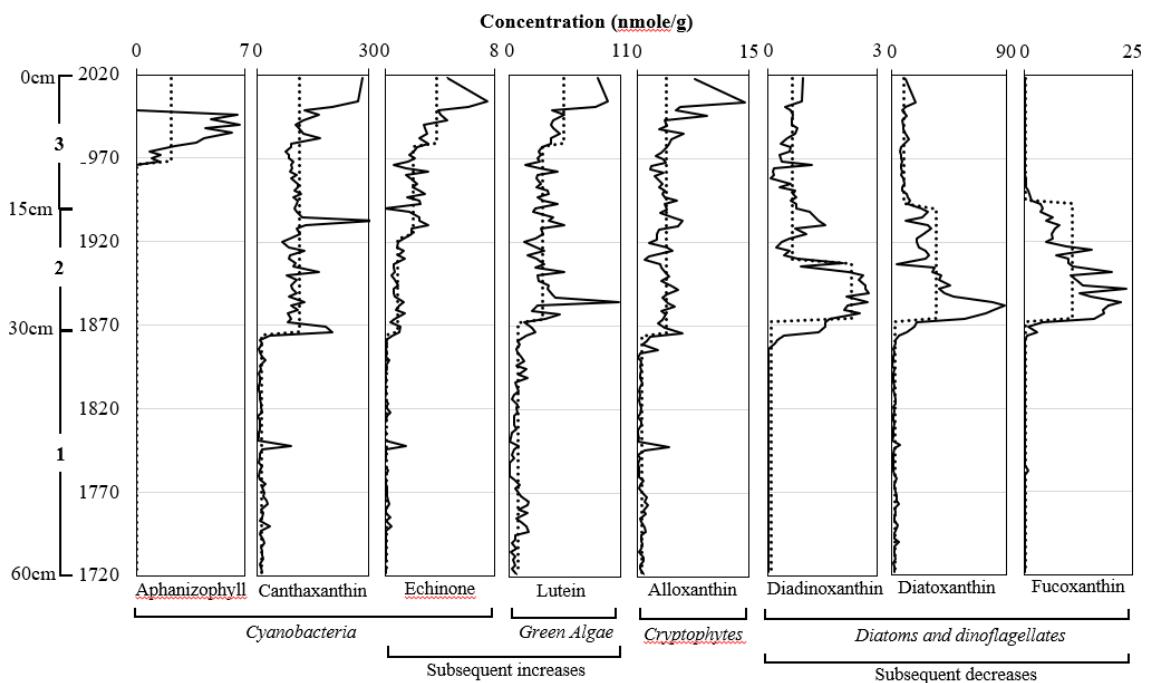
Algal pigments associated with specific algal groups all showed significant increases, of approximately 5-10 fold, from low, stable values to higher, more variables values (Fig. 2-6). Following the initial shift, many of the algal pigments exhibited a subsequent increase or decrease in concentration at ~15 cm (corresponding with ~1945 ± 13 years) (Fig. 2-6). Cyanobacterial pigments, canthaxanthin and echinone, green algae pigments, and cryptophyte pigments displayed an increasing trend up core.

Concentration (nmole/g)

Pheophytin *a*

Chlorophyll *a*

β-carotene

All primary producers

Fig. 2-5 Concentrations of algal pigments representative of all algal taxa throughout the Goshen Bay core. Dotted lines indicate significant regime shifts (Rodionov, 2004) using a target p-value=0.05, cutoff length=20, and tuning constant=2.

Aphanizophyll did not experience a significant shift at ~30 cm, but instead elevated significantly at ~10 cm, which coincides with the subsequent transitions observed in other algal pigments. The pigments that experienced a subsequent decrease did not return to pre-regime shift concentrations, suggesting the ecosystem was still largely influenced by anthropogenic activities.

Next generation sequencing (NGS) of eDNA samples detected 278 phytoplankton and 65 higher plant DNA sequences throughout the 21 total sediment samples. However, only 50 of the phytoplankton sequences were detected to the species level, 62 to genus, and 27 to order. Most sequences could generally only be classified at the kingdom level: 68 bacillariophyta (diatoms), 34 chlorophyta (green algae), 25 eustigmatophyta, 45
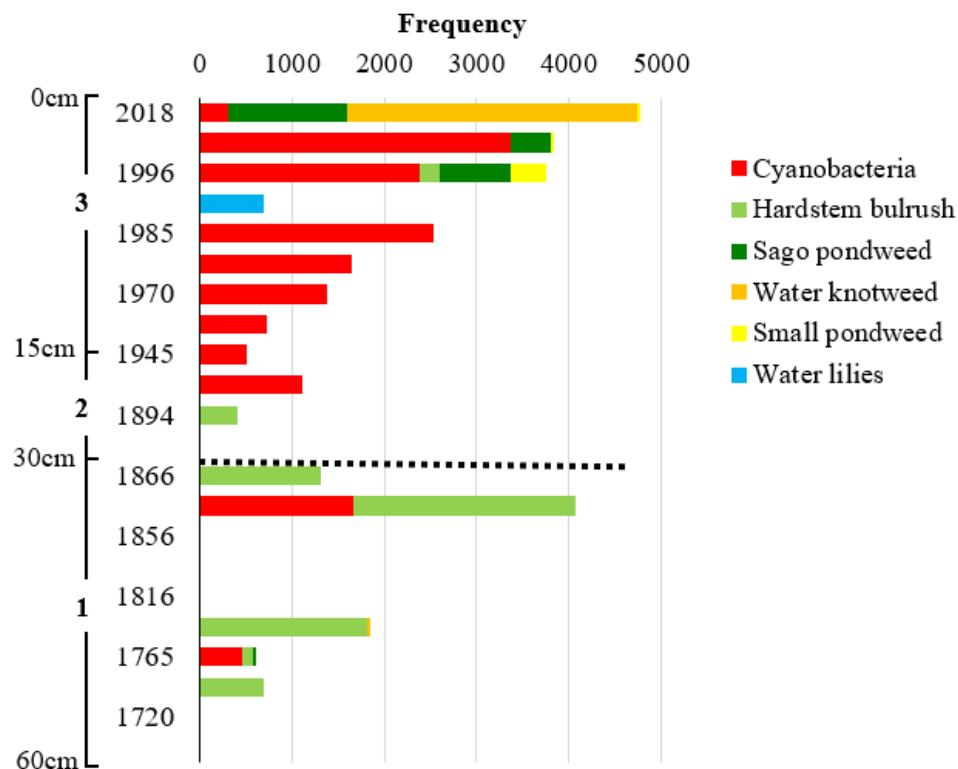
Fig. 2-6 Concentrations of specific algal pigments throughout the Goshen Bay core. Dotted lines indicate significant regime shifts (Rodionov, 2004) using a target p-value=0.05, cutoff length=20, and tuning constant=2.

streptophyta, and 63 unknown sequences. Cyanobacteria taxa were detected in only two sediment samples below 30 cm; however, in the recent sediments (above 30 cm) they were detected in 11 (out of 12) samples in higher frequencies, suggesting an increase in cyanobacteria populations above 30 cm, which matches cyanobacteria pigment results (Fig. 2-7). Cyanobacterial frequencies ranged from 0 to 3,377 sequences detected. All the genera of cyanobacteria that were identified are known to be toxic to humans and/or animals.

Higher plant samples had 27 detected to the species level, 22 to genus, 12 to family, and 4 to the order level. Hardstem bulrush (*Schoenoplectus acutus*) was the only native aquatic macrophyte detected in historic sediments (Fig. 7). Within the top 6 cm of sediment samples, small pondweed (*Potamogeton berchtoldii*), sago pondweed

(*Stuckenia pectinata*), hardstem bulrush, water smartweed (*Persicaria amphibia*), and water lilies (*Nymphaea*) were all detected. Food crops identified included beets (*Beta vulgaris*), scarlet gourds (*Coccinia samburuensis*), plums/cherries/peaches (*Prunus*), apples/pears (Maloideae family), and sunflowers (*Atractylodes*). Invasive species detected included crofton weed (*Ageratina adenophora*), wild hops (*Bryonia alba*), and smooth crabgrass (*Digitaria ischaemum*). The presence of dandelions (*Sonchus*) was only detected in the 30.5 cm sample, which fits the overall chronology developed from the ^{137}Cs results but highlights the limitation in the method because clearly dandelions have been present in Utah since the late 1800s.
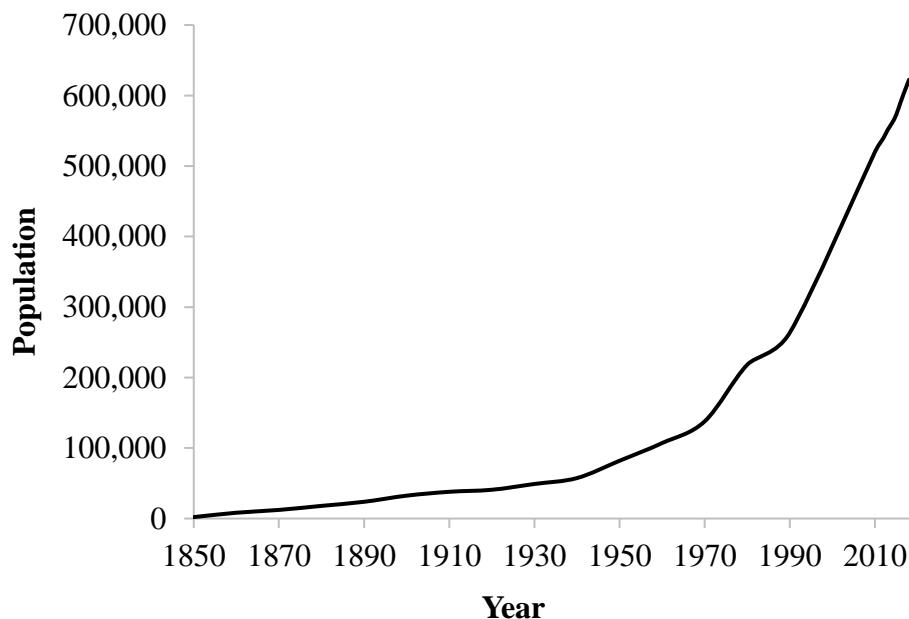
Fig. 2-7 Frequency of aquatic plants and cyanobacteria detected with eDNA in the Goshen Bay core. Dashed line indicates ~30 cm, where the other proxies experienced significant regime shifts.

Discussion

I identified three independent facies throughout the sediment core that correspond to significant transitions in the proxy data sets. The data contained in the sediment cores collectively indicate a large, significant regime shift from mesotrophic to eutrophic lake conditions at ~30 cm, which corresponds with ~1869 ± 25 years. I attribute this initial regime shift largely to the introduction of common carp in 1883 due to the abrupt transition in the proxies. Ongoing nutrient additions due to the growing population in the valley (Fig. 2-8) appear to lead to consistent eutrophication through the last century and result in a subsequent transition at ~15 cm, which corresponds with ~1945 ± 13 years. The results suggest that the lake shifted from a mesotrophic, clearwater, macrophyte-dominated state to its current eutrophic, turbid, phytoplankton-dominated state. Independently, there may be multiple explanations for each of the proxies examined; however, when examined in combination they make a compelling argument that the lake underwent a regime shift from mesotrophic to eutrophic conditions that was driven by anthropogenic forcing.

Unit 1 (~1640-1869): Pre-regime shift

C:N ratios, δ^{15}N isotopes, LOI, and algal pigments in the Goshen Bay and Provo Bay cores indicate a period of mesotrophic, macrophyte-dominated lake conditions in the lake's history. Calculated ages from ^{137}Cs dating suggest this period lasted until ~1869 ± 25 years, which coincides with the introduction of common carp in 1883 (Fig. A2). C:N values in the Provo Bay core during this period had a mean of ~15, indicating a mix of organic matter sources including both plant and algal material. Organic matter content

Fig. 2-8 Population growth within the Utah Lake value has grown exponentially, resulting in continuous increased nutrient loading to the lake. Data was obtained from www.worldpopulationreview.com.

during this period ranged from 1.26% to 6.42% and 1.04% to 7.29% in the Goshen Bay and Provo Bay cores, respectively. The Goshen Bay core exhibits lower percentages of organic matter in this section of the core relative to more recent layers (Fig. 3), which likely indicates a lower abundance of phytoplankton in early years (as C:N ratios did not shift significantly in this core). The opposite is seen in the Provo Bay core (Fig. 4), where the percentage of organic matter in this facies is the highest observed in any of the cores. This likely results from Provo Bay's historical dominance by macrophytes (Brotherson 1981), which have greater organic matter content than phytoplankton due to their large physical structure, and thus result in a decrease in C:N and organic matter despite an increase in phytoplankton. The majority of the intact plant remains preserved in the Goshen Bay and Provo Bay cores were located in this section as well, supporting

historical reports of abundant macrophyte communities in these areas during this period (Bushman 1980 and references therein). Additionally, gastropod shells preserved in the cores were located throughout this section, further suggesting a greater abundance of macrophytes as gastropod grazing has been found to be an important factor in maintaining healthy submerged macrophyte communities (Jones and Sayer 2003). Intact plant and gastropod remains in the Bird Island core did not reflect this same pattern as the coring location was reflective of a more open-water site that would not have contained abundant macrophytes to the same degree. Concentrations of pheophytin *a*, a degradation product of chlorophyll *a*, in the Goshen Bay core are extremely low during this period, ranging from 0 to 57 nmole/g, indicating a good preservation environment in the lake sediments featuring minimal mixing and disturbance after deposition (Fig. 5). The abundant macrophyte community during this period would have helped stabilize the sediments to prevent sediment resuspension. The mean $\delta^{15}N$ values (Fig. 3 & Fig. 4) prior to ~1869 ± 25 years was within the range of natural terrestrial sources, approximately 0-5‰ (Finlay and Kendall 2007). Altogether, the presence of intact macrophyte and gastropod remains, organic matter contents, stable sediments, and natural $\delta^{15}N$ values indicates that the lake featured a clearwater state with an abundant macrophyte community, specifically within Goshen Bay and Provo Bay, and was largely undisturbed by anthropogenic activities.

Unit 2 (~1869-1945): Post-regime shift

Due to the rapid and coordinated nature of the transitions in many of the proxy data sets, I conclude that the initial impact to the lake was driven by the introduction of

common carp in Utah Lake in ~1883. Based on the modeled results for the depth-time profile, the 30 cm horizon represents a date between 1842 and 1892 (Fig. A2), which corresponds with the known introduction date of common carp. Within 20 years, lake managers reported the impact that the common carp were having on the lake ecosystem, indicating the rapid growth rate of the carp population within the lake. The impact due to European settlement and population growth in the valley likely would have appeared to occur would have resulted in a more gradual transition over a longer period of time in the proxy data sets. The input of raw sewage and effluent from wastewater treatment plants would have increased gradually over time due to population growth in the region up until the construction of the wastewater treatment plants in ~1945. This is also observed as a gradual increase in echinone, lutein, and alloxanthin pigment concentrations (representative of cyanobacteria, green algae, and cryptophyte communities) through this period as nutrient loading to the lake increased alongside population growth (Fig. 6).

Pheophytin *a* is an indicator of the amount of overall pigment degradation in the sediment. The significant increase in pheophytin *a* (Fig. 5) following the regime shift indicates a fundamental change in the lake environment, likely due to increased mixing and aeration of the sediment associated with the loss of benthic primary producers, leading to increased pigment degradation rates. The high concentration of many of the algal pigments observed during this period likely experienced *more* degradation than the pigments prior to the regime shift.

Despite greater degradation rates, the pigment concentrations are notably greater during this time period suggesting that the phytoplankton communities substantively increased in this time period. Chlorophyll-*a* and β-carotene, pigments that represent all

primary producers, also experienced a significant increase at this time, indicating an overall increase in algal production (Fig. 5). Canthaxanthin and echinone pigments, representative of cyanobacteria, displayed a significant increase during this time. eDNA results also indicate an increase of cyanobacteria detected in more recent years (Fig. 7). Other algal pigments detected increased significantly as well and include specific pigments representing green algae, cryptophytes, diatoms, and dinoflagellates (Fig. 6).

The proxies indicate a simultaneous loss of macrophytes along with the increase in phytoplankton production. The increase in organic matter in the Goshen Bay core, combined with no significant change in the C:N ratios, indicates an increasing phytoplankton community. The significant decrease in organic matter in the Provo Bay core, combined with the significant decrease in C:N ratios, indicates a loss of macrophytes despite an increasing phytoplankton community due to the large biomass of macrophytes (Fig. 4). This corresponds with historical records that indicate that Provo Bay and Goshen Bay were historically more abundant in macrophytes than it is today. This discrepancy may also be a result of the Goshen Bay core being collected further off-shore in a deeper location, which would add weight to the argument that phytoplankton increase in the overlying water column boosted organic matter in the Goshen Bay core, while the shorter water column in the Provo Bay core would have suppressed the phytoplankton signal in the organic matter. The increase in cyanobacteria (Fig. 6 & Fig. 7) aligns with the decrease in native hardstem bulrush observed in macrophyte eDNA results. Macrophyte eDNA results are somewhat limited as the only native aquatic macrophyte detected in historic sediments was hardstem bulrush, which are emergent macrophytes. The relative abundance of these macrophytes appeared to decline following

the regime shift (Fig. 7), but this could be attributed to a deterioration in the preservation environment, as indicated by the algal pigments, rather than a true loss of macrophytes (which are still present to a lesser extent in Utah Lake). A change in the preservation environment could also explain the recent increase in other aquatic macrophytes, such as small pondweed, sago pondweed, and water knotweed, which simply may not have had sufficient time to degrade in the sediments (Fig. 7). It is important to note that the use of eDNA is still an emerging tool in the field of paleolimnological studies and is best used in combination with other well-tested proxies to provide additional insight into changing communities rather than as an independent proxy.

The increase in $\delta^{15}N$ values can be attributed to increasing input of effluent from wastewater treatment plants along with population growth. Both the Provo Bay and Goshen Bay core displayed significant increases in $\delta^{15}N$ values just after ~1869 ± 25 years (Fig. 3 & Fig. 4). Wastewater effluent is known to be isotopically enriched in $\delta^{15}N$, typically 10-15‰, due to the bacteria preferentially processing the lighter ^{14}N isotope during the denitrification process (Heaton 1986; Anderson and Cabana 2006; Finlay and Kendall 2007). This is consistent with the results of Bushman (1980) that indicate that WWTPs may be among the major sources of nutrients in Utah Lake. Approximately 230 tons/year of phosphorus loading is associated with the discharge from WWTPs (PSOMAS and SWCA 2007).

Overall, the lake underwent a significant regime shift in the late 19th century, likely resulting from the introduction of common carp. During this period, the lake exhibited a loss of macrophytes and an increase in phytoplankton abundance, particularly

cyanobacteria. The increased nutrient loading resulted in a shift from clearwater, mesotrophic condition to eutrophic, turbid conditions featuring harmful algal blooms.

Unit 3 (~1945-Present): Continued Cultural Eutrophication

Continued nutrient loading to Utah Lake resulted in a subsequent transition in more recent years following the initial regime shift. Algal pigments that exhibited a subsequent transition to increased concentrations included echinone and lutein (Fig. 6). This increase can be attributed to the continued increase of nutrients from the construction of WWTPs and a growing population in the surrounding region. Aphanizophyll did not experience an initial increase along with the other pigments, but instead exhibits elevated values at ~10 cm (~1970 ± 12 years) which aligns with the secondary transition observed in the other pigments (Fig. 6). It is a pigment associated with *aphenozomenon flos-aquae*, which is a species of cyanobacteria that is present in Utah Lake harmful algal blooms (Randall et al. 2019). Pigments that exhibited a subsequent transitional decrease in concentration included diadinoxanthin, diatoxanthin, and fucoxanthin (Fig. 6). However, none of the concentrations returned to the natural levels prior to human settlement, which indicates that the lake is still largely influenced by anthropogenic impacts. Many cities around the lake had constructed WWTPs by 1954, which could explain the subsequent transitional decrease observed in some of the pigments. Utah Lake continues to be faced with the impacts of cultural eutrophication and harmful algal blooms as external nutrient loading to the lake continues.

Conclusion

This study shows that the introduction of common carp and nutrient loading were likely the main driver of a regime shift from a clearwater, macrophyte-dominated regime to the current turbid, phytoplankton-dominated regime in Utah Lake. However, ongoing nutrient additions have led to a persistent increase in lake phytoplankton production with increased cyanobacterial presence. Additionally, the construction of wastewater treatment plants has contributed to maintaining the eutrophic state of the lake by influencing the source and processing of nutrients. The current eutrophic state of Utah Lake can be largely attributed to human influence, as the timing of the significant regime shift aligns with human activities within the watershed.

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CHAPTER 3

PRIMARY PRODUCTION MODELING MAY IMPROVE RESTORATION

PLANNING IN A SHALLOW, EUTROPHIC LAKE

Abstract

Benthic primary production can play an important functional role in lakes by improving water quality and clarity. This is accomplished via several mechanisms, including stabilizing sediments against resuspension, competing with phytoplankton for nutrients, and providing zooplankton refugia. However, eutrophic lakes which have lost their benthic communities can be notoriously difficult to restore to clear-water conditions, as turbid communities are likewise self-stabilizing. As benthic primary production in nutrient-rich lakes is primarily limited by light availability, predictive ecosystem models can provide guidelines for the water clarity levels necessary to re-establish a dominant benthic primary producer community, considering lake-specific traits. Here, I describe the benthic, planktonic, and total primary productivity of a large, turbid (mean Secchi depths = ~0.25 m), shallow lake (Utah Lake, USA), and explore the potential for altering plant community structures for improving lake restoration plans. I found present-day (2018) primary production in Utah Lake to be strongly dominated (~ 99%) by phytoplankton. Models indicate that a transition to benthic dominance would be possible at current water clarity conditions when the lake is at low pool water levels, or with water clarity increases of 0.9 m (at 2018 water levels), or 2.5 m at full pool (last attained in 2011). However, I discuss potential complications in restoration strategies given the effects of wind mixing on sediment resuspension at low water levels. Analyzing wind-protected lake areas (Goshen Bay, Provo Bay) separately, I identify a necessary increased

water clarity of 0.3 m (from 2018 means) for benthic dominance in these areas, which may be possible to attain via nutrient loading efforts which reduce water column Chlorophyll *a* concentrations to ~18 μg L^{-1} (2018 mean lake-wide values = ~40 μg L^{-1}). Overall, I provide a first estimate of the likely historical water clarity conditions in Utah Lake, in fitting with literature and paleolimnological analyses, and also present lake restoration guidelines for contemporary managers interested in returning the lake to historical conditions.

Introduction

Cultural eutrophication remains an important global issue, despite advances in nutrient loading reduction strategies. Urbanization, agricultural practices, and wastewater loading continue to increase nutrient concentrations in many lakes. Poor water quality conditions can have considerable economic and ecological impacts, including a loss of local recreation revenue and harmful impacts on fish and other aquatic life by reducing food and habitat (Carpenter et al. 1998; Dodds et al. 2008). Water managers routinely use a wide variety of mitigation strategies to minimize the effects of anthropogenic activities. However, these strategies can be time-consuming, costly, and ineffective in complex lake ecosystems (Chislock et al. 2013). Nutrient reduction strategies alone may be insufficient to return a lake to its pre-impact conditions (Jeppesen et al. 2005; Brothers et al. 2017) due to the multiple and complex drivers of eutrophication. There is thus a growing need for lake management and restoration strategies which incorporate our current understanding of aquatic ecosystem functioning for improved success.

Given the complexity of factors controlling eutrophic conditions, lake management and restoration strategies are increasingly considering the functional

potential of plant community structure (Smith and Schindler 2009). Regime shift theory, which centers on the idea that ecosystems do not respond gradually to perturbations, but instead can shift between alternative self-stabilizing "regimes", provides a useful framework to better understand how the role of lake primary production (PP) conditions may be able to help us understand and manage phytoplankton dominance. Shallow lakes often exhibit one of two self-stabilizing regimes: a clear-water, macrophyte-dominated regime or a turbid, phytoplankton dominated regime (Scheffer et al. 1993). Research has historically focused on the role of phytoplankton on aquatic processes and water quality, and only recently has it begun to more consistently examine the role of periphyton and submerged macrophytes on lake ecosystem dynamics and functioning (Vadeboncoeur et al. 2002; Hilt et al. 2017). Due to logistical difficulties, benthic periphyton PP is not frequently measured in lake ecosystem studies; however, it can be modeled using established PP models to provide current and potential estimates. The integration of benthic periphyton (attached algae) and submerged macrophyte PP into our understanding of lake ecosystem functioning could enhance the development of lake management strategies, given the potentially important functional role of benthic PP in improving lake water quality and clarity (Schindler and Scheuerell 2002; Vadeboncoeur and Steinman 2002; Dodds 2003). Mechanistically, benthic PP can reinforce a clearwater state by promoting piscivore control over planktivorous fish (Blindow et al. 1992), providing habitat refuge for zooplankton (Burks et al. 2002; Genkai-Kato 2007), reducing sediment resuspension from wind mixing (Barko and James 1998; Hilt and Gross 2008), and sequestering water column nutrients to the sediments (reviewed by Hilt et al. 2017). However, the self-stabilizing mechanisms of phytoplankton-dominated regimes can make

macrophyte recolonization difficult (Hilt 2006) due to increased turbidity from sediment resuspension and disturbance from fish and birds (Hilt 2006 and references therein; Hidding et al. 2016).

Nutrient reduction strategies can lead to significant improvements in water quality and clarity, though the natural re-establishment of functionally valuable submerged macrophyte communities can be slow or absent (Jeppesen et al. 2005; Hilt et al. 2006). This has led to an increased consideration of submerged macrophytes in guiding management strategies. Previous research has largely focused on biomanipulation strategies to initiate regime shifts (Shapiro and Wright 1984; Moss et al. 1996; Søndergaard et al. 2008). Food web manipulation typically involves the removal or addition of fish stocks to beneficially manipulate the food web (Hansson et al. 1998). The removal of fish stocks has the potential to increase light transparency and promote macrophyte recovery (Gulati et al. 1990), as well as increase predation by zooplankton on phytoplankton (Henrikson et al. 1980; Reinertsen et al. 1990) via direct and indirect food-web interactions. However, even successful attempts to reduce the populations of detrimental invasive fish species (such as the common carp) are typically unable to completely extirpate such species from a system, making long-term management strategies potentially interminable and costly. The physical planting of submerged macrophytes to re-establish their presence in aquatic systems has been found to have a positive impact on water clarity in warm, shallow lakes (Liu et al. 2018) as well as coastal ecosystems (Lefcheck et al. 2018). Such efforts can be combined with large-scale enclosures to protect returning submerged macrophyte communities from multiple

stressors including wave-driven resuspension events and grazing by fish (Chen et al. 2009).

Despite the many management techniques available, the science behind managing eutrophic lakes is complex and inexact. Liere and Gulati (1992) suggest that each lake must be studied independently prior to implementation of restoration management techniques because the outcome of a given method can be difficult to predict. The National Research Council (1992) suggest that while restoration attempts in shallow, well-mixed, eutrophic lakes can be effective in the short-term, it is more difficult to maintain long-term improvements in a shallow lake than in deep, stratified lakes due to a greater importance and complexity of internal nutrient loading mechanisms (e.g., Welch et al. 1988). Large, abrupt changes in water levels have also been found to initiate regime shifts (Scheffer et al. 1993), which can pose an additional management challenge for shallow lakes that experience significant annual water level fluctuations. In such instances, management techniques must consider the effects of fluctuating lake levels, which affects littoral habitat availability as well as light supply to the sediments, and thus the ability of benthic primary producers to re-establish.

This research applies functional ecology and regime shift theory to provide a novel restoration strategy for a large, shallow, eutrophic lake (Utah Lake, USA) which is subject to natural major interannual water level fluctuations and frequent wind-driven resuspension events. Paleolimnological analyses, combined with historical reports, indicate that the lake historically featured clearer waters with greater macrophyte coverage than observed today (see Chapter 1). I thus use *in situ* data and primary production (PP) modeling to calculate periphyton and phytoplankton gross PP to predict
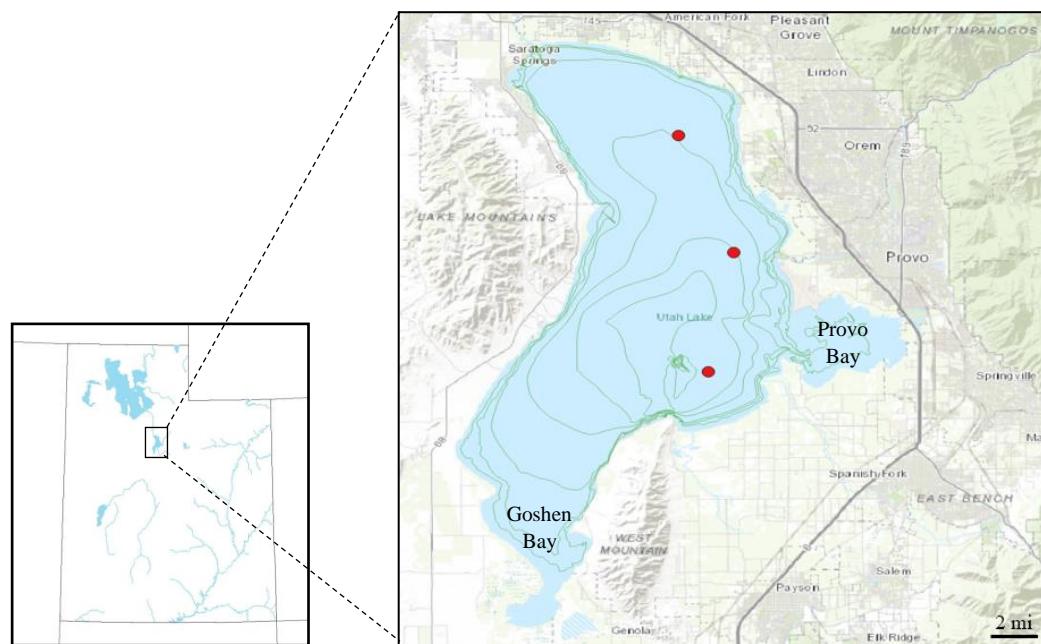
how lake PP partitioning will respond to water clarity management at various water levels, providing guidance into the light requirements necessary to re-establish benthic dominance. By examining a lake with extremely poor water quality conditions that is known to historically feature a clearwater, macrophyte-dominated state, modeling the water clarity necessary for benthic dominance provides insight into the lake's historical water clarity, as well as water clarity targets for contemporary lake management strategies. I hypothesize that the conditions necessary for establishing a clear-water state are attainable within the range of recent water level fluctuations and argue that the active re-establishment of benthic primary producers in Utah Lake should be considered a key component in long-term cost-effective strategies aimed at improving the lake's water quality.

Study Site Description

Utah Lake is a large (surface area = 385 km²), shallow (max. depth = 4.3 m) lake located in north-central Utah (Fig. 3-1). It features several hallmark indicators of a turbid (average Secchi depth = ~0.25 m), eutrophic (mean annual total phosphorus = 80 µg/L) lake, including recurrent harmful algal blooms (HABs) since the 1970s (Strong 1974). Whether or not Utah Lake experienced a historical regime shift to phytoplankton dominance is not yet fully understood. Previous reports indicate that the lake historically (in the late 19th Century and early 20th Century) featured a healthy submerged macrophyte community (Bushman 1980 and references therein). Tanner (1931) measured Secchi depths ranging from 0.15 to 1 m, indicating that the lake was occasionally turbid during that period, but also historically exhibited clearer water than it does today (the maximum recorded Secchi depth in 2018 was 0.3 m; Utah Lake Data Explorer,

https://udwq.shinyapps.io/UtahLakeDataExplorer/). By the early-to-mid 20th Century there were reports of increasing turbidity and species shifts to more turbid-adapted submerged macrophytes, such as broadleaf pondweed (*Stuckenia striata*, previously *Potamogeton latifolius*; Bingham 1975 and references therein; Bushman 1980 and references therein). While substantial submerged macrophyte communities have been reported as recently as the 1970s, particularly in Goshen Bay and Provo Bay (Brotherson 1981), they have only rarely been observed in more recent years (Janetski 1990; Miller and Crowl 2006; pers. comm. K. Landom). Due to its large surface area, Utah Lake is highly susceptible to wind-driven sediment resuspension events, which are frequently considered to be a primary barrier to the establishment of submerged macrophyte communities, although the lake also features two bays (Goshen Bay and Provo Bay) which are relatively protected from the prevailing winds (Fig. 1). However, the establishment of littoral-zone primary producers may be further complicated in Utah Lake by its shallow sediment slope and location in a watershed which features high interannual hydrological fluctuations, as well as the lake's use as a controlled reservoir, increasing interannual water-level fluctuations and regularly exposing large areas of land. Since the 1930s, the lake's surface water levels have risen and fallen by approximately 4 m. In addition to these physical challenges to macrophyte communities, the 1881 introduction of invasive benthic-feeding common carp (*Cyprinus carpio*) is believed to have severely reduced the abundance of macrophytes (Miller and Crowl 2006; Miller and Provenza 2007) by destabilizing lake sediments and exacerbating lake turbidity (Rivera et al. 2013), with high nutrient enrichment to the lake likely exacerbating the loss of submerged macrophytes (Scheffer et al. 1993; Hidding et al. 2016). This is supported by

Fig. 3-1 Map of Utah Lake with bathymetry contours at 0.3 m intervals (green lines) and buoy locations (red dots). Adapted from the Utah Department of Environmental Quality (DEQ).

paleolimnological proxy datasets indicating the existence of a transitional period in the lake's recent history, marking a decrease in macrophyte communities coinciding with the period of carp introduction (Chapter 1 of this thesis; Bolland 1974).

Methods

Analyses

To examine the water quality conditions necessary for a historic dominance of benthic primary producers in Utah Lake, I reconstructed the benthic and planktonic partitioning of the lake's PP across a gradient of water clarity and water levels. In these analyses, I considered a submerged macrophyte presence covering 30% of the lake's surface area to represent a critical threshold for indicating benthic dominance over planktonic processes (Canfield et al. 1984; Hilt and Gross 2008 and references therein).

Long-term modeled gradients involved increasing the lake's mean annual water clarity by up to 3 m, at 0.1 m intervals for the first meter and then every 0.5 m thereafter. Due to high interannual water level fluctuations in Utah Lake, the lowest lake elevation in the past 80 years was 3 m below full pool (1,365 m above sea level; Utah Lake Data Explorer). Full pool is here defined as the lake surface elevation of 1,368 m above sea level (a.s.l.), which since 1985 has been established as the controlled maximum lake level. Given that water levels influence the light availability to the lake sediment surface, which is a primary limitation of benthic periphyton PP (Vadeboncoeur et al. 2008), I modeled PP at full pool, 2018 water levels (1,367 m a.s.l.), and at low-pool (the 80-year minimum water level; 1,365 m a.s.l.). I also ran separate analyses for Goshen Bay and Provo Bay (Fig. 1) as historical records emphasized the presence of submerged macrophytes in these locations, which are also where many contemporary algal blooms reportedly form (Bradshaw et al. 1973; Brotherson 1981; pers. comm. S. Daly, DWQ). Being relatively sheltered from wind-driven sediment resuspension events, I also considered them independently as potentially promising restoration sites within Utah Lake. I only modeled the bays at 2018 and full-pool water levels, as they would be dry at low-pool water levels. Provo Bay represents 6.5%, and Goshen Bay 7.5%, of the total lake surface area.

Although phytoplankton production-to-Chlorophyll a (Chl a) concentration relationships have been previously established in lakes (e.g., del Giorgio and Peters 1993), Utah Lake's water clarity is strongly influenced by sediment resuspension dynamics. I thus assume that its phytoplankton productivity may not follow the same pattern as that established for lakes whose turbidity is primarily determined by algal

biomass. To account for Utah Lake's potentially unique light environment, I applied

light-integrated models for planktonic (Silsbe and Malkin 2015) and benthic periphyton

PP (Vadeboncoeur et al. 2008; Brothers et al. 2016) to estimate the rates of phytoplankton

and periphyton PP in Utah Lake. Lacking lake-specific algal photosynthesis-irradiance

(PI) curve parameters, I calibrated the phytoplankton production model to 2018 using

measured contemporary PP rates. Although I recognize the importance of competitive

interactions between macrophytes and periphyton in eutrophic lakes (Vadeboncoeur and

Steinman 2002; Hidding et al. 2016), I here broadly consider the light conditions required

for periphyton PP to be analogous to conservative initial thresholds for the light

requirements of submerged macrophytes as well, which would play an important role in

stabilizing sediments, competing with phytoplankton for nutrients, and providing fish and

macroinvertebrate habitat (Sand-Jensen and Borum 1991; Blindow et al. 1992;

Søndergaard and Moss 1998; Jeppesen et al. 2012).

Whole-Lake Primary Production Measurements

Contemporary lake metabolism rates were calculated using a diel oxygen

technique (Staehr et al. 2010). Dissolved oxygen, water temperature, and other relevant

water quality variables were measured every 15 minutes from April 11th to October 31st,

2018 at three buoys (near Provo Bay, Bird Island, and Vineyard) operated and maintained

by the Utah Division of Water Quality (Fig. 1). The average monthly metabolism rates of

April and October were applied to remaining months for which no data were available.

Wind speeds were obtained from the National Center for Environmental Information

(NCEI) from a weather station at the Provo Airport. Daylight hours were determined

from sunrise and sunset time obtained online (https://sunrise-sunset.org/). The salinity of

Utah Lake was assumed to be 0.9 ppt (Merritt 2017).

The diel open-water dissolved oxygen technique is based on the governing

equation (Odum 1956):

$$\text{(Eq. 1) } \Delta O_2/\Delta t = GPP - R - F - A$$

where GPP is gross primary production, R is ecosystem respiration, F is the physical gas

flux with the atmosphere, and A is all other processes that result in changing DO

concentrations.

Piston velocity, k (m hr^{-1}), was calculated (following Jahne et al. 1987; Cole and Caraco

1998; Wanninkhof 1992) as:

$$\text{(Eq. 2) } k = [(2.07 + 0.215U_{10}^{1.7})/100] * [(0.0476T^3 + 3.7818T^2 - 120.1T + 1800.6)/600]^{-0.5}$$

where U_{10} = wind speed, at a height of 10 m, (m sec^{-1}) and T = water temperature (°C).

Physical oxygen exchange with the atmosphere, F (g O_2 m^{-2} h^{-1}), was calculated (from

Staehr et al. 2010) as:

$$\text{(Eq. 3) } F = k \ (O_{2meas} - O_{2sat})$$

where k = the piston velocity (m hr^{-1}) and O_2 is in mg L^{-1}. Net ecosystem production per

hour, NEP_{hr} (g O_2 m^{-3} h^{-1}), was calculated (from Cole et al. 2000) as:

$$\text{(Eq. 4) } NEP_{hr} = \Delta O_2 - F/Z_{mix}$$

where Z_{mix} is assumed to be the average lake depth (Utah Lake = 3.2 m). The proportion of NEP during daylight hours, $NEP_{daytime}$ (g O_2 m^{-3} daylight period^{-1}), was calculated as the mean daytime NEP_{hr} multiplied by the number of daylight hours. Hourly ecosystem respiration (R_{hr}, g O_2 m^{-3} h^{-1}) was calculated as the mean nighttime NEP_{hr}, as no photosynthesis occurs at night, and assuming nighttime respiration is equal to daytime respiration. Respiration for the entire 24-hour day period, R_{day}, was calculated as R_{hr} multiplied by 24 hours; and the respiration only during daylight hours, $R_{daytime}$ (g O_2 m^{-3} daylight period^{-1}), was calculated as R_{hr} multiplied by the number of daylight hours. GPP (g O_2 m^{-3} d^{-1}) and NEP (g O_2 m^{-3} d^{-1}) for the whole system were calculated (from Staehr et al. 2010) as:

$$\text{(Eq. 5) } GPP = NEP_{daytime} + R_{daytime}$$

$$\text{(Eq. 6) } NEP = GPP - R_{day}$$

GPP and NEP were converted to g C m^{-3} d^{-1} by dividing by 2.67 (assuming a respiratory quotient of 1). Following Staehr et al. (2010), I used monthly mean depth (m) at each buoy to convert volumetric rates to areal production rates and to adjust for water level fluctuations throughout the year (Table 3-1). Lastly, I calculated the lake-area weighted production rates based off the approximate lake surface area represented by each buoy (Vineyard = 105 km^2, Provo = 131 km^2, Bird Island = 149 km^2). Although the diel oxygen curve approach technically integrates benthic and planktonic PP, given the off-shore

Table 3-1 Average monthly water depth (m) at DWQ buoy locations.

Month	Provo Bay	Vineyard	Bird Island
January	2.49	2.45	2.60
February	2.59	2.56	2.70
March	2.68	2.64	2.79
April	2.76	2.72	2.87
May	2.69	2.66	2.80
June	2.63	2.59	2.74
July	2.38	2.35	2.49
August	2.17	2.13	2.28
September	1.95	1.91	2.06
October	2.01	1.98	2.12
November	2.07	2.03	2.18
December	2.06	2.03	2.17

location of these monitoring stations and the very low Secchi depths, I considered these

PP values to essentially represent phytoplankton production in Utah Lake.

Phytoplankton Production Modeling

The R package Phytotools (Silsbe and Malkin 2015 and references therein) was

used to calculate phytoplankton production in the water column. The incident command

simulates photosynthetically active radiation (PAR) across a defined time period (2018),

latitude (40.2130°), longitude (-111.8025°), elevation (1,368 m), and time zone (-6

Universal Coordinated Time). PAR (μmol m^{-2} s^{-1}) was determined monthly for all of

2018, using a Linke turbidity factor = 3.5 and subtracting the irradiance reflected off the

water's surface from PAR values following Kirk (2011). Photosynthesis-irradiance (PI)

curve parameters (Fig. A3) were calibrated to match the mean annual GPP (g C m^{-2} year^{-1})

measured in Utah Lake via the diel oxygen curve approach (described above), using

the Jassby and Platt (1976) model fitted by the Nelder-Mead method (Silsbe and Malkin,

2015). I applied a light utilization efficiency parameter (the initial slope of the PI curve,

α), of 7.53 g C m^2 (g Chl a mol)$^{-1}$, derived from another shallow eutrophic lake (West Basin of Lake Erie; Smith et al. 2005). I then adjusted the value of the irradiance at the inflection of α and light-saturated maximum productivity (I_k), applying 2018 measured Utah Lake water clarity data, so that the modeled mean phytoplankton PP matched Utah Lake's measured 2018 phytoplankton PP. This provided an I_k value of 33 μmol m^{-2} s^{-1} and a maximum light-saturated production rate of ~250 mg C m^{-3} hr^{-1}.

Utah Lake's total phytoplankton production was calculated (using Silsbe and Malkin 2015) as a function of irradiance, light attenuation (K_d, m^{-1}), algal PI parameters, maximum mixing depth (Z_{max}), and monthly Chl a concentrations (μg L^{-1}). Z_{max} was 4.3 m at full pool, 3 m at 2018 water levels, and 1.2 m at low-pool levels. Goshen Bay and Provo Bay had a Z_{max} of 2.7 m at full pool and 1.5 m at 2018 water levels. The bays are too shallow to exist at full pool and therefore I only analyzed contemporary and full-pool water levels within the bays. Mean monthly Chl a concentrations from 2018 were used for model calibration to the diel oxygen curves. For modeling phytoplankton PP with changes in water clarity, monthly Chl a was calculated by applying 2018 monthly trends in Chl a concentrations to mean annual Chl a values derived from the measured relationship (Eq. 7, $r^2 = 0.16$, $p < 0.0001$) between water clarity and Chl a concentrations from 2017-18 (Fig. A4; Utah Lake Data Explorer), using the equation:

$$(Eq.\ 7)\ Chl\ a = 10.204992 + 2.1807127/(Z_{Secchi}) + 1.0670865/(Z_{Secchi})^2$$

Due to regular water column mixing, mean monthly Chl a concentrations measured at the surface were assumed to be uniform across the water column. Light attenuation values

were calculated from mean monthly 2018 Secchi depths (Table 3-2, Utah Lake Data

Explorer). Light attenuation calculated from Secchi depths using standard methods (Idso

and Gilbert 1974) were found to underestimate light transmission in Utah Lake

(measured by the DWQ in 2019), which I attributed to the predominance of resuspended

sediments, rather than algal biomass, as the primary driver of water clarity in Utah Lake.

Attenuation coefficients (K_d) were therefore calculated as $K_d\ (m^{-1}) = 0.89 + 0.536/Z_{Secchi}$,

which was derived from concurrently measured Utah Lake Secchi depths and light

attenuation (2019, DWQ), following the exponential decay relationship described by Idso

and Gilbert (1974). Although PP models are based on estimates of PAR at various lake

water depths, I here present necessary water clarity changes in Secchi depths (rather than

K_d) as they may provide a more meaningful tool and target for lake managers.

Table 3-2 Average 2018 monthly Secchi depths, daylength, solar radiation, and Chlorophyll *a* values for Utah Lake. Values in parentheses represent the average Chl *a* concentrations from 1978-2016 (Utah Lake Data Explorer) used for long-term phytoplankton models.

Month	2018 Secchi Depth (m)	Average Daylength (hr)	Solar Radiation ($\mu mol/m^2 s$)	Chlorophyll *a* ($\mu g/L$)
January	0.21	10	4761.0	21
February	0.21	11	4862.2	21
March	0.21	12	4908.2	21
April	0.21	13	4899.0	21
May	0.23	14	4862.2	27.4
June	0.18	14	4830.0	53
July	0.2	14	4820.8	97.5
August	0.23	13	4839.2	71.6
September	0.15	12	4857.6	39.5
October	0.30	11	4834.6	30.8
November	0.19	10	4765.6	14.6
December	0.21	9	4715.0	21

Benthic Periphyton Production

The shallow sediment slope of Utah Lake provides a high potential for supporting littoral benthic PP. I focus on benthic periphyton as its productivity in lakes is well-established in models (e.g., Vadeboncoeur et al. 2008), while further considering that the improved light climate from periphyton dominance would be a necessary precursor for the re-establishment of submerged macrophytes, which provide a key structural distinction between turbid and clearwater regimes. However, the presence of periphyton alone can greatly improve the resistance of sediment to shear stress/resuspension events (Vignaga et al. 2012) and influence regime shifts in shallow lakes (Genkai-Kato et al. 2012).

Table 3-3 Total surface area (% and m^2) associated with depth intervals within Utah Lake (and the individual bays) based off the bathymetry contour maps, assuming a full lake level at 1,368 m.

Depth (m)	Surface Area (m^2)	Total SA (%)
0-1.2	61,763.80	16.06
1.2-1.5	18.93	0.005
1.5-2.1	27,842.82	7.24
2.1-2.7	40,638.07	10.57
2.7-3.4	109,891.15	28.58
3.4-3.7	70,289.28	18.28
3.7-3.8	49,836.23	12.96
3.8-4.0	22,541.21	5.86
4.0-4.3	1,678.50	0.44
TOTAL	**384.5 km^2**	**100%**

Depth (m)	Goshen Bay (m^2)	Total SA (%)	Provo Bay (km^2)	Total SA (%)
0-1.5	11,010,000	38.2	16,910,000	68.1
1.5-2.1	6,310,000	21.9	7,620,000	30.7
2.1-2.7	11,490,000	39.9	300,000	1.2
TOTAL	**28.81 km^2**	**100**	**24.83 km^2**	**100**

I adopted a standard benthic PP model which assumes that periphyton production in Utah Lake is light, rather than nutrient, limited (Vadeboncoeur et al. 2008; Brothers et al. 2016). I applied a conservative maximum, light-saturated rate of PP (BP_{max}) value of 30 mg C m^{-2} hr^{-1} based on literature values for periphyton in lakes (Vadeboncoeur et al. 2008; Vander Zanden et al. 2011; Brothers et al. 2016 and references therein). Following Brothers et al. (2016), I_k (value of the irradiance at the inflection of α and light-saturated maximum productivity) was calculated as:

$$\text{(Eq. 8) } I_k = 334.5 * e^{-Z*Kd} + 68.$$

The maximum benthic periphyton at a specific depth, BP_{maxZ} (mg C m^{-2} hr^{-1}), was calculated at each bathymetric depth interval for each month of the year. To account for both the positive effects of light access on benthic PP as well as the negative effects of wave action at shallower depths, separate calculations were made for depth gradients above and below 50% surface light availability, with the depth at 50% light availability assumed to feature the highest rates of benthic PP (following Brothers et al. 2016). When the light at a depth interval was greater than 50% surface light, BP_{max} (mg C m^{-2} hr^{-1}) was calculated as:

$$\text{(Eq. 9) } BP_{maxZ} = [(15/(\ln(0.5)/-K_d))*Z]+15.$$

When less than 50% surface light was available to the sediment surface, the following equation was used:

$$\text{(Eq. 10) } BP_{maxZ} = BP_{maxZ50} * [(2 * PAR_Z) - 0.1]$$

where PAR_Z (µmol m^{-2} s^{-1}) is the fraction of I_0 at a given depth (Z, m). Periphyton

production at each depth (mg C m^{-2} h^{-1}) was then calculated in half-hour intervals using

the equation:

$$\text{(Eq. 11)} \quad BP_Z = BP_{maxZ} * \tanh[(I_{0,t}) * \sin(\pi * (t / daylength)) * e^{-Kd * Z} / I_k]$$

where $I_{0,t}$ was the surface irradiance at time, t (h). Production intervals were summed

over the course of the day and divided by 2 to calculate the rate of production per day,

then multiplied by the percentage of total surface area for that depth to determine the

area-weighted production. The sum across all depths represented the daily periphyton

production throughout the lake.

Secchi depths from 2018 were obtained from the Utah DWQ (Table 3-2). Secchi

depths were measured at 8 locations throughout the lake on two consecutive days each

month. The average monthly Secchi depth was used to calculate light attenuation (K_d, m^{-1}) using the same equation described for phytoplankton models. The sediment surface

area across water depth intervals was calculated using bathymetry contours obtained from

the Utah DWQ (Table 3-3). As with phytoplankton PP models, month-specific daylength

(h) and solar radiation (µmol m^{-2} s^{-1}) were obtained through online calculators (based on

the 15th of each month; www.timeanddate.com, www.cableizer.com; Table 3-2).

Results

Contemporary (2018) Utah Lake Primary Production

The whole-lake gross primary production (GPP) of Utah Lake in 2018 was

calculated from *in-situ* measurements to be 568 g C m^{-2} year^{-1} (Table 3-4). Pooling data

from all stations, monthly measured GPP ranged from 15.0-182 g C m^{-2} month^{-1}.
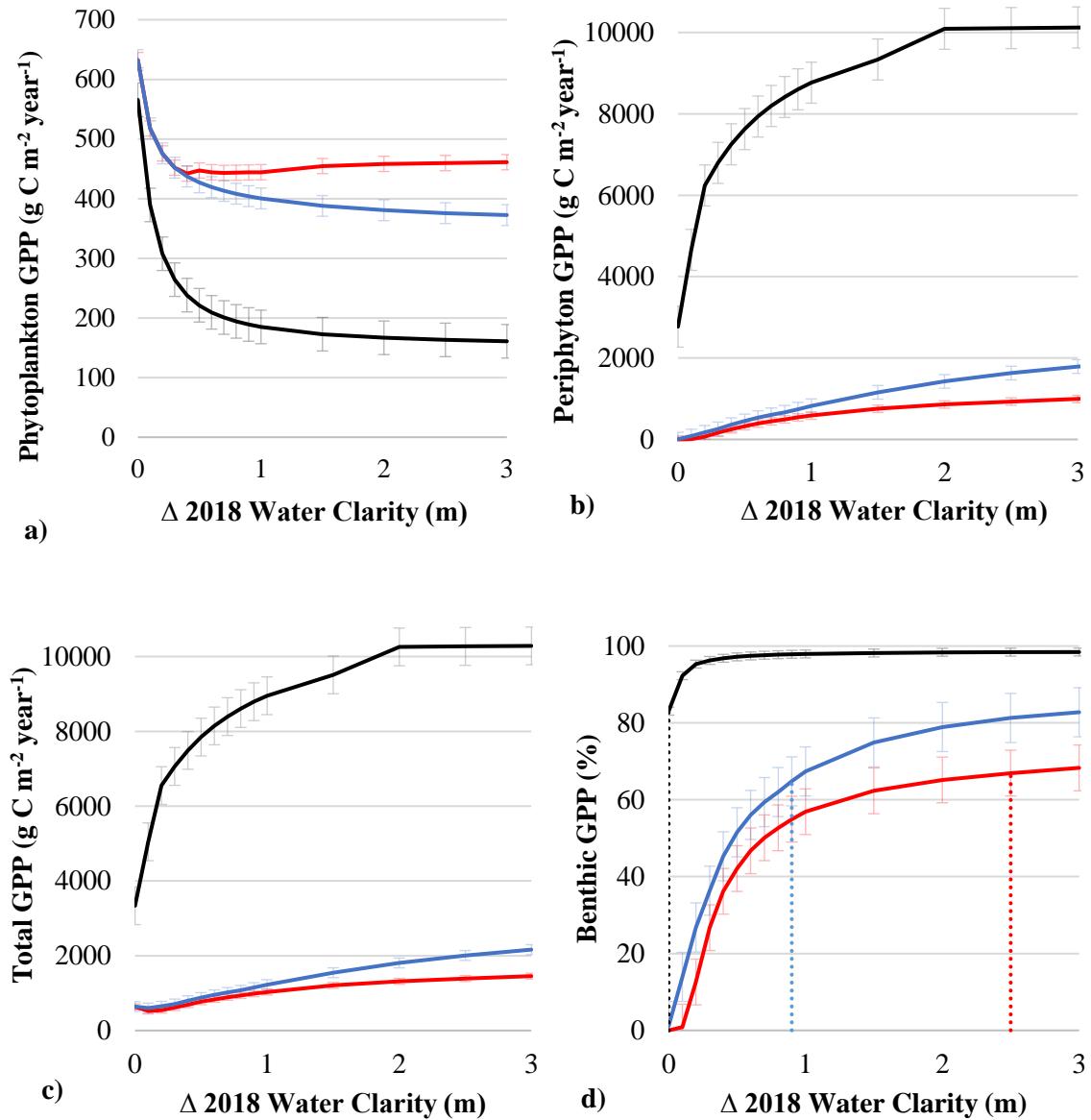
Monthly modeled 2018 phytoplankton PP ranged from ~15.8 to 143 g C m^{-2} month^{-1}, indicating that the model PI-curve parameters reasonably-well reflected the measured inter-seasonal range of variability of phytoplankton PP in Utah Lake (Table 3-4). Given extremely poor light conditions in 2018 (Secchi depths typically < 0.3 m), contemporary modeled benthic periphyton production was minor, representing roughly 1% of Utah Lake's annual modeled PP (Table 3-4). In sum, monthly whole-lake modeled PP was largely in agreement with measured values. I therefore considered it to be a valid model with which to compare benthic versus planktonic PP dominance along a gradient of water clarity and surface water levels.

Table 3-4 Monthly areal GPP rates (g C m^{-2} month^{-1}) from monitoring stations, phytoplankton model, and periphyton models for 2018, applying a 2018 lake elevation of 1,367 m (1.2 m below full pool) and 2018 mean monthly Chlorophyll *a* concentrations and Secchi depths (Table 3-2). The whole-lake modeled GPP estimate is the sum of the phytoplankton and periphyton estimates for 2018.

Month	Bird Island Measured PP	Provo Bay Measured PP	Vineyard Measured PP	Phytoplankton Modeled PP	Periphyton Modeled PP	Whole-lake Modeled GPP	Whole-lake Measured PP
January	20.72	28.46	24.13	16.97	0.03	17.00	24.28
February	21.55	29.65	25.15	18.48	0.03	18.51	25.29
March	22.24	30.63	26.00	24.60	0.04	24.64	26.12
April	25.40	26.50	20.95	27.55	0.04	27.59	24.56
May	32.67	33.80	27.69	43.44	0.54	43.98	31.7
June	38.03	53.66	44.90	71.19	0.04	71.23	45.22
July	134.34	182.56	30.04	143.19	0.04	143.23	122.26
August	107.79	168.66	100.16	106.96	0.5	107.46	126.4
September	57.81	101.11	87.64	36.74	0.02	36.76	80.68
October	15.05	26.67	23.64	40.14	5.79	45.93	21.35
November	17.38	23.68	20.01	11.20	0.03	11.23	20.24
December	17.31	23.68	19.93	15.80	0.03	15.83	20.16
TOTAL	**510**	**729**	**450**	**556**	**7.13**	**563**	**568**
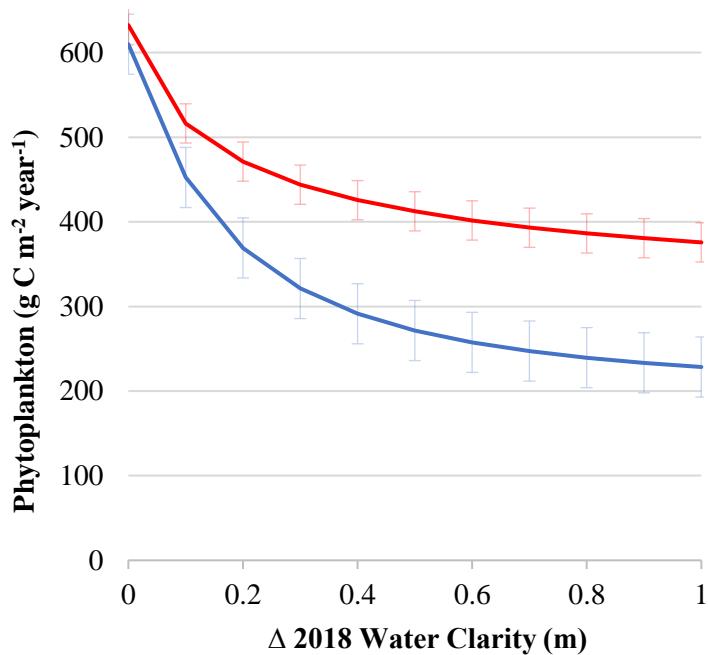
Historical Primary Production Modeling

Primary production was modeled along a 3 m water clarity gradient at full pool, contemporary (2018), and low-pool (80-year minimum) water levels. Modeled trends in areal annual phytoplankton PP reflected both the influence of water column thickness as well as the effect of decreasing phytoplankton biomasses associated with higher water clarities, with the greatest PP declines occurring at low-pool water levels (Fig. 3-2a). Increases in modeled periphyton productivity, on the other hand, reflected the interaction between the lake morphometry and changes in light availability at the sediment surface. Along a water clarity gradient from mean 2018 Secchi depths to 3 m increased clarity, annual periphyton production increased dramatically, from ~0 to 1,800 g C m^{-2} year^{-1} considering either full pool or contemporary water levels, or from ~2,770 to 10,160 g C m^{-2} year^{1} at low-pool water levels (Fig. 3-2b). Whole-lake GPP (phytoplankton + periphyton) followed the same pattern as periphyton GPP (Fig. 3-2c) due to the elevated periphyton production rates, yet still reflects the influence of water column thickness allowing for greater phytoplankton production. The percentage of periphyton production relative to whole-lake PP increased rapidly with increasing water clarity, particularly within the first 1 m increase in water clarity (Fig. 3-2d). High water levels exhibit the lowest percentage of periphyton production due to the added water column thickness. These models indicate that a benthic dominance threshold would be surpassed with water clarity increases of 2.5 m at full pool, 0.9 m at contemporary water levels, and at current water clarity conditions at low-pool (Fig. 3-2).
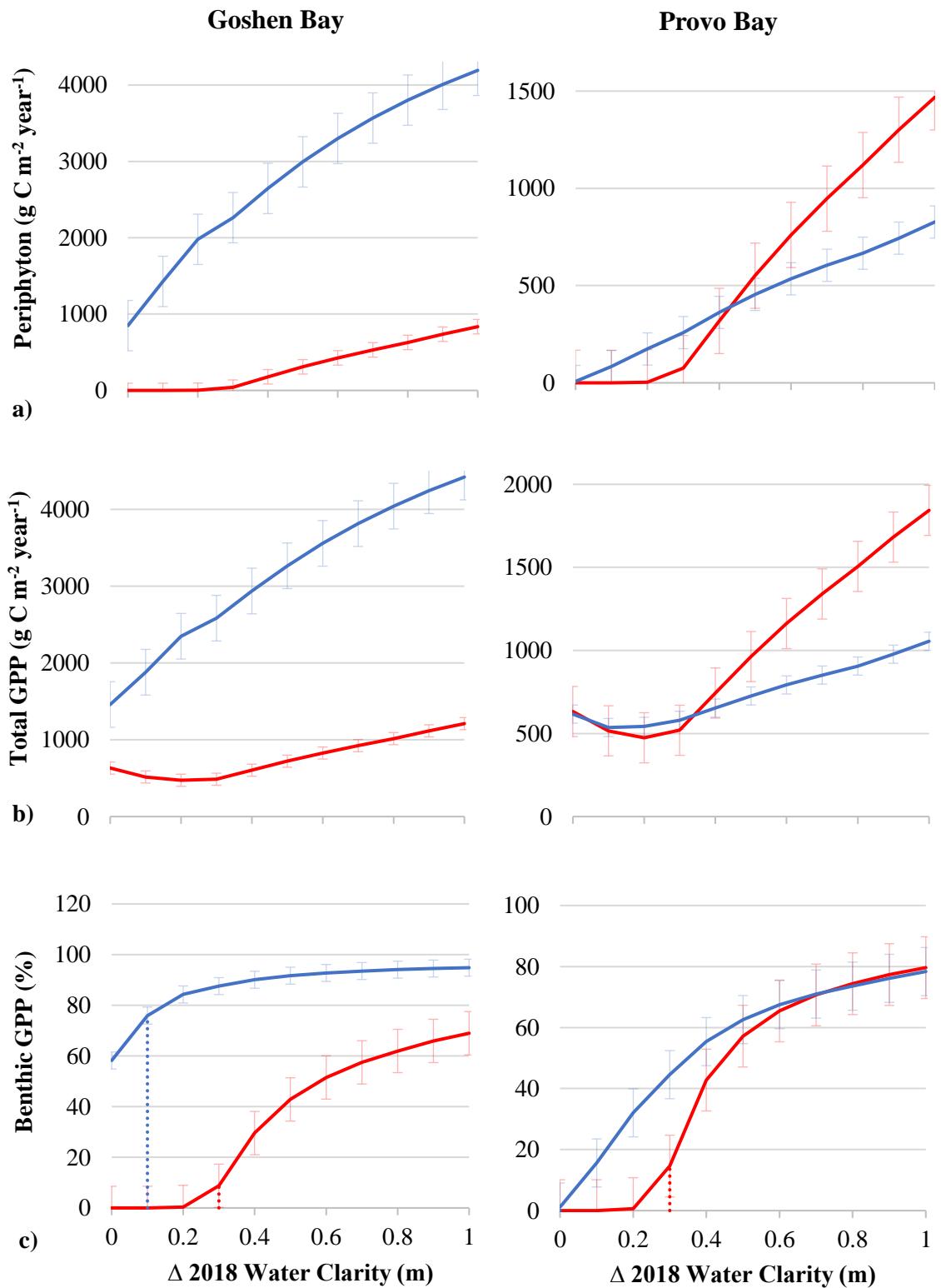
Fig. 3-2 Phytoplankton PP (a, g C m^{-2} year^{-1}), periphyton PP (b, g C m^{-2} year^{-1}), total GPP (c, g C m^{-2} year^{-1}), and percentage of benthic GPP (d, %) modeled at a whole-lake scale along a gradient of increasing water clarity at full pool (red lines), contemporary water levels (blue lines; 1.2 m below full pool), and minimum water levels (black lines; 3 m below full pool). The Secchi depth of 0 m represents the mean monthly Z_{Secchi} from 2018 (Table 3-2), with every number thereafter indicating an increase of that amount from the current mean value. The dashed lines indicate the 30% areal benthic dominance threshold associated with each water level.

Model estimates for phytoplankton and periphyton PP were also made along a gradient of increasing water clarity conditions in Utah Lake's two sheltered bays, Provo Bay and Goshen Bay. Annual phytoplankton production decreased with increasing water clarity in both Provo Bay and Goshen Bay (Fig. 3-3). Annual periphyton production increased exponentially with increasing water clarity (Fig. 3-4a). Provo Bay periphyton production rates were substantially smaller than Goshen Bay periphyton production rates at increases water clarities. Although the model indicates that in Provo Bay, no water clarity improvements would be necessary at current water levels to allow for benthic dominance, this is slightly misleading due to the basin's morphometry. This model indicated that water clarity in Provo Bay and Goshen Bay would need to be increased by a minimum of 0.3 m to allow for benthic dominance at full pool (Fig. 3-4b).


Fig. 3-3 Phytoplankton PP (g C m^{-2} year^{-1}) modeled in Goshen Bay and Provo Bay at full pool (red lines) and contemporary water levels (blue lines; 1.2 m below full pool). The Secchi depth of 0 m represents the mean monthly Z_{Secchi} from 2018 (Table 3-2), with every number thereafter indicating an increase of that amount from the current mean value.

Goshen Bay

Provo Bay

Fig. 3-4 Periphyton PP (a, g C m^{-2} year^{-1}), total GPP (b, g C m^{-2} year^{-1}), and percentage of benthic GPP (c, %) modeled in Goshen Bay (left column) and Provo Bays (right column) along a gradient of increasing water clarity at full pool (red lines) and 2018 water levels (blue lines; 1.2 m below full pool). The Secchi depth of 0 m represents the mean monthly Z$_{Secchi}$ from 2018 (Table 3-2), with every number thereafter indicating an increase of that amount from the current mean value. The dashed lines indicate the 30% benthic dominance threshold associated with each water level.

Discussion

This study demonstrates that primary production modeling can provide lake managers with precise water clarity targets to promote benthic primary production to levels required for influencing whole-lake ecosystem functioning. Such models may provide an effective tool to improve restoration planning in shallow, eutrophic lakes. Utah Lake's 2018 PP rates, calculated from measured diel oxygen curves, fell within the expected range of phytoplankton PP given literature relationships based on mean lake Chl *a* concentrations (del Giorgio and Peters 1993). As water quality variables were not available for the winter months, diel oxygen curve calculations may have overestimated full-year mean PP rates. However, this was unlikely to significantly influence the phytoplankton model (which provided low PP rates during winter months; Table 3-4), or the general modeled trend between phytoplankton and periphyton PP. I also noted that due to Utah Lake's large surface area and fetch , off-shore wind speeds were likely greater than wind speeds on land (Desai et al. 2009), although I had to use wind speeds taken from a nearby land-based weather station for calculating the lake surface oxygen exchange in the diel oxygen curves approach. While this may have slightly inflated lake metabolism estimates as the lake was often super-saturated with dissolved oxygen, the good fit between my measured PP rates and those expected from the literature (as described above) indicate that this was likely a minor effect and is also unlikely to

significantly influence the modeled PP relationships. With regards to the model

parameters, I note that future improvements to the models may include measured lake-

specific algal photosynthetic parameters, although I consider the literature estimates

adopted here to be appropriate for a first examination of these potential processes in Utah

Lake.

I found present-day (2018) primary production in Utah Lake to be strongly

dominated (~ 99%) by phytoplankton. However, models indicate that a transition to

benthic dominance would likely occur with water clarity increases, or water level

decreases. Regarding restoration options available to lake managers, I considered water

levels to be predominantly controlled by regional climatic variability, while water clarity

might be partly influenced by nutrient abatement strategies (influencing the

phytoplankton biomass component of light attenuation, but not the sediment resuspension

component). Specifically, nutrient abatement, such as tertiary treatment of wastewater

effluent, may be an effective way to limit phytoplankton production (Schindler 1974;

Conley et al. 2009), but it does not directly address the role that suspended sediments

play in limiting light access to the sediments. Given contemporary (2018) water levels

and mean Secchi depths (0.25 m), Utah Lake's water clarity would need to increase by a

minimum of 0.9 m (i.e. to 1.15 m) to allow for benthic dominance at a whole-lake scale

(Fig. 3-2). Based on the measured 2017-2018 relationship between Chl *a* and water

clarity in Utah Lake (Eq. 7), this increase in water clarity is theoretically attainable via

nutrient abatement efforts which reduce the water column Chl *a* concentrations to ~13 μg

L^{-1}. However, while this relationship is derived from empirical data, measured Secchi

depth readings did not surpass 0.4 m during the measured period, while Chl *a*

concentrations were frequently less than 13 µg L^{-1}, indicating that current sediment

resuspension rates may represent a barrier to nutrient-abatement water clarity targets

beyond 0.4 m Secchi depths. A whole-lake increase in Secchi depths to 1.15 m does not

therefore appear likely based on nutrient reductions alone.

These models indicate that low-pool water levels would allow for benthic

dominance with no increases in water clarity. There is support in the literature for

indicating that lakes experiencing major drawdowns in water levels can provide ideal

habitats for submerged macrophytes (e.g., Van Geest et al. 2005; reviewed by Jeppesen et

al. 2015). Furthermore, submerged macrophytes (identified as *Stuckenia pectinata*) were

observed in several shallow locations in Utah Lake beginning in 2016 (pers. comm. K.

Landom), which coincided with a relatively low water level year (~ 1 m below 2018

levels). However, drastically reduced water levels can also introduce a critical risk of

increasing turbidity due to sediment resuspension from wind mixing (Lawson et al. 2007;

reviewed by Jeppesen et al. 2015), which would further limit benthic periphyton growth.

This effect may be especially apparent in lakes which have become eutrophic (Lisi and

Hein 2018), and may thus impede the natural regeneration of submerged macrophyte

communities in Utah Lake. As this is likely a factor linking to lake-specific morphometry

and sediment characteristics, as well as the physiological characteristics of Utah Lake's

benthic primary producers, further research is needed to determine whether macrophytes

and benthic periphyton could establish quickly enough in this lake to reduce sediment

resuspension.

At high-pool water levels, the greater thickness of the water column would reduce

wind-driven sediment resuspension, potentially allowing for improved sediment stability.

While transparency may increase at such high-water levels (Lisi and Hein 2018), the greater water column thickness also means that the light would need to travel a longer distance to reach the sediment surface for promoting benthic PP. The model thus indicates that benthic dominance at high pool would require an increase in water clarity of 2.5 m (i.e. to Secchi depths of 2.75 m). Even though such maximum water levels occur infrequently (roughly once per decade), I consider them to provide a conservative estimate of water clarity requirements as the lake's benthic primary producer community must be able to tolerate such conditions to allow for a sustained shift to benthic PP dominance (Hunt and Jones 1972; Hofmann et al. 2008). As the water clarity-Chl a relationship measured for 2017-2018 represents lower water levels (and thus likely higher resuspension rates) than is here considered, I did not consider it appropriate for producing a necessary Chl a reduction guideline for water clarity. However, it is likely that both reductions in sediment resuspension as well as Chl a biomass in the water column would be necessary to increase mean Utah Lake Secchi depths to 2.75 m.

This analysis underlines the important challenges that resuspension and fluctuating water levels play in designing Utah Lake restoration plans. By reducing or eliminating the effect of sediment resuspension, while maximizing the potential impact of nutrient reduction measures on controlling water clarity, high-pool years may provide the best opportunity for re-establishing benthic primary producers in Utah Lake. If water clarity can be managed by continued nutrient abatement measures in subsequent years (following high-pool water levels) to allow for a sustained shift to benthic PP dominance, lake managers may be able to maintain the lake at its historical clearwater, macrophyte-dominated state by capitalizing on the nutrient sequestration and sediment resuspension-

reducing effects of a healthy community of benthic primary producers (as reviewed in Hilt et al. 2017). However, more information is required to fully predict whether Utah Lake's water clarity at a whole-lake scale could be increased to such a degree at high water levels. The time-consuming nature and cost of many restoration approaches (Chislock et al. 2013) necessitates a need for lake managers to identify strategies that will be most effective.

A more viable approach for lake managers may be to target increasing water clarity within the shallow, wind-sheltered areas of the lake (Goshen Bay and Provo Bay, Fig. 1), where the light conditions necessary for benthic periphyton and submerged macrophyte establishment may be more attainable. The models indicate that water clarity would need to improve by a minimum of 0.3 m in these bays (i.e. to Secchi depths of 0.55 m) to allow for benthic dominance (Fig. 5). The current Chl *a*-water clarity relationship (Eq. 7) indicates that this would require a reduction of Chl *a* concentrations in these bays to roughly 18 μg L^{-1}. Although this is also above the previously-described 0.4 m threshold apparent in that measured relationship, by being sheltered from wind-driven resuspension it is likely that the water clarity in these bays is more strongly determined by phytoplankton biomass, and thus greater increases in water clarity may be possible. Together, Goshen Bay and Provo Bay represent ~14% of Utah Lake (by surface area). Therefore, if submerged macrophyte communities were to eventually establish themselves across the full area of these two bays, broader positive food web and water clarity effects may extend to the whole-lake scale (Canfield et al. 1985).

I note that these models examine only the basic light requirements and lake morphometry dynamics that would determine what is possible for primary producers in

Utah Lake, and that they do not consider interactions with higher trophic levels, such as

grazing by fish (e.g., Miller and Crowl 2006), or the effects of water level management

on fish (e.g., Glassic and Gaeta 2019). Regarding the effects of a regime shift to benthic

dominance on fish productivity, our models indicate that such a regime shift would be

accompanied by a net increase in whole-lake PP, indicating potentially widespread

benefits to the lake food web, despite reductions in phytoplankton PP (Vadeboncoeur et

al. 2002; Vander Zanden et al. 2002; Sierszen et al. 2003; Brothers et al. 2013).

Regarding the negative effects of introduced carp on potential macrophyte recover

efforts, efforts are already underway in Utah Lake, to remove five million pounds of

common carp annually (USFWS 2010). Given both the direct grazing and indirect

resuspension effects of carp on submerged macrophytes, the continued success of these

carp reduction measures is likely necessary for the re-establishment of submerged

macrophyte communities. While both periphyton and submerged macrophytes can

produce positive effects on water quality (as discussed previously), periphyton can also

have a direct negative shading effect on submerged macrophytes (e.g., Roberts et al.

2003), underscoring that the minimum water quality improvements here described will

likely need to be surpassed, along with a successful return of periphyton grazers such as

aquatic snails, for a full recovery of submerged macrophytes. Indeed, herbivores have the

greatest impact on plant abundance during conditions of high abiotic stress, such as light

limitation (Silliman et al. 2013), and releasing submerged macrophytes from the light-

suppressing effects of periphyton growth on their surface may make them more resilient

to grazing by common carp (Hidding et al. 2016). If a healthy, carp-resistant submerged

macrophyte community is able to establish and maintain clear-water conditions in Utah

Lake, this may therefore ultimately reduce the necessity for ongoing carp reduction efforts.

I propose a two-tiered restoration approach for Utah Lake, combining nutrient abatement with additional management strategies, as the required increase in water clarity can likely only be partially met by nutrient mitigation efforts (Jeppesen 2005). Reducing nutrient loading into Utah Lake will decrease phytoplankton production and thus Chl *a* concentrations (Schindler 1974; Conley et al. 2009), though at the whole-lake scale, water level fluctuations and the role of sediment resuspension on water clarity may impede the effectiveness of such nutrient reduction measures (with the possible exception of high-pool conditions, when sediment resuspension is reduced). I therefore propose that restoration efforts be focused primarily on wind-sheltered bays (Provo Bay and Goshen Bay), where nutrient mitigation effects on water clarity may be maximized. In addition to nutrient abatement, current management strategies to improve water clarity that may be beneficial for Utah Lake, especially in more wind-exposed areas of the lake, may include large-scale enclosures, potentially in addition to ongoing biomanipulation efforts and macrophyte transplantation (Liu et al. 2018; Lefcheck et al. 2018; Chen et al. 2009). Macrophytes do not always return on their own very readily following nutrient reductions in lakes (Jeppesen et al. 2005), so active macrophyte planting in key areas may be necessary. While additional research would help improve the planning and optimizing of lake management strategies, my results indicate that a return to clearwater conditions in Utah Lake is viable and may improve upon fish removal strategies which have not yet led to the desired return in vegetation coverage.

Conclusion

Records and paleolimnological analyses indicate that Utah Lake historically exhibited a clearwater state that supported an abundant macrophyte community, particularly within Provo Bay and Goshen Bay (Brotherson 1981; Chapter 1 of this thesis). I here show that water level fluctuations interacting with sediment resuspension may preclude the necessary water clarity increases for whole-lake scale benthic primary production dominance. However, if efforts are focused on Provo Bay and Goshen Bay, water clarity would need to increase by 0.3 m to promote benthic dominance, which may be possible given reduced resuspension effects anticipated in these areas. Improving water clarity through a combination of nutrient reductions strategies, ongoing biomanipulation, macrophyte transplantation, and large-scale enclosures may thus be an effective approach to increase vegetation coverage throughout Utah Lake.

I show that primary production (PP) modeling may be used to improve restoration planning in shallow, eutrophic lakes by providing lake managers with historically and ecologically-relevant, lake-specific water clarity targets. Without accounting for the light requirements necessary for benthic primary producers to become re-established in lakes, nutrient loading reductions to lakes may potentially be either insufficient at restoring clear-water conditions, or alternatively, may over-shoot water clarity thresholds, in both cases representing an inefficient use of management resources. Furthermore, applying benthic PP dominance to lake management strategies may allow lake managers to maintain long-term improvements in water clarity and water quality by utilizing the ecosystem services provided by clear-water states (Hilt et al. 2017), thus further minimizing the resources necessary for lake management.

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CHAPTER 4

CONCLUSION

Cultural eutrophication is expected to persist as a major issue for waterbodies worldwide. Understanding the lake dynamics that lead to and maintain these eutrophic conditions is thus essential for future improved lake management and restoration efforts. The aim of this research was to describe the pre- and post-eutrophication ecosystem characteristics of Utah Lake, and identify the transitional period and main driver(s) from clearwater to turbid conditions. Additionally, I incorporated the lake's historical plant community structure (which featured a healthy benthic primary producer community) into ecosystem models to determine the increase of water clarity required to return to this historic state, accounting for contemporary interannual shifts in lake water levels.

Chapter 1 provided the necessary framework and background information for this thesis. I first introduced the larger issue at stake, cultural eutrophication, and the difficulties managers face with remediation efforts. I addressed the history of Utah Lake, which has experienced a high degree of cultural eutrophication that has caused both ecological and economic impacts to the region. Given high wind-driven sediment resuspension and major lake-shore fluctuations from interannual water level shifts, Utah Lake remediation efforts face major obstacles and nutrient reduction alone may not be sufficient. The multi-proxy paleolimnological approach and the water clarity necessary for benthic production were explored in more detail in Chapters 2 and 3.

In chapter 2, I described the pre- and post-eutrophication ecosystem health of Utah Lake using a paleolimnological approach. Additionally, I identified the transitional dates of the regime shift to provide insight into the main drivers of eutrophication. I

attribute the significant regime shift to anthropogenic forcing in the lake, specifically the introduction of common carp around 1881. A combination of proxy data sets indicated a recent transition in the lake's history to greater phytoplankton dominance. eDNA and pigment results specifically showed an increase in cyanobacteria abundance, which are associated with harmful algal blooms. Dating models using peaks of ^{137}Cs associated with nuclear testing, indicated that the depth horizon of this shift was associated with ~1869 ± 25 years, which considering the abrupt nature of the transition correlates well with the introduction of carp. Isotope results indicated a shift in δ^{15}N to higher values associated with wastewater treatment plant effluent. The continued input of wastewater effluent further impacted the lake ecosystem following the initial transition, leading to continued increases in some algal pigments. Overall, I demonstrated that Utah Lake underwent a regime shift to greater phytoplankton dominance and a loss of macrophytes due to anthropogenic forcing. Pending research includes radiocarbon dating to establish a better chronology deeper in the cores, zooplankton and diatom analyses to provide more detailed lake conditions, and additional geochemistry analyses.

Chapter 3 involved modeling the water clarity necessary to allow for sustained benthic primary production (including submerged macrophytes and periphyton) in Utah Lake, marking a return to its historical conditions defined in Chapter 2. However, eutrophic lakes which have lost their benthic communities can be notoriously difficult to restore to clear-water conditions. An increase in water clarity both at the whole-lake scale, which could be difficult due to its size, and within the isolated bays, that historically contained abundant submerged macrophytes, could produce conditions that would favor the dominance of benthic primary producers within the lake. Currently,

primary production in Utah Lake is largely dominated by phytoplankton (~99%). However, the lake is morphologically suited to exhibit greater periphyton dominance due to its shallow nature if water clarity improvements are made. Primary production modeling indicates that in order to re-establish macrophyte dominance in Provo Bay and Goshen Bay, water clarity needs to increase by at least 0.3 m. Models indicate that this may be attainable via reduced nutrient loading efforts which reduce water column Chlorophyll a concentrations to ~18 μg L^{-1} (2018 mean lake-wide values = ~40 μg L^{-1}). Combining nutrient reduction strategies with other existing approaches that promote benthic primary production dominance in shallow, eutrophic lakes, such as biomanipulation, large-scale enclosures, and submerged macrophyte planting, may be necessary for Utah Lake remediation efforts. Overall, I provided a first estimate of the likely historical water clarity conditions in Utah Lake, in fitting with literature and paleolimnological analyses, and also present lake restoration guidelines for contemporary managers interested in returning the lake to historical conditions.

This research provides critical information about the lake's history to guide future lake management efforts. I suggest that lake managers continue to prioritize the current carp removal efforts, as well as reduce the amount of external nutrient loading to the lake. Since 2009, the June Sucker Recovery Program has successfully reduced the abundance and biomass of the common carp population by removing them on a full-time basis (Gaeta et al. 2018). Previous studies have indicated that removal of 75% of the carp would lead to beneficial changes in the lake environment (USFWS 2010); however, combining these efforts with other remediation strategies may make it more feasible to achieve the goal of re-establishing submerged macrophytes to benefit the native fish
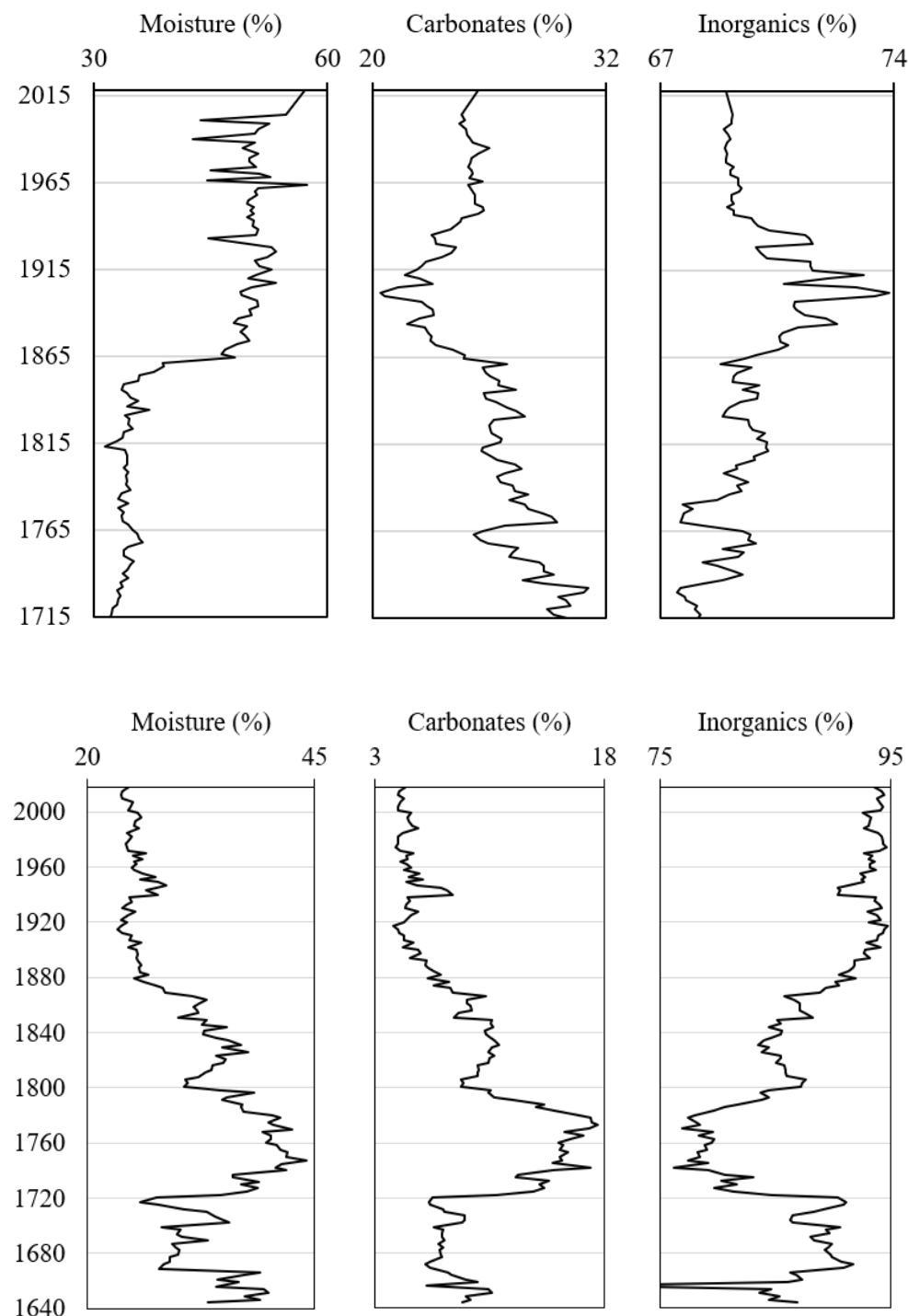
community. Wastewater treatment plants (WWTPs) discharging directly into the lake and its tributaries are currently only required to provide secondary treatment to effluent, which does not include the removal of nutrients. Requiring WWTPs to provide tertiary treatment would greatly reduce the nutrient loading to Utah Lake. In addition to nutrient abatement and to promote a shift back to greater benthic dominance, lake managers should also prioritize improving water clarity to reduce light limitation to benthic producers. Areas that are best suited to for increased macrophyte abundance can be targeted based off lake morphometry and the historical presence of large macrophyte stands in Goshen Bay and Provo Bay.

Cultural eutrophication is expected to pose a growing challenge to lake managers in the future as anthropogenic threats to lake ecosystems increase. The population within the valley is expected to roughly double within the next 30 years (Kem C. Gardner Policy Institute, https://gardner.utah.edu/demographics/population-projections/), which will in turn double the pressure on WWTPs and water bodies in the basin. In the case of Utah Lake, managers will be faced with how to restore the natural mesotrophic conditions of the lake. This study has shown that Utah Lake historically exhibited a greater abundance of macrophytes and has shifted to greater phytoplankton dominance in recent years due to the introduction of common carp and continued external nutrient loading. In addition to reducing nutrient loading to Utah Lake, managers will need to prioritize improving water clarity to create the necessary conditions for submerged macrophytes and benthic periphyton establishment. Overall, I provided the necessary baseline lake conditions and insight into the primary drivers of eutrophication in Utah Lake to guide lake management and restoration efforts.
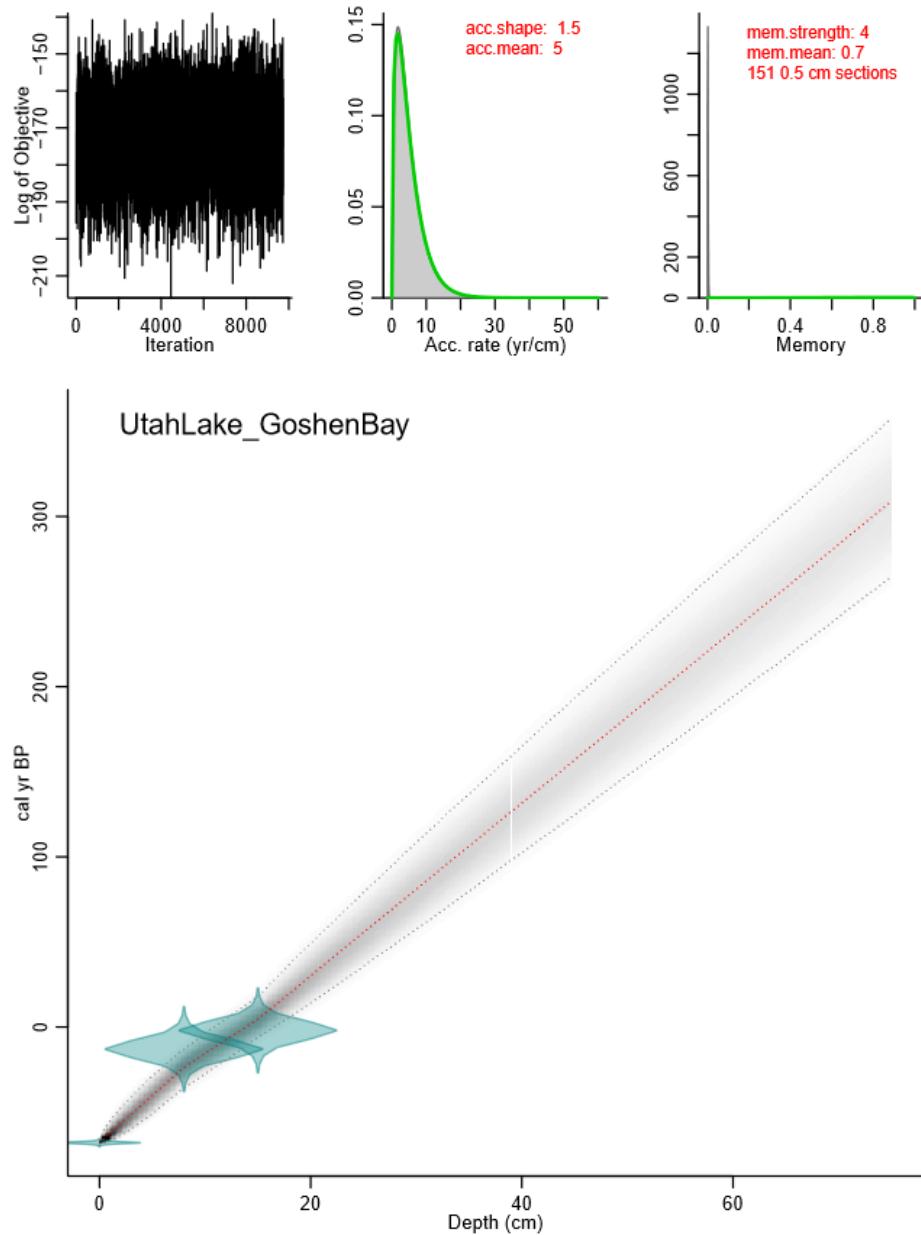
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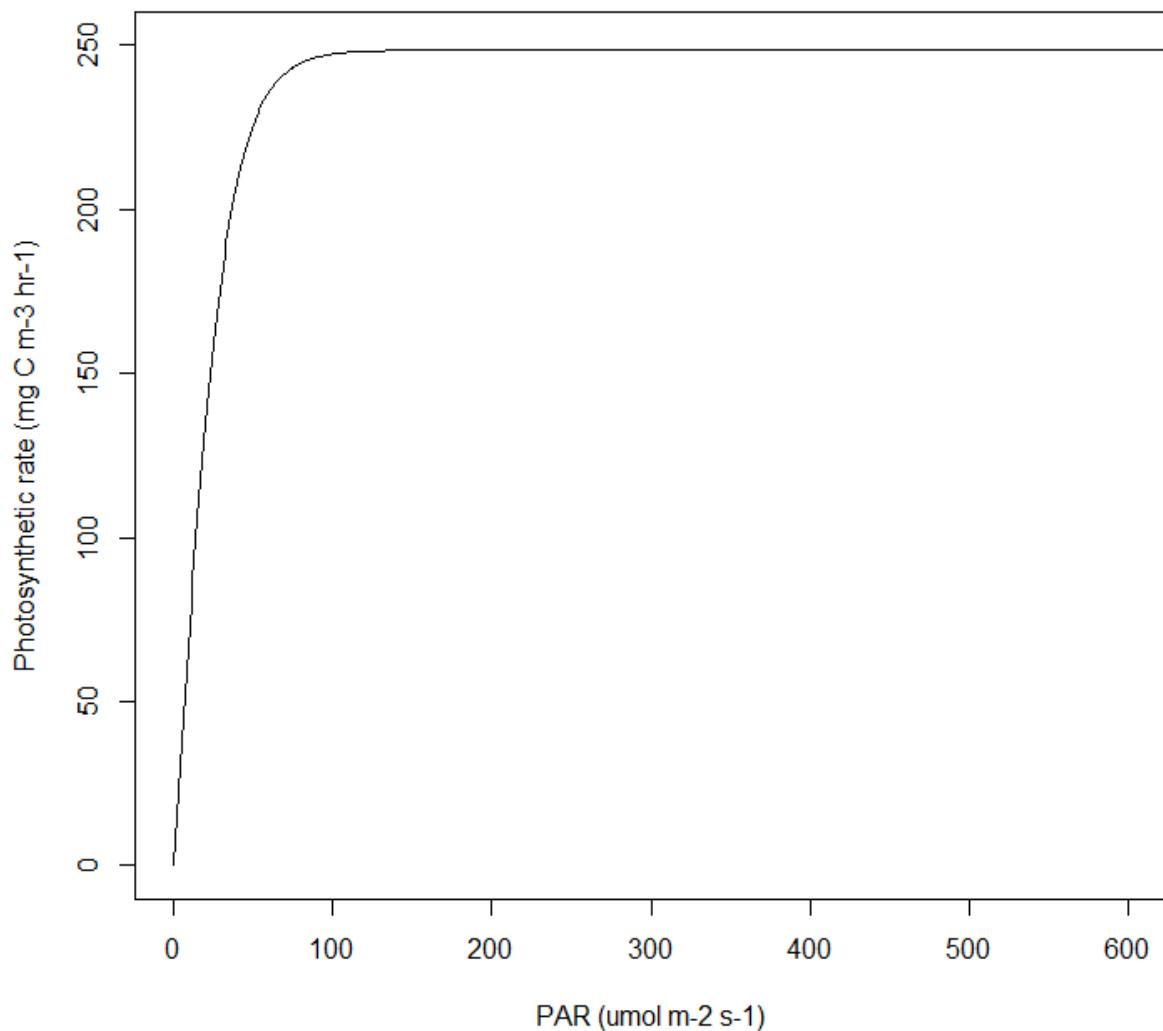
APPENDIX

Fig. A1 Loss-on-ignition results for Goshen Bay (top) and Provo Bay (bottom) sediment cores.
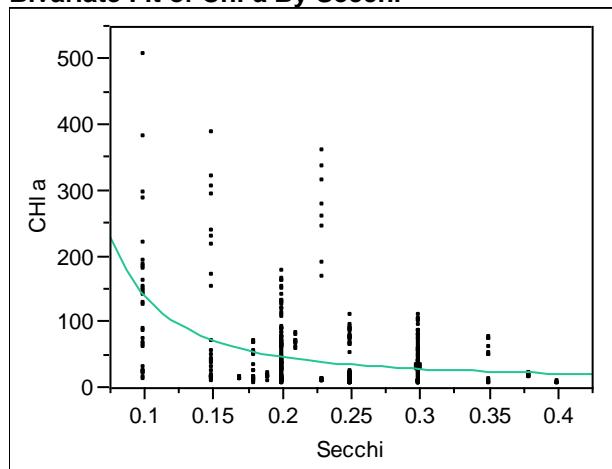
Fig. A2 Results of the BACON modeling to establish a depth-time profile for Utah Lake sediment cores. The blue points represent the ^{137}Cs dates, with uncertainty, that were included in the model. All years are in cal yr BP (1950 = present). The red line indicates the mean of the modeled profile and the gray band represents the associated uncertainty.

Fig. A3 Calibrated photosynthesis-irradiance (PI) curve for Utah Lake phytoplankton production based off values measured in the West Basin of Lake Erie (Smith et al. 2005).

Bivariate Fit of Chl *a* By Secchi

── Transformed Fit to Reciprocal

Transformed Fit to Reciprocal

Chl a = 10.204992 + 2.1807127*Recip(Secchi) + 1.0670865*Recip(Secchi)^2

Summary of Fit

RSquare	0.162213
RSquare Adj	0.158602
Root Mean Square Error	60.40256
Mean of Response	47.68225
Observations (or Sum Wgts)	467

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	2	327777.9	163889	44.9199
Error	464	1692889.9	3648	**Prob > F**
C. Total	466	2020667.9		<.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	10.204992	24.17227	0.42	0.6731
Recip(Secchi)	2.1807127	8.482499	0.26	0.7972
Recip(Secchi)^2	1.0670865	0.663713	1.61	0.1086

Fig. A4 Measured relationship between water clarity and Chlorophyll *a* concentrations from 2017-18 data.