

Final Report to the Utah Division of Water Quality

Littoral-Benthic Primary Production in Utah Lake

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Executive Summary

Utah Lake is a shallow, hypereutrophic lake that exhibits the typical characteristics of cultural eutrophication, including recurrent harmful algal blooms. High water column nutrients, phytoplankton chlorophyll-*a*, and poor water clarity (associated with both wind-driven resuspension and phytoplankton biomass) indicate that the primary productivity of this lake is dominated by phytoplankton. Thus, Utah Lake likely features a self-stabilizing regime whereby sediment resuspension and high phytoplankton biomass perpetuate turbid conditions, precluding the development of submerged macrophytes or benthic algal primary production. However, historical reports anecdotally state that Utah Lake once featured a healthy submerged macrophyte community, indicating that the lake's waters were historically clearer than in recent decades. We investigated the nearshore (littoral) sediments of Utah Lake for buried macrofossil remains, specifically the presence of the species *Chara aspera* (stonewort), which was historically reported in Utah Lake and is considered an indicator species for clearwater conditions in lakes due to a high light requirement for growth. We also measured and modeled rates of gross primary production (GPP) in the lake, including nearshore zones where submerged macrophytes, *Stuckenia pectinata* (Sago pondweed), have been observed in recent years following invasive common carp removal efforts. Our goal was to combine evidence of historical submerged macrophytes with primary production models to estimate the current and historical rates of benthic and planktonic GPP in Utah Lake.

Sediments from 20 nearshore sediment cores yielded no positive identifications of *C. aspera* oospores. We discuss several potential explanations for the apparent absence of oospores, and consider the most likely explanation to be that the cores extracted from the lake bed did not overlap with the historical location of *C. aspera* in the lake. We outline an improved sampling strategy for follow-up studies. Regarding contemporary lake GPP rates, area-weighted offshore (pelagic) primary production in 2018 ranged from $\sim 30 \text{ g C m}^{-2} \text{ month}^{-1}$ (January – April, October to December) to $\sim 160 \text{ g C m}^{-2} \text{ month}^{-1}$ (July), providing an overall mean value of $\sim 550 \text{ g C m}^{-2} \text{ y}^{-1}$. Productivity models indicate that benthic algal production likely represents $\sim 1\%$ of Utah Lake's contemporary (2018) total primary production. Contemporary measurements of offshore free-water GPP rates thus likely represent phytoplankton production alone.

Regarding the historical rates and distribution of primary production in Utah Lake, a literature analysis indicated that >70% of Utah Lake's surface area would likely need to feature benthic primary production for significant reductions of sediment resuspension, promoting a stable clear-water regime at the whole-lake scale. This level of coverage would correspond to mean Secchi depths of ~1 m (2018 mean Secchi depths, for comparison, are ~0.2 m) and chlorophyll *a* concentrations of ~20 $\mu\text{g L}^{-1}$ (2018 mean = ~40 $\mu\text{g L}^{-1}$), given Utah Lake's bathymetry at full-pool water level (thus providing maximum light requirement values). At this higher historical water clarity, our models indicate that Utah Lake's primary productivity would remain dominated by phytoplankton at 2018 and high-pool water levels (~1% benthic GPP at the whole-lake scale in both cases). Even at low-pool water levels, benthic primary production would only represent ~23% of the whole-lake annual GPP. Although our model does not account for changes in lake nutrient dynamics, it indicates that at high water levels (2018 and full-pool), increased water clarity is associated with increased areal phytoplankton GPP rates, as more production can occur at deeper layers of the water column (even when accounting for a concurrent decrease in chlorophyll *a* concentrations). Thus, Secchi depths of 1 m (projected historical conditions) are associated with 9 to 18% greater total lake areal GPP rates (at 2018 and full-pool water levels, respectively) compared to measured 2018 GPP rates.

Dissolved oxygen measurements made from mid-May until mid-June 2019 allowed for a direct comparison of near-shore (littoral) and offshore (pelagic) aquatic metabolism dynamics in Utah Lake. Volumetric rates of primary production were significantly greater in the near-shore zones (mean = $31.2 \pm 2.5 \text{ mg O}_2 \text{ L}^{-1} \text{ d}^{-1}$) compared to off-shore measurements (mean = $11.0 \pm 2.9 \text{ mg O}_2 \text{ L}^{-1} \text{ d}^{-1}$, $p < 0.0001$). However, higher near-shore GPP rates were paired with much greater community respiration rates (mean = $68.4 \pm 2.9 \text{ mg O}_2 \text{ L}^{-1} \text{ d}^{-1}$) compared to off-shore measurements (mean = $30.0 \pm 3.3 \text{ mg O}_2 \text{ L}^{-1} \text{ d}^{-1}$, $p < 0.0001$). Thus, the more structurally-complex and productive near-shore zones were also more net heterotrophic (featuring more negative net ecosystem production rates) during our period of measurement, indicating that organic matter removal by the littoral food webs featuring submerged macrophytes may be more effective than that in the pelagic zone. We conclude that historically clearer waters in Utah Lake may have permitted higher rates of primary production than those measured in 2018, but also potentially lower rates of algal biomass accumulation in the water column due to a more effective and robust consumer community.

Introduction

Aquatic primary production in lakes can regulate dissolved oxygen saturation and provide essential support for aquatic food webs. However, excessive nutrient loading often results in the proliferation of phytoplankton and cyanobacteria in lakes, at the expense of light-limited benthic periphyton and submerged macrophytes, which can result in algal fouling and harmful algal blooms. Submerged macrophytes can thus be useful indicators of lake water quality, as they require light penetration through the water column to permit their photosynthesis. Macrophytes also physically stabilize sediments, reducing turbidity from wind-driven resuspension and improving multiple ecosystem functions and services of lakes (Hilt *et al.*, 2017). Little information is available regarding the historical submerged macrophyte community

of Utah Lake (Utah). Prior to the 1980s, Utah Lake reportedly featured over 100 stands of *Stuckenia striata* (Ruiz & Pav.) ranging in area from approximately 1 to 40 m², and up to 2.4 m deep (Brotherson 1981 and references therein). Other submerged macrophyte species that have reportedly grown in Utah Lake, including *Ceratophyllum demersum* L., *Elodea canadensis* Michx., *Utricularia minor* L., *Myriophyllum spicatum* L., and *Chara aspera* L., have reportedly been extirpated from the lake (Brotherson, 1981; Miller and Crowl, 2006). The loss of historical species, such as *C. aspera* and *C. demersum*, may be due to multiple factors, including carp invasion, anthropogenic eutrophication of the lake, and/or increased lake level fluctuations following its damming in 1872 (Janetski, 1990; Miller and Crowl, 2006; Landom, Dillingham and Gaeta, 2019). It is also possible that the decline in submerged macrophytes was not the result of any individual stressor but rather the cumulative effect of multiple stressors, such as algal shading combined with carp grazing (Hidding *et al.*, 2016). Today, submerged macrophytes are rare in Utah Lake, though communities of *Stuckenia pectinata* L. are extant (Miller and Crowl, 2006) and are returning sporadically to certain areas of the lake following long-term intensive carp removal efforts (Landom, Dillingham and Gaeta, 2019). Such partial (incomplete) returns of submerged macrophytes are indicative of an “unstable clear state,” rather than a full recovery. Such unstable clear states can result when internal restoration efforts (such as carp removal) are not accompanied by reductions in external nutrient loading (Hilt *et al.*, 2018).

We carried out field campaigns and analyzed data from Utah Lake to improve our understanding of the lake’s current and possible historical primary production rates, and the potential role of littoral-benthic primary production in this system. We sought to confirm reports (Miller and Crowl, 2006 and references therein) of *C. aspera* (stonewort) in Utah Lake and investigate the distribution of this macrophyte around the periphery of the lake, as this species is widely considered to be a key clear-water indicator species for lakes (Hilt *et al.*, 2006; Lambert-Servien *et al.*, 2006). We analyzed 24-hour (diel) dissolved oxygen (DO) curves from the lake to assess its current primary productivity, and compared littoral to pelagic aquatic metabolism rates. We predicted that nearshore sites associated with the initial return of submerged macrophytes in Utah Lake would feature higher measured rates of primary production compared to turbid pelagic sites featuring only phytoplankton production (following Brothers *et al.*, 2013a).

Sampling Design & Methods

Macrophyte Oospore Analysis



Figure 1. Utah Lake, showing locations of off-shore monitoring stations (white circles), nearshore sondes (white stars), and nearshore sediment core retrieval sites (triangles). Yellow triangles were each sampled once (two cores retrieved, August 2019), and red triangle sites were sampled a second time in October 2019 (three additional cores from each)

documented by GPS and photographs. When retrieving sediments, care was taken to minimize the physical disturbance to the immediate sediment area being cored, and where boat or human traffic was evident, sheltered/undisturbed sites were sought out for sampling. However, as our analyses was solely to examine the deepest (oldest) sediments for *C. aspera* oospores, and sediment cores were not intended for dating, the potential effects of local surface sediment disturbance were not considered to be critical to the success of the analysis. Clear polycarbonate tubes were used by hand to retrieve the sediment and promptly photographed. Cores were then labeled and carefully transported back to Utah State University (USU)

The target species of submerged macrophyte in this study, *C. aspera*, produces distinctive oospore remains that are deposited in the immediate sediments below which the plant is growing (S. Hilt, *pers. comm.*). We therefore planned an initial sampling campaign to retrieve near-shore sediment cores around the periphery of the lake, as it is unlikely that the oospores would be transported to deeper lake sites (Fig. 1). Furthermore, we chose near-shore sites based on accessibility by automobile and waders, considering that appropriate near-shore sites would be too shallow for boat access. Sites for measuring aquatic metabolism rates in near-shore macrophyte recovery areas were selected by Kevin Landom, based on submerged macrophyte monitoring results in Utah Lake (Rivera, Landom and Crowl, 2013; Landom, Dillingham and Gaeta, 2019).

In August 2019, we collected 14 sediment cores from seven littoral locations in Utah Lake to assess the historical presence of *C. aspera* (Figs. 1, 2). All selected sites were



Figure 2. Undergraduate research assistant, Angelia Klein, retrieving sediment core near Provo Bay, Utah Lake (August 2019)

where they were stored at ~4°C until analyzed. Following preliminary data from offshore paleoanalyses (J. Brahney, *pers. comm.*), our aim was to retrieve 30 to 50 cm long sediment cores to ensure that we reached a deep enough sediment layer that would represent the mid-to-late 19th Century period during which *C. aspera* was still present in Utah Lake (Miller and Crowl, 2006 and references therein). However, water levels during our sampling period were relatively high, and potentially higher than average water levels in the mid-late 19th Century, potentially influencing the spatial



Figure 3. Utah Lake sediment core taken with Russian peat corer in October, 2019.

overlap of our nearshore sampling compared to the historical littoral zone location. Nearshore sediments were generally rocky and difficult to core using PVC coring tubes, and only 10-15 cm of material could be retrieved from most sites. We therefore returned for a second sampling campaign in October 2019 to the east shore of Utah Lake, where historical reports indicate the greatest prevalence of submerged macrophytes (Janetski, 1990). During this second campaign, we used a Russian peat coring device which permitted longer (up to ~30 cm) sediment cores (Figs. 3, 4). During this second campaign, three sediment cores were retrieved from two sites, within and directly outside of Provo Bay (Fig. 1).

Sediments were analyzed for macrophyte macrofossil remains using a top/bottom investigation. A small amount (~1 teaspoon) of material was sieved with 400 μm and 100 μm mesh sizes, with materials being retained from both size fractions. Most macrophyte macrofossil remains were expected to be found in the 400 μm size fraction (S. Hilt, *pers. comm.*). A dissecting microscope with a white background was used to scan for macrophyte remains. For each analyzed sediment subsample, the frequency of macrofossil remains was documented (i.e., counts of macrofossil remains identified per gram of material analyzed), and all unanalyzed sediments were stored for future possible analyses.



Figure 4. Retrieval of sediment cores using Russian peat corer in Provo Bay (October 2019)

Contemporary Aquatic Metabolism Measurements

We quantified lake aquatic metabolism rates using diel dissolved oxygen (DO) curves (Staeher *et al.*, 2010) using the R Package “LakeMetabolizer” (Winslow *et al.*, 2016). Although diel DO curves can be problematic in shallow, heterogeneous lakes (Van de Bogert *et al.*, 2012; Brothers *et al.*, 2017), Utah Lake is consistently mixed due to its high surface area (~380 km²) and shallow mean depth (3.2 m). DO and temperature loggers (miniDOT,

Precision Measurement Engineering) were installed (fixed to an anchor weight 0.2 m above the sediment surface) on May 14th, 2019 at shallow, littoral sites (Powell Slough and Spanish Fork) where returning submerged macrophyte communities have been observed (K. Landom, *pers. comm.*), and were retrieved on June 11th (Fig. 1, Table 1). Pelagic (offshore) metabolic parameters were calculated from three permanent monitoring stations installed and maintained by the Utah Division of Water Quality (Fig. 1). Dissolved oxygen and water temperature were measured every 15 minutes from April 11th to October 31st, 2018. Measurements were made by multiparameter sondes (Yellow Springs Instruments, Yellow Springs, OH) deployed at approximately 0.8 m depth. The mean monthly metabolism rates of April and October were applied to months for which data were unavailable (January to March, November, December). Wind speeds were measured at 10 m height and obtained from the National Centers for Environmental Information (NCEI) from an adjacent weather station (Provo Airport). Daylight hours were determined from local daily sunrise and sunset times. The salinity of Utah Lake was assumed to be 0.9 ppt (UDEQ, n.d.). We calculated the lake-area weighted production rates by approximating the lake surface areas represented by each buoy (Vineyard = 105 km², Provo = 131 km², Bird Island = 149 km²), and applied a respiratory quotient of one when converting aquatic metabolism rates to carbon values (for comparison with model outputs). Given the offshore location of these monitoring stations (with water depths typically between 2 to 3 m) and low Secchi depths (mean = 0.2 m in 2018) that would preclude any local benthic PP, we expected these PP values to represent only phytoplankton production.

Table 1: Littoral miniDOT sites (May 14th – June 11th, 2019)

Location Name	Geographic Coordinates	Water Depth at Deployment (m)	Water Depth at Pull (m)
Powell Slough 1	40.265°N, 111.745°W	0.95	1.3
Powell Slough 2	40.264°N, 111.746°W	1.2	1.55
Spanish Fork	40.175°N, 111.740°W	1.15	1.5

Primary Production Modeling

We used established models to estimate phytoplankton and periphyton gross primary production (GPP) in Utah Lake across a gradient of current and historical water clarity and water levels. Given the high water level fluctuations of Utah Lake, and the appreciable effect this would have on the GPP within the lake (considering both available water volume for phytoplankton GPP and distance of sediment surface to incoming solar radiation), we calculated productivity at 2018 water levels (1,367 m above sea level), low-pool (1,365 m above sea level, the lowest recorded lake level in 80 years), and high-pool levels (1,368 m above sea level, the controlled maximum lake level since 1985). We tested increases in the lake's 2018 mean annual water clarity by up to 3 m (roughly equivalent to this lake's mean depth, and the maximum Secchi depth recorded since 1989), at 0.1 m intervals for the first meter and then every 0.5 m thereafter.

For phytoplankton production, we used the R package “phytotools” (Silsbe & Malkin, 2015 and references therein). Although phytoplankton GPP is often closely related to chlorophyll *a* (chl *a*) concentrations in lakes (e.g., del Giorgio & Peters, 1993), Utah Lake's water clarity is strongly influenced by sediment resuspension dynamics, which complicates the relationship when integrating productivity across the full water column. We thus assumed that areal phytoplankton GPP 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 resuspension-driven light environment, we applied light-integrated models for planktonic GPP (Silsbe and Malkin, 2015). Photosynthetically active radiation (PAR) was simulated across a defined time

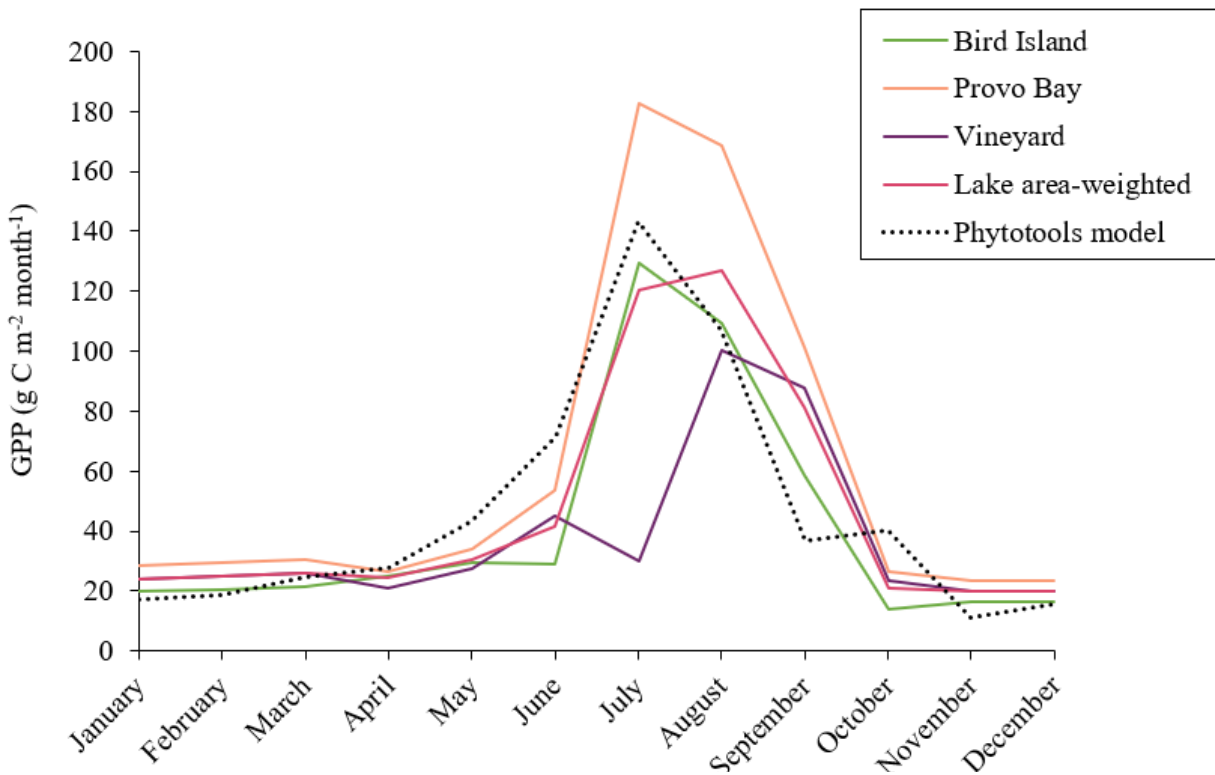


Figure 5. Monthly areal GPP rates ($\text{g C m}^{-2} \text{ month}^{-1}$) in 2018 from the three monitoring stations (green, orange, and purple lines), a lake area-weighted estimate (red line), and phytoplankton model for 2018 (black dashed line), applying a lake elevation of 1,367 m (1.2 m below full pool), and mean monthly chl *a* concentrations and Secchi depths.

period (2018), latitude (40.2130°), longitude (-111.8025°), elevation (1,368 m), and time zone (-6 Universal Coordinated Time). PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was determined for each month of 2018 using a Linke turbidity factor of 3.5, subtracting the irradiance reflected off the water's surface from PAR values following Kirk (2011). Photosynthesis-Irradiance (PI) curve parameters of phytoplankton were calibrated to match the mean annual contemporary GPP rates, measured in Utah Lake via the diel oxygen curve approach, using the Jassby & Platt (1976) model fitted by the Nelder-Mead method (Silsbe and Malkin, 2015). We applied a light utilization efficiency parameter (α , the initial slope of the PI curve) of $7.53 \text{ g C m}^{-2} (\text{g chl } a \text{ mol})^{-1}$, derived from another shallow eutrophic lake (West Basin of Lake Erie; Smith et al., 2005). We 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 and chl *a* data, calibrating the modeled mean phytoplankton PP to Utah Lake's measured 2018 phytoplankton PP (by DO curves), producing an I_k value of $33 \mu\text{mol m}^{-2} \text{s}^{-1}$. Although this value is relatively low (e.g., reported I_k values for four algal species range from 56-233 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in Gilbert et al., 2000), it was considered to be appropriate for this general analysis, and well-represented the independently measured monthly 2018 lake productivity rates (Fig. 5).

Utah Lake's total phytoplankton production was calculated (using Silsbe & Malkin, 2015) as a function of irradiance, light attenuation (K_d , m^{-1}), PI parameters, maximum mixing depth (Z_{max} , in this case assumed to be the lake depth at each given monitoring site), and monthly surface water measured chl *a* concentrations ($\mu\text{g L}^{-1}$). Z_{max} was 4.3 m at full pool, 3 m at 2018 water levels, and 1.2 m at low-pool levels. For modeling phytoplankton GPP with changes in water clarity, monthly chl *a* was derived from the measured relationship (Eq. 1, $r^2 = 0.05$, $p < 0.0001$, $n = 502$) between water clarity and chl *a* concentrations from 1989-2019 (Fig. 6; UDEQ, n.d.), using the equation:

$$\text{(Eq. 1) Chl } a = 14.294628 + 5.3231568/(Z_{\text{Secchi}})$$

Due to regular full water column mixing, chl *a* concentrations were assumed to be uniform across the water column. This equation was calculated using chl *a* measurements which were uncorrected for pheophytin, as they represented the most available long-term data, and may also provide the most accurate data (Stich and Brinker, 2005). Light attenuation values were calculated from mean monthly 2018 Secchi depths (UDEQ, n.d.). Light attenuation coefficients (K_d) were calculated by adapting the relationship with Secchi depths (Z_{Secchi}) described by Idso & Gilbert (1974) to the relationship between these variables calculated from Utah Lake data in 2018 ($r^2 = 0.29$, $p = 0.0134$, $n = 20$), providing the equation:

$$\text{(Eq. 2) } K_d (\text{m}^{-1}) = 0.89 + 0.536/Z_{\text{Secchi}}$$

Although PP models are based on estimates of PAR at various lake water depths, we 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.

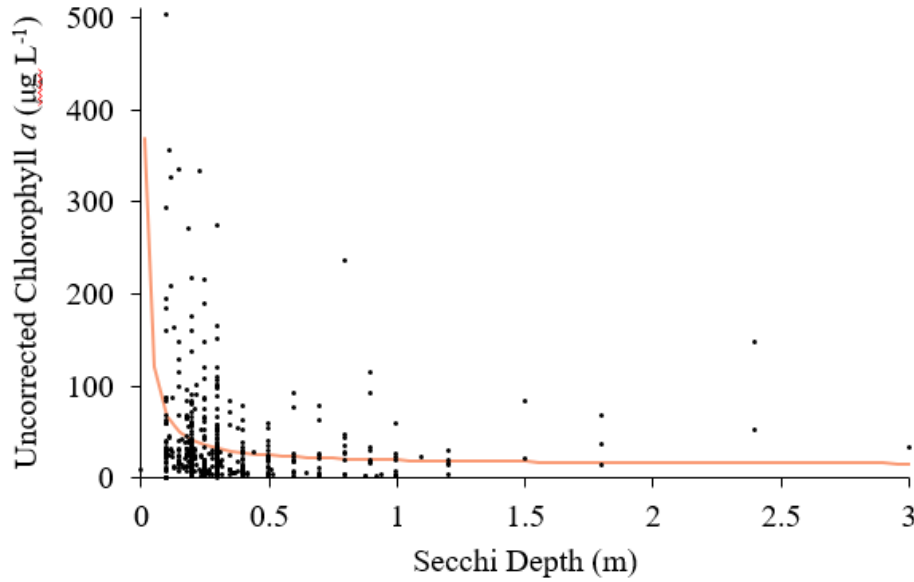


Figure 6. Measured relationship (orange line; $r^2 = 0.05$, $p < 0.0001$, $n = 502$) between Secchi depths (m) and chl *a* concentrations ($\mu\text{g L}^{-1}$) from 1989-2019.

Benthic periphyton GPP in Utah Lake was modeled assuming that it would be primarily limited by light, rather than nutrients (Brothers et al., 2016; Vadeboncoeur et al., 2008). We applied a conservative maximum GPP rate (BP_{\max}) of $30 \text{ mg C m}^{-2} \text{ hr}^{-1}$ based on literature values for periphyton in lakes (Brothers et al., 2016 and references therein; Vadeboncoeur et al., 2008; Vander Zanden et al., 2011). Following Brothers et al. (2016), I_k was calculated as:

$$\text{(Eq. 3) } I_k = 334.5 * e^{-Z * K_d} + 68$$

The maximum benthic periphyton production at a specific depth, $BP_{\max Z}$ ($\text{mg C m}^{-2} \text{ hr}^{-1}$), 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 scouring 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} ($\text{mg C m}^{-2} \text{ hr}^{-1}$) was calculated as:

$$\text{(Eq. 4) } BP_{\max Z} = [(15 / (\ln(0.5) / -K_d)) * Z] + 15$$

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

$$\text{(Eq. 5) } BP_{\max Z} = BP_{\max Z50} * [(2 * PAR_Z) - 0.1]$$

where PAR_Z ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) is the fraction of I_0 at a given depth (Z , m), and $BP_{\max Z50}$ is the maximum periphyton productivity at the depth of 50% surface light ($30 \text{ mg C m}^{-2} \text{ hr}^{-1}$). Periphyton production at each depth ($\text{mg C m}^{-2} \text{ h}^{-1}$) was calculated in half-hour intervals using the equation:

$$\text{(Eq. 6) } BP_Z = BP_{\max Z} * \tanh[(I_{0,t}) * \sin(\pi * (t / \text{daylength})) * e^{-K_d * Z} / I_k]$$

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 two 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 is the daily periphyton production throughout the lake. Secchi depths from 2018 were obtained from the Utah DWQ. Light attenuation (K_d , m^{-1}) was calculated from Secchi depths using the same equation described for the phytoplankton model. The sediment surface area across water depth intervals was calculated using bathymetry contours obtained from the Utah DWQ. As with the phytoplankton PP model, month- and location-specific daylength (h) and solar radiation ($\mu mol\ m^{-2}\ s^{-1}$) were applied from the 15th day of each month. To

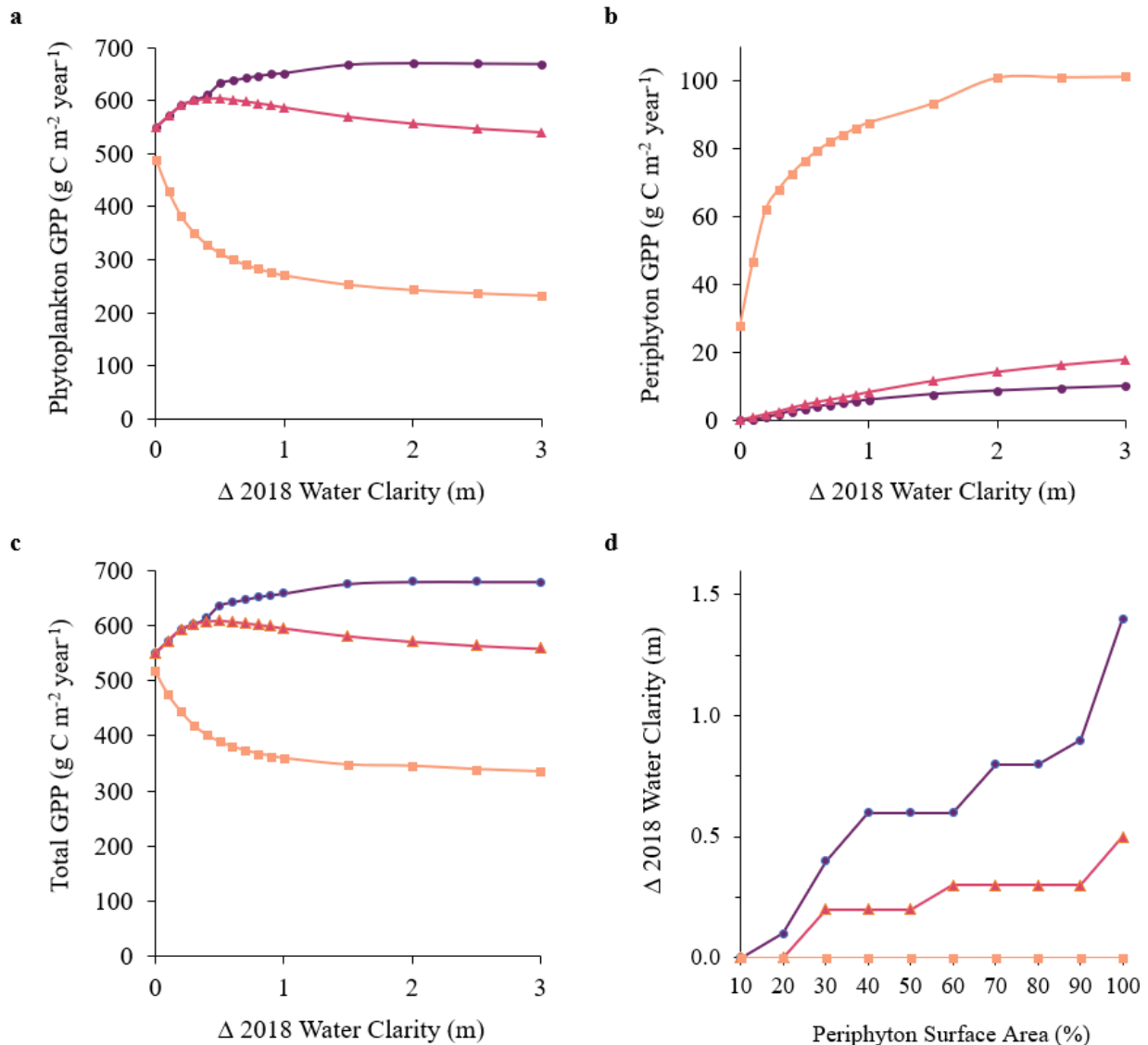


Figure 7. Phytoplankton PP (A), periphyton PP (B), total GPP (C), and the total surface area of lake sediments supporting BPP (D) modelled at a whole-lake scale along a gradient of increasing water clarity. Water levels modelled include full pool (purple), contemporary water levels (pink), and minimum water levels (orange). Δ 2018 Water Clarity refers to Secchi depth, with 0 m representing the mean monthly Z_{Secchi} from 2018 (0.2 m).

assess what fraction of sediment surface area had the potential to support benthic GPP, we applied a conservative benthic light access of 1% surface PAR (Vadeboncoeur et al., 2014).

To compare current vs. historical rates of GPP in Utah Lake, we considered literature reports of how benthic GPP affects water clarity in various lake types. The literature suggests that a benthic GPP occurrence across 5-30% of the sediment surface area decreases phytoplankton biomass via zooplankton grazing, 31-70% BPP coverage is necessary for increased nutrient competition effects, higher sediment nutrient retention, and potential allelopathic effects on phytoplankton, and >70% of benthic GPP coverage is necessary for strong controlling effects on reducing resuspension (following Hilt et al., 2006; Table 3 in Hilt & Gross, 2008 and references therein). We thus considered that Utah Lake, given its susceptibility to sediment resuspension, would have historically needed to have >70% benthic GPP coverage to support a self-stabilizing clear-water regime featuring a robust submerged macrophyte community.

Results

Detailed analyses of sediments from August and October 2019 cores, as well as a separate offshore cores collected in 2019, revealed no *C. aspera* oospore macrofossils. However, a good temporal agreement was obtained between the measured and modeled phytoplankton GPP (Fig. 5). Considering all model outputs (for comparison between phytoplankton and periphyton GPP, as well as current and historical GPP rates), Utah Lake's 2018 GPP was $550.1 \text{ g C m}^{-2} \text{ y}^{-1}$, which was almost entirely phytoplankton ($550 \text{ g C m}^{-2} \text{ y}^{-1}$). Given Utah Lake's bathymetry, a historical coverage of 70% of its sediment surface area by benthic primary producers would require Secchi depths to increase by 0.8 m from 2018 mean values (0.2 m; Fig. 7d).

Primary production models showed that phytoplankton GPP would likely initially increase slightly with improved water clarity, except at low-pool water levels, where phytoplankton GPP would sharply decrease (Fig. 7a). Conversely, modeled periphyton GPP displays the strongest positive response at low-pool water levels, and only a slight increase in productivity at 2018 and full-pool levels (Fig. 7b). Given the generally much greater rates of phytoplankton vs. periphyton GPP, total lake GPP (the sum of phytoplankton and periphyton GPP) generally follows the same pattern as that described for phytoplankton (Fig. 7c). Ultimately, the model thus indicates that at 0.8 m greater Secchi depths (compared to 2018 values), the total GPP of Utah Lake may be $602.3 \text{ g C m}^{-2} \text{ y}^{-1}$ (at 2018 water levels), 9% greater than 2018 GPP rates. An analysis of the proportional representation of benthic GPP at the whole-lake scale reveals that periphyton GPP can

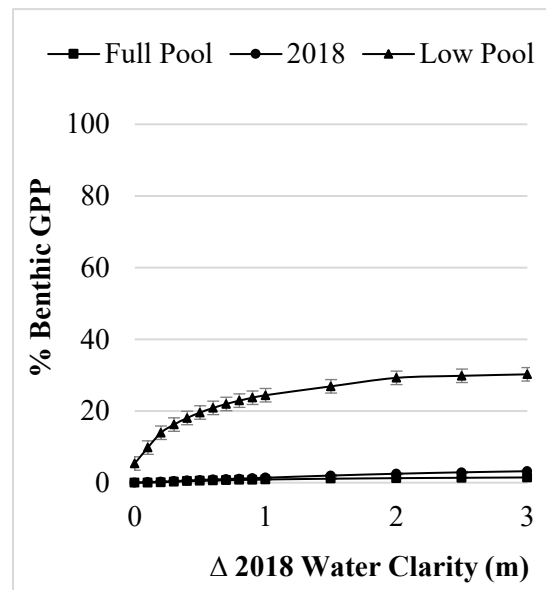


Figure 8. Fraction of benthic GPP vs. water clarity. Triangles represent low-pool water levels, circles and squares represent 2018 and high pool levels, respectively. Confidence intervals represent standard errors.

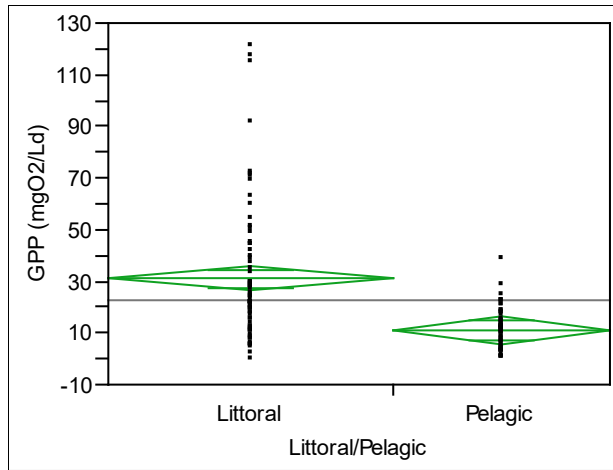


Figure 9: Littoral vs. off-shore (pelagic) GPP measured in spring 2019. Mean diamonds represent upper and lower 95% confidence intervals, overlap marks, and group mean values.

substantially compensate for declines in phytoplankton GPP, but only at low-pool water levels (Fig. 8).

Regarding aquatic metabolism rates measured from mid-May to mid-June in 2019, volumetric GPP rates measured from the near-shore (littoral) sites were significantly greater in the littoral zones (mean = 31.2 ± 2.5 mg O₂ L⁻¹ d⁻¹) compared to pelagic measurements (mean = 11.0 ± 2.9 mg O₂ L⁻¹ d⁻¹, $p < 0.0001$; Fig. 9). However, community respiration (CR) rates were also much greater in the littoral zone (mean = 68.4 ± 2.9 mg O₂ L⁻¹ d⁻¹) compared to pelagic measurements (mean = 30.0 ± 3.3 mg O₂ L⁻¹ d⁻¹, $p < 0.0001$; Fig. 10), resulting in a more negative net ecosystem production (NEP) in the littoral zone (Fig. 11).

Discussion

There are several possible explanations for the lack of *C. aspera* macrophyte remains in our collected sediment cores. These include: 1) cores were taken from locations that did not historically contain these submerged macrophytes, 2) coring depths (sediment core lengths) were insufficient to reach a historical macrophyte layer, 3) wave action may have destroyed macrofossil remains, and/or 4) anecdotal records of the prevalence of *C. aspera* in Utah Lake are false. Of these, we consider the most likely explanation to be the first; that our sampling locations did not overlap with the *C. aspera* macrophyte beds. *C. aspera* have elsewhere been observed as occurring off-shore from the wave-zone disturbance and emergent macrophyte (reed) beds of lakes (Y. Vadeboncoeur, *pers. comm.*). As our sampling efforts focused on the littoral zone during a high-water year, it is likely that the sediment cores we retrieved in 2019 were too shallow for finding the depth-layer at which *C. aspera* beds would have been prevalent in the 1800s. We therefore recommend that future studies carry out coring depth transects from

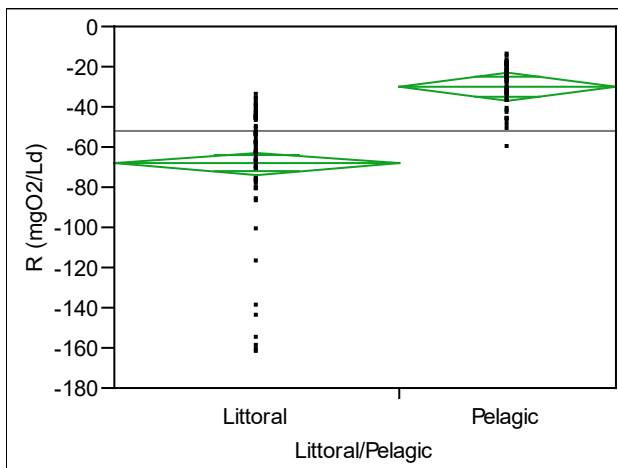


Figure 10: Littoral vs. off-shore (pelagic) CR measured in spring 2019. Mean diamonds represent upper and lower 95% confidence intervals, overlap marks, and group mean values.

near- to off-shore sites, by boat. Although coring depth may not have been a factor in our sampled sites, longer sediment cores are also more likely to be collected further offshore, making it more likely to reach the 1800s sediment layer. This approach would thus more decisively determine the location (or historical presence) of *C. aspera* beds in Utah Lake. Parallel sediment core studies from offshore sites have indeed retrieved plant microfossils in offshore locations.

This analysis cannot conclusively determine whether the historical submerged macrophyte community of Utah Lake occupied 70% of the lake's sediment surface area, or whether mean historical Secchi depths were in the range of 1 m. We can only report the results of our productivity models and literature analysis that together indicate that 1 m mean Secchi depths would likely be required for Utah Lake to have had enough macrophytes to significantly reduce lake-wide resuspension, creating the necessary conditions for the large macrophyte beds that were reported historically. Since 1989, fewer than 4% of measured Secchi depths from standardized monitoring campaigns have been 1 m or greater, most of those being from 1989, 1991, and 2006, and the maximum recorded Secchi depth in 2018 was 0.3 m (Utah Department of Environmental Quality (UDEQ), n.d.). However, 12 Secchi depth measurements taken from 1929 to 1931 included values of up to 1 m (Tanner, 1931; as reported in Bushman, 1980), though it is impossible to say how common these conditions were at that time, or in the previous century. Our primary production models indicate that 1 m Secchi depths would be associated with greater periphyton production rates than those observed in 2018 (ranging from $\sim 5 \text{ g C m}^{-2} \text{ y}^{-1}$ at full-pool water levels to $84 \text{ g C m}^{-2} \text{ y}^{-1}$ at low-pool), and variable responses in phytoplankton production rates (ranging from $\sim 283 \text{ g C m}^{-2} \text{ y}^{-1}$ at low pool to $\sim 647 \text{ g C m}^{-2} \text{ y}^{-1}$ at full pool). Thus, even at the water clarity conditions necessary to establish historically-reported submerged macrophyte growth in Utah Lake, phytoplankton production likely maintained a dominating role in food web dynamics.

We also note that these productivity models indicate that phytoplankton GPP may be higher at 1 m Secchi depths compared to 2018 Secchi depths, at 2018 and full-pool water levels, even when accounting for lower chl *a* concentrations in the water column. This modeling outcome captures the effect of self-shading by phytoplankton in the water column, as well as non-algal shading, which currently limits phytoplankton production at deeper layers of the water column. Although higher phytoplankton productivity at lower concentrations with clearer waters may initially be counter-intuitive, the efficiency of primary production in algae is not always closely bound with algal biomass (Baulch *et al.*, 2009). Studies from other lakes have also shown that greater water clarity and structural complexity in primary producer communities can result in higher annual rates of primary production (Blindow *et al.*, 2006; Brothers *et al.*, 2013a), and that these conditions can also result in more effective consumption and respiration of that primary production (Brothers *et al.*, 2013b). As a result, “inverted trophic pyramids” (i.e., large metazoan community biomasses supplied by low algal biomasses) are not uncommon in productive aquatic environments where rapid algal production is tightly coupled with algal consumption (Vadeboncoeur and Power, 2017). Thus, with respect to these model outputs for Utah Lake, it should not be assumed that higher modeled primary production with greater water

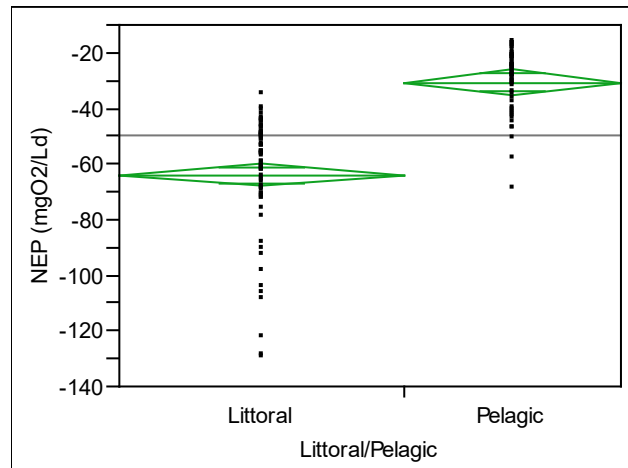


Figure 11. Littoral vs. off-shore (pelagic) net ecosystem production measured in spring 2019. Mean diamonds represent upper and lower 95% confidence intervals, overlap marks, and group mean values.

clarity means greater algal biomass accumulation or biofouling. Indeed, a comparison of the littoral vs. pelagic aquatic metabolism measurements in 2019 supports this argument, as the littoral GPP rates were higher (presumably associated with more complex primary producer communities observed in these locations), though the resulting NEP at the littoral sites was more negative, indicating that more organic matter was being consumed at the littoral sites vs. the pelagic sites. Although a more detailed analysis of the net heterotrophy measured in the lake during this period is impossible with the given data (and beyond the scope of this report), it is worth noting that during the 2019 measurement period, both littoral and pelagic sites were net heterotrophic, indicating that more organic matter was being consumed than was being produced during that period of measurement. Furthermore, the rate at which consumption/respiration exceeded primary production was greatest in the littoral zone. This difference between locations could potentially reflect a seasonal pattern at either site, whereby previously accumulated organic matter is being consumed (Staeher *et al.*, 2010; Finlay *et al.*, 2019), or it may indicate that a surplus of organic matter is available for mineralization at the littoral sites. This surplus could be either loaded into the lake from the watershed (del Giorgio *et al.*, 1999; Lapierre *et al.*, 2013), or even potentially transported from off-shore phytoplankton that was less-effectively consumed offshore and transported via convective or other currents.

We conclude that there is a high potential for Utah Lake to feature littoral-benthic primary production that plays an important functional role. The shallow lake zones which are today becoming clear enough to support the initial return of submerged macrophytes appear to feature higher primary production rates than recent historical pelagic measurements, indicating a potential (and tentative) link between water clarity and areal GPP rates in the lake, worthy of further investigation.

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