

Primary production modeling identifies restoration targets for shifting shallow, eutrophic lakes to clear-water regimes

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Abstract: Benthic primary production (BPP) plays an important functional role in lakes, improving water quality by stabilizing clear-water regimes. Shallow, eutrophic lakes lacking BPP communities can be difficult to restore because self-stabilizing feedbacks of phytoplankton dominance can impede the establishment of BPP. BPP in lakes is light limited, and ecosystem models can provide guidance for determining the water clarity necessary to re-establish BPP dominance. We developed a multi-tiered framework for the restoration of shallow, eutrophic lakes that incorporates multiple turbidity sources, lake morphometry, and water-level fluctuations to determine water-clarity thresholds above which BPP dominance may be established. We present a case study applying this restoration target framework to a large, shallow lake (Utah Lake, Utah, USA), where water clarity was greatly impeded by sediment resuspension and high algal biomass. Our analysis, which used commonly available lake-monitoring data, indicated that a return to BPP dominance is possible in Utah Lake, particularly if external nutrient loading to its shallow, wind-protected bays is reduced. Our novel framework incorporates regime shift theory to improve shallow, eutrophic lake restoration efforts. By incorporating ecological feedbacks when identifying the restoration targets necessary for returning a lake to a self-stabilizing, clear-water regime, this restoration target framework offers economical and logistical advantages over strategies that focus solely on phytoplankton management or fish biomanipulation.

Key words: regime shift, periphyton, water clarity, eutrophication, restoration, shallow lakes, water level, macrophyte, phytoplankton

Cultural eutrophication remains a critical global issue as urbanization, agricultural practices, and insufficient wastewater treatment continue to increase nutrient loading to many waterbodies (Frei et al. 2021). Eutrophication can lead to poor water-quality conditions that have considerable economic impacts, including a loss of local recreation revenue, and ecological impacts, including reduced food and habitat for aquatic life (Dodds et al. 2009). Excessive nutrient loading can result in cyanobacterial blooms with high concentrations of cyanotoxins that are harmful to lake

users and aquatic organisms (Chaffin et al. 2019). Blooms are projected to continue to increase (Glibert 2017), and advances in restoration and management strategies for shallow, eutrophic lakes are in high demand.

Water managers have historically adopted a variety of mitigation strategies to minimize or reverse the effects of anthropogenic activities on lakes. However, these strategies can be time-consuming, costly, and ineffective (Chislock et al. 2013). For instance, reduced P loading into Lake Erie (USA/Canada border) initially reduced in-lake P concentrations

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(Dove and Chapra 2015), yet eutrophic and hypoxic conditions persisted (Zhou et al. 2013), potentially because of within-lake biological feedbacks (Brothers et al. 2017). Furthermore, declines in phytoplankton production may be met with concerns that commercially and culturally valuable fisheries may be negatively affected (Evans et al. 2011). Elsewhere, nutrient reduction strategies have likewise been insufficient to return lakes to their pre-impact conditions because of the multiple drivers and consequences of eutrophication, as well as prolonged internal nutrient loading from the sediments (Jeppesen et al. 2005, Hilt et al. 2018). A greater incorporation of ecosystem functioning into lake-restoration strategies could improve their likelihood of success.

In-lake primary production is often dominated by phytoplankton (planktonic algae and prokaryotes, typically nutrient limited) or by a benthic community composed of periphyton (algae attached to macrophytes and lake sediments, typically light limited). Although the literature on eutrophication and lake food webs has historically focused on phytoplankton dynamics (Vadeboncoeur et al. 2002, Brothers and Vadeboncoeur 2021), benthic primary producers can play a critical structural and foodweb role (Hilt et al. 2017, Vander Zanden and Vadeboncoeur 2020). Despite the importance of primary production to lake ecosystem dynamics, it can be difficult to accurately measure rates of primary production (reviewed by Staehr et al. 2012), leading many studies to estimate rates using chlorophyll *a* (Chl *a*) concentrations as an analogue of algal biomass (e.g., following del Giorgio and Peters 1993). However, benthic algal Chl *a* concentrations are poorly linked to benthic primary production (BPP) rates (Baulch et al. 2009, Vadeboncoeur and Power 2017), and periphyton biomass is not a reliable trophic indicator because it can be very high even in pristine lakes (Vadeboncoeur et al. 2021). Nevertheless, water column parameters such as Chl *a* and Secchi depth provide lake-management agencies with rapid and relatively cheap information about the conditions of a given lake and can be used together to inform calculations of BPP and planktonic primary production rates. Incorporating such parameters into estimates of benthic and planktonic production facilitates the development of more ecologically relevant restoration targets that account for the role of benthic producers in addition to phytoplankton.

The competitive trade-offs between benthic and planktonic primary producers are at the core of regime shift theory and alternate stable states in lakes. Lakes often do not respond gradually to perturbations but instead shift between alternative self-stabilizing regimes that are separated by ecological tipping points (Scheffer et al. 1993). BPP reinforces clear-water conditions by promoting piscivore control over planktivorous fish (Blindow 1992), providing habitat for zooplankton (Genkai-Kato 2007), reducing sediment resuspension from wind mixing (Barko and James

1998), allelopathically inhibiting phytoplankton growth (Hilt and Gross 2008), and sequestering water-column nutrients to the sediments (reviewed by Kufel and Kufel 2002, Hilt et al. 2017). However, the self-stabilizing mechanisms of phytoplankton-dominated regimes can inhibit the colonization of both submerged macrophytes and periphyton because of shading from phytoplankton and sediment resuspension, as well disturbance from herbivorous fish and birds (Hilt et al. 2006 and references therein, Hidding et al. 2016). Despite the beneficial and self-stabilizing ecosystem effects of a clear-water regime, guidance remains scarce on how lake managers should utilize the functional and strategic potential of plant community structure (e.g., the partitioning between phytoplankton and periphyton) and regime shift theory in attaining desirable clear-water conditions.

Management and restoration strategies in eutrophic lakes have often focused on biomanipulation to initiate regime shifts (Shapiro and Wright 1984, Søndergaard et al. 2008). The removal of fish can directly and indirectly promote submerged macrophyte recovery, increasing water transparency (Miller and Crowl 2006, Jeppesen et al. 2007, Guo et al. 2022) through reduced sediment bioturbation and by facilitating increased zooplankton grazing (Reinertsen et al. 1990). However, even successful attempts to reduce populations of invasive fish species are not guaranteed to extirpate such species from a lake, making long-term management strategies potentially interminable and costly. Although strategies involving biomanipulation often produce significant improvements in water quality and clarity, the re-establishment of functionally valuable submerged macrophyte assemblages can be slow or absent, hindering the long-term recovery of clear-water conditions (Jeppesen et al. 2005, Hilt et al. 2006). It may, thus, be necessary for management strategies to include external nutrient reductions, with the explicit goal of re-establishing a self-stabilizing BPP community (rather than a transient reduction of phytoplankton gross primary production [GPP]; Hilt et al. 2018). The physical planting of submerged macrophytes to re-establish their presence in aquatic systems has had a positive impact on water clarity in shallow lakes (Liu et al. 2018) and coastal ecosystems (Lefcheck et al. 2018). Such efforts can be combined with large-scale enclosures to protect returning submerged macrophyte assemblages from multiple stressors including wave-driven resuspension events and grazing or physical uprooting by fish (Chen et al. 2009, Li et al. 2021). However, the response of BPP to increased water clarity is also linked to lake morphometry (Vadeboncoeur et al. 2008, Brothers et al. 2016), making the effects of reduced nutrient loading potentially lake specific. Therefore, further efforts accounting for lake-specific conditions are necessary to identify appropriate lake-specific restoration targets to make management and restoration efforts efficient.

We developed a conceptual framework to improve restoration targets for turbid, shallow lakes (Fig. 1). We present this restoration target framework as it applies to large, shallow, eutrophic Utah Lake (Utah, USA; Fig. 2), which is subject to major water-level fluctuations and frequent wind-driven resuspension. Based on in situ data and GPP modeling, we calculated periphyton and phytoplankton GPP to predict how lake GPP partitioning responds to water-clarity management at multiple water levels, providing guidance on the light attenuation requirements necessary to establish BPP dominance and, thus, a self-stabilizing, clear-water regime. We hypothesized that the conditions necessary for establishing a clear-water regime are attainable, given the likely historical occurrence of such a regime in this lake. If so, the targeted establishment of BPP in Utah Lake should be considered a key component in strategies aimed at improving this lake's water quality.

METHODS

Restoration target framework

We developed a framework that involves modeling benthic and planktonic GPP as variable functions of light availability and water-column thickness to identify the conditions necessary for BPP dominance (Fig. 1). This framework uses commonly available lake-monitoring data as inputs for calculations and provides output guidance targets in terms of Secchi depths and water-column Chl *a* concentrations for use by management and restoration agencies. The areal BPP coverage necessary to permit a stable, clear-water regime is often sensitive to lake-specific controls of lake turbidity, which our framework assesses by examining the relationship between water clarity (Secchi depths, representing non-algal and algal turbidity) and water-column Chl *a* (reflecting algal turbidity alone). This framework focuses conceptually on periphyton production because it

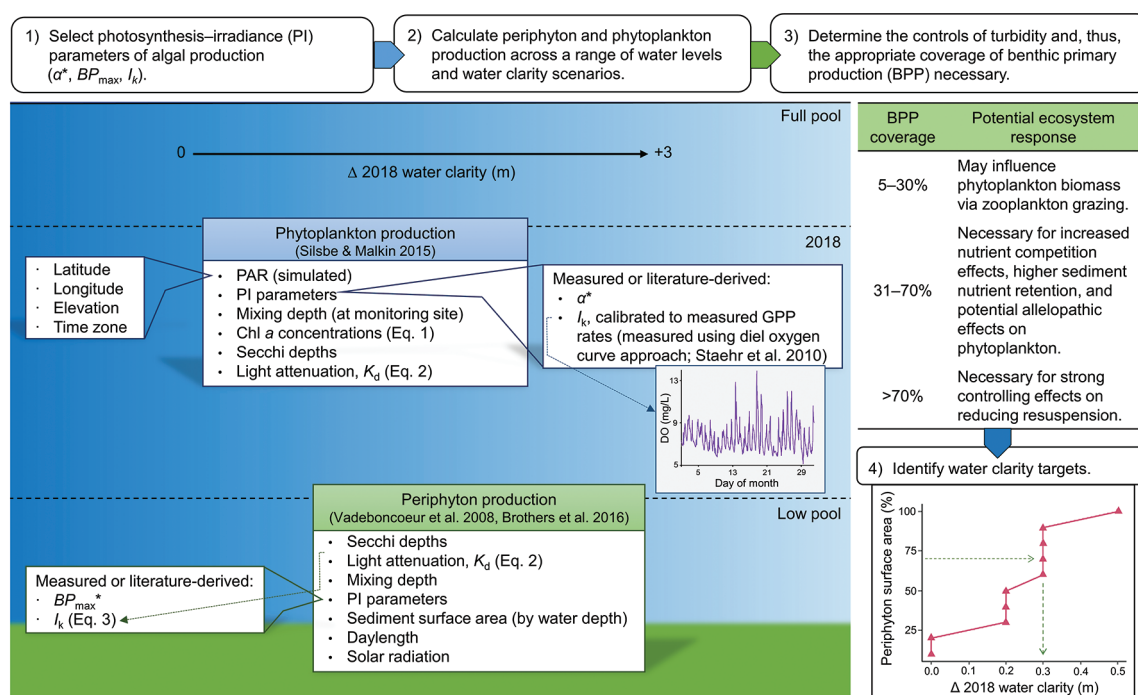


Figure 1. Conceptual workflow detailing water level and water clarity modeling scenarios for improving restoration targets for turbid, shallow lakes as well as required data inputs. This workflow was applied to a case study with light-integrated benthic and planktonic primary production models for shallow and eutrophic Utah Lake in Utah, USA. Phytoplankton (blue) and periphyton (green) production were modeled for Utah Lake along a gradient of increasing water clarity at 0.1-m intervals up to 3 m (indicated by blue fading) at full pool (controlled maximum lake level; 1368 m a. s. l., solid black line), 2018 water levels (1367 m a. s. l., upper dashed black line), and low pool (lowest lake elevation; 1365 m a. s. l., lower dashed black line). All data incorporated in the models were lake specific except where * indicates literature-derived values. Data included monthly chlorophyll *a* (Chl *a*) concentrations, photosynthetically active radiation (PAR), and photosynthesis-irradiance (PI) parameters, which included light attenuation (K_d), light utilization efficiency (α), light-saturated maximum rate of periphyton productivity (BP_{max}), and the irradiance at the inflection point (I_k , calibrated to measured gross primary production [GPP] from the diel dissolved oxygen curve approach for phytoplankton production). Modeled periphyton surface area along the gradient of increased water clarity shown in step 4 (pink triangles) was used to determine the necessary increase in water clarity based on the appropriate benthic primary production (green dashed arrows; e.g., 70% surface area requires an increase of 0.3 m).

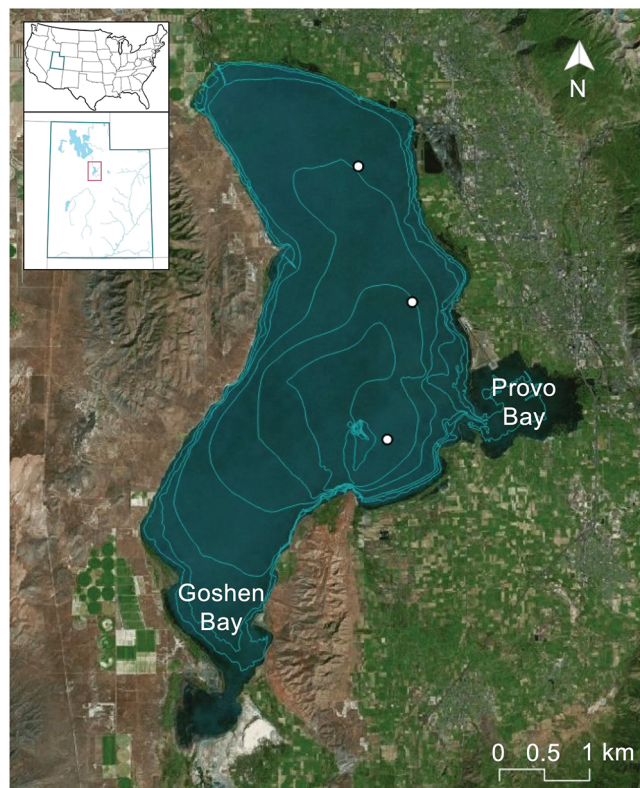


Figure 2. Map of Utah Lake in Utah, USA, with buoy locations (white circles) and bathymetry contours at 0.3-m intervals (blue lines).

often dominates benthic production (Brothers and Vadeboncoeur 2021), and the light conditions required by periphyton can generally be considered analogous to conservative thresholds required by submerged macrophytes. However, we report the current light attenuation and modeled future improvements in light attenuation as an additional verification of our models.

Applying the restoration framework to Utah Lake

To assess the usefulness of our framework, we applied it to Utah Lake, a lake identified as a good candidate for restoration of a clear-water regime. Utah Lake is a large (surface area = 385 km²), shallow (2018 mean depth = 3.2 m) lake located in north-central Utah (Fig. 2). It has several hallmark indicators of a turbid (2018 mean Secchi depth = ~0.2 m), eutrophic (mean annual total P = 80 µg/L) lake, including recurrent harmful algal blooms since the 1970s (Randall et al. 2019). Historical reports indicate that the lake had high water transparency and clear-water indicator submerged macrophytes (*Chara aspera*; Lambert-Servien et al. 2006) that are no longer observed today (Bushman 1980, Miller and Crowl 2006 and references therein).

Because of its large surface area and shallow depth, Utah Lake is highly susceptible to wind-driven sediment resuspension that may be a primary barrier to re-establishment of a

clear-water, macrophyte-dominated regime. However, the lake has 2 bays (Goshen Bay and Provo Bay) that are relatively sheltered and may, thus, be less affected by prevailing winds (Fig. 2). The partitioning between planktonic and benthic GPP in Utah Lake is further affected by its shallow sediment slope and high interannual hydrological fluctuations (~4-m water-level loss and gain since the 1930s; Fig. S1). In addition to these physical challenges to macrophyte assemblages, the introduction of invasive benthic-feeding Common Carp (*Cyprinus carpio* Linnaeus, 1758) has contributed to reduced submerged macrophyte abundance by destabilizing lake sediments and exacerbating lake turbidity (Miller and Crowl 2006, King 2019). High nutrient loading has also exacerbated the decline of submerged macrophytes (Hogsett et al. 2019).

We applied light-integrated models for monthly planktonic (Silsbe and Malkin 2015) and benthic periphyton GPP (Vadeboncoeur et al. 2008, Brothers et al. 2016) with lake-specific and literature-derived photosynthesis–irradiance (PI) curve parameters (Table 1) to account for a sediment resuspension-driven light environment. For both planktonic and benthic GPP, we modeled increases in Utah Lake’s 2018 mean monthly water clarity (ranging from 0.18–0.3 m; Table S1) by up to 3 m (roughly equivalent to the lake’s mean depth and the maximum Secchi depth recorded since 1989) at 0.1-m intervals for the 1st m and then every 0.5 m thereafter. Because water levels strongly influence light availability to the lake sediment surface, we modeled GPP at full pool (controlled maximum lake level; 1368 m a. s. l.), 2018 water levels (1367 m a. s. l.), and low pool (lowest lake elevation in the past 90 y, occurring in 1935, 1989, and 1992; 1365 m a. s. l.) (UDEQ 2019; <https://udwq.shinyapps.io/UtahLakeDataExplorer/>; Fig. 1). We analyzed water-clarity of both Goshen Bay and Provo Bay (Fig. 2) separately from the rest of the lake and only up to 1 m (as opposed to 3 m for the rest of the lake) because sheltered bays featuring shallow depths and reduced wind-driven sediment resuspension can be more responsive than off-shore areas to restoration strategies (Qin et al. 2006).

Phytoplankton production modeling

We calculated Utah Lake’s gross phytoplankton GPP with the package *Phytotools* (version 1.0; Silsbe and Malkin 2015) in the R statistical environment (version 4.1.0; R Project for Statistical Computing, Vienna, Austria) as a function of irradiance, light attenuation (K_d/m), PI-curve parameters, maximum mixing depth (Z_{max} , assumed to be the lake depth at each given monitoring site), and monthly surface-water-measured Chl *a* concentrations (µg/L) (Table 1). Using *Phytotools*, we simulated photosynthetically active radiation (PAR) across a defined time period (2018) given the latitude (40.2130°), longitude (−111.8025°), elevation (1368 m a. s. l.), and time zone (−6 Universal Coordinated Time) for Utah Lake. We used a Linke turbidity

Table 1. The variables and associated values/units for each parameter modeled in the phytoplankton and periphyton models. Data were collected in Utah Lake by the Utah Department of Environmental Quality, except when * indicates that data were obtained from the literature. Max = maximum, PAR = photosynthetically active radiation, PI = photosynthesis–irradiation.

| Model | Parameter | Variable | Value (unit) |
|---------------|------------------------|--|--|
| Phytoplankton | Bathymetry | Max mixing depth (Z_{\max}) | 4.3 m (full pool), 3 m (2018), 1.2 m (low pool) |
| | Irradiance/ PAR | Time period of interest | 2018 |
| | | Latitude, longitude | 40.21°, −111.80° |
| | | Elevation | 1368 m |
| | | Time zone | −6 Universal Coordinated Time |
| | | Light attenuation (K_d) | Eq. 2: K_d (m) |
| | PI-curve parameters | Light utilization efficiency (α)* | 7.53 g C m ^{−2} g Chl <i>a</i> ^{−1} mol ^{−1} |
| | | Irradiance at inflection of α and light-saturated max productivity (I_k) | 33 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (calibrated from diel oxygen measurements) |
| | | Monthly Chl <i>a</i> | Eq. 1: Chl <i>a</i> ($\mu\text{g/L}$) |
| Periphyton | Bathymetry | Proportion of sediment surface area at given depth (Z) | Unitless |
| | Irradiance/ PAR | Solar radiation (I_0) | $\mu\text{mol m}^{-2} \text{s}^{-1}$ |
| | | Daylength | h |
| | | Light attenuation (K_d) | Eq. 2: K_d (m) |
| | PI-curve parameters | Light-saturated max rate of periphyton productivity (BP_{\max})* | 15, 30, 150 mg C m ^{−2} h ^{−1} |
| | | Irradiance at inflection of BP_{\max} and light-saturated max productivity (I_k) | Eq. 3: I_k ($\mu\text{mol m}^{-2} \text{s}^{-1}$) |
| | | Max BP at specific depth ($BP_{\max Z}$) | Eq. 4 or Eq. 5: $BP_{\max Z}$ (mg C m ^{−2} h ^{−1}) |
| | | Periphyton production at each depth, ½-h intervals | Eq. 6: BP_Z (mg C m ^{−2} h ^{−1}) |

factor of 3.5 to determine monthly PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for all of 2018, and we subtracted the irradiance reflected off the water's surface from the PAR values.

To model phytoplankton production, we determined PI parameters from both measured variables and literature-derived values. We applied a literature-derived light utilization efficiency parameter (α , the initial slope of the curve) of 7.53 g C m^{−2} g Chl *a*^{−1} mol^{−1} that was measured in another shallow, eutrophic lake (West Basin of Lake Erie; Smith et al. 2005) because of a lack of lake-specific PI-curve parameters. However, a literature-derived value of the irradiance at the inflection of α and light-saturated maximum productivity (I_k) was not available for a suitably similar lake. We therefore derived an I_k value for our model by calibrating it to directly measured GPP rates in the lake. Specifically, we measured 2018 GPP rates (g C m^{−2} y^{−1}) in Utah Lake following the diel oxygen curve approach described by Staehr et al. (2010; details in Appendix S1), which remains the most commonly used method for estimating GPP despite its associated uncertainties (see Brothers and Vadeboncoeur 2021). Given the off-shore locations of the monitoring stations used for the diel oxygen curve approach (with water depths typically between 2–3 m) and low Secchi depths (mean = 0.2 m in 2018) that would preclude any local benthic GPP, we considered these GPP values to represent only

phytoplankton production. Using the Jassby and Platt (1976) model (Silsbe and Malkin 2015) and applying 2018 measured water-clarity data, we adjusted I_k so that the modeled phytoplankton GPP reflected the 2018 measured diel oxygen curve approach GPP rates, providing an I_k value of 33 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. S2). Although this value is somewhat below the range typical for lakes described in the literature (e.g., reported I_k values for 4 algal species ranged from 56–233 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in Gilbert et al. 2000), it provided a good overlap with the seasonality of measured monthly 2018 lake productivity rates (Fig. 3) and was thus considered appropriate for this analysis. Z_{\max} was 4.3 m at full-pool levels, 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 levels and 1.5 m at 2018 water levels. We analyzed only contemporary and full-pool water levels within the bays because the sediments in these areas would be largely exposed at low-pool levels.

For modeling phytoplankton GPP with changes in water clarity, we derived monthly Chl *a* using the equation:

$$\text{Chl } a = 14.29 + 5.32/Z_{\text{Secchi}}, \quad (\text{Eq. 1})$$

where Z_{Secchi} is the Secchi disk depth (m). This equation was developed from the long-term relationship between water

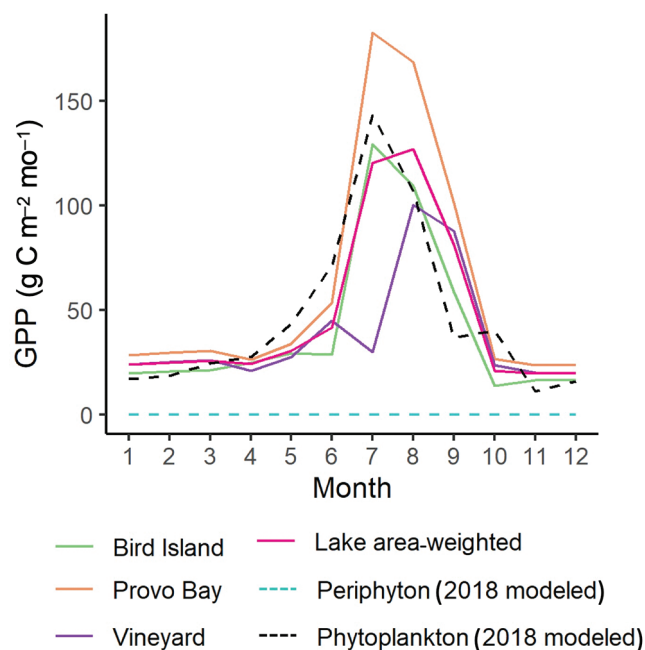


Figure 3. Monthly areal gross primary production (GPP) rates ($\text{g C m}^{-2} \text{mo}^{-1}$) in 2018 from 3 monitoring stations on Utah Lake, Utah, USA, a lake area-weighted estimate, phytoplankton model results for 2018, and periphyton model results for 2018 at a lake elevation of 1367 m (1.2 m below full pool) and mean monthly chlorophyll *a* concentrations and Secchi depths (Table S1).

clarity and measured Chl *a* (uncorrected for pheophytin) from 1989 to 2019 ($r^2 = 0.05$, $p < 0.0001$, $n = 502$) (UDEQ 2019; Fig. S3). We assumed Chl *a* concentrations to be uniform across the water column because of regular full water-column mixing.

We calculated light attenuation values from mean monthly 2018 Secchi depths (UDEQ 2019). We calculated light attenuation coefficients (K_d) by adapting the relationship with Secchi depths (Z_{Secchi}) described by Idso and Gilbert (1974) to the relationship between these variables calculated from Utah Lake data in 2018 ($r^2 = 0.29$, $p = 0.01$, $n = 20$), providing the equation:

$$K_d = 0.89 + 0.536/Z_{\text{Secchi}}. \quad (\text{Eq. 2})$$

Periphyton production modeling

We adopted a BPP model that assumes gross periphyton production in Utah Lake is limited only by light (Vadeboncoeur et al. 2008, Brothers et al. 2016) and that uses commonly available lake monitoring data (Table 1). We obtained monthly Secchi depths from 2018 from the Utah Department of Environmental Quality (UDEQ) (UDEQ 2019; Table S1). We then calculated K_d from Secchi depths by using the same equation described for the phytoplank-

ton model (Eq. 2). To calculate the sediment surface area across water-depth intervals, we used bathymetry contours obtained from UDEQ. Month- and location-specific day-length (h) and the amount of light reaching the surface of the lake (i.e., solar radiation because our model did not include cloud cover estimates; I_0 [$\mu\text{mol m}^{-2} \text{s}^{-1}$]) were applied from the 15th d of each month. Light-saturated maximum rates of periphyton photosynthesis (BP_{max}) reported in the literature can range from <30 to $>400 \text{ mg C m}^{-2} \text{h}^{-1}$, so we applied a conservative range of values including 15, 30, and $150 \text{ mg C m}^{-2} \text{h}^{-1}$ (Vadeboncoeur et al. 2008, Vander Zanden et al. 2011, Brothers et al. 2016 and references therein). For the separate analyses of the sheltered bays, we only modeled periphyton GPP assuming $BP_{\text{max}} = 30 \text{ mg C m}^{-2} \text{h}^{-1}$ to allow a more straightforward comparison between lake areas. Following Brothers et al. (2016), we calculated I_k as:

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

where Z is the lake's sediment surface depth (m) being modeled. We calculated the maximum benthic periphyton production at specific depths, $BP_{\text{max}Z}$ ($\text{mg C m}^{-2} \text{h}^{-1}$), at each bathymetric depth interval for each month of the year. To account for both the positive effects of light access on benthic GPP and the negative scouring effects of wave action at shallower depths, we made separate calculations for depth gradients above and below 50% surface light availability, assuming that the depth at 50% light availability captures the highest rates of BPP (following Brothers et al. 2016). When the light at a depth interval was $>50\%$ surface light, we calculated $BP_{\text{max}Z}$ ($\text{mg C m}^{-2} \text{h}^{-1}$) as:

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

and when $<50\%$ surface light was available to the sediment surface, we used the following equation:

$$BP_{\text{max}Z} = BP_{\text{max}Z50}(2\text{PAR}_Z - 0.1), \quad (\text{Eq. 5})$$

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

$$BP_Z = \Sigma(BP_{\text{max}Z} \tanh\{I_{0,t} \sin[\pi(t/\text{daylength})]e^{-K_d Z}/I_k\})/2, \quad (\text{Eq. 6})$$

where $I_{0,t}$ was the surface irradiance at time t (h). We then multiplied periphyton production at each depth 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.

To assess what fraction of sediment surface area had the potential to support BPP, we applied a conservative benthic

light access of 1% surface PAR (Vadeboncoeur et al. 2014). Literature indicates that a BPP coverage of 5 to 30% of the sediment surface area may influence phytoplankton biomass via zooplankton grazing; 31 to 70% BPP coverage is necessary for increased nutrient competition effects, higher sediment nutrient retention, and potential allelopathic effects on phytoplankton; and >70% BPP coverage is necessary for strong controlling effects on reducing resuspension (following Hilt et al. 2006, Table 3 in Hilt and Gross 2008 and references therein).

Macrophyte light compensation

To assess whether macrophyte establishment would be possible with modeled improvements in water clarity, we determined light compensation points for Utah Lake submerged macrophyte species. The UDEQ measured light profiles in Utah Lake in 2019, when the lake was at full pool. We computed K_d at each site on each sampled date by regressing $\ln(\text{PAR})$ by depth in R, according to North Temperate Lakes Long-Term Ecological Research methodology (NTL LTER 2022; <https://lter.limnology.wisc.edu/protocol/light-extinction>). We compared light profiles with literature values for macrophyte light compensation point, the PAR level at which net growth is 0, to predict sites where submerged macrophyte establishment may be successful. Light compensation points for species documented in Utah Lake (*Ceratophyllum demersum*, *Elodea canadensis*, *Myriophyllum spicatum*, *Stuckenia pectinata*, *Potamogeton praelongus*; Brotherson 1981, Miller and Crowl 2006) range from 3.5 to 45 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Madsen and Sand-Jensen 1991, Sand-Jensen and Madsen 1991). We entered observed PAR levels with associated depths into a logistic regression, which tested the likelihood of a given depth being below a light compensation point of 7, 10, and 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$, representing the most reported light compensation values across the above-listed taxa. Finally, we tested the effects of improvements in water clarity by increasing 2019 Secchi depths based on modeled light conditions following the computed relationship between Secchi depth and K_d in Utah Lake.

We made 2 key assumptions in the analyses of macrophyte light compensation: 1) calculations assumed only submerged macrophyte growth (i.e., emergent macrophytes and the possible complicating effect of periphyton shading was excluded), and 2) calculations assumed light conditions at the sediment–water interface. Thus, the light compensation depths may be considered conservative estimates given that emergent macrophytes are above the sediment–water interface. In Utah Lake, the historical presence of *Chara aspera*, a clear-water indicator species (Lambert-Servien et al. 2006) that has not been observed in recent years (Miller and Crowl 2006), suggests that conservative estimates are appropriate because this species typically grows near the sediment surface.

RESULTS

Primary production modeling

Utah Lake has extremely low light transmission; therefore, modeled 2018 gross BPP was minor ($0.07 \text{ g C m}^{-2} \text{y}^{-1}$), representing roughly 1% of the lake's annual modeled GPP (Fig. 3). Thus, our assumption that the lake area-weighted annual GPP of Utah Lake in 2018 calculated from in situ measurements ($\sim 560 \text{ g C m}^{-2} \text{y}^{-1}$) represents only phytoplankton GPP is appropriate. Monthly measured GPP ranged from ~ 13 to $182 \text{ g C m}^{-2} \text{mo}^{-1}$, and monthly modeled gross 2018 phytoplankton GPP ranged from ~ 11 to $143 \text{ g C m}^{-2} \text{mo}^{-1}$ (for a total of $556 \text{ g C m}^{-2} \text{y}^{-1}$). The agreement between the measured and modeled inter-seasonal range of variability indicates that our phytoplankton model PI-curve parameters were suitable. Given the agreement between measured and modeled GPP ($r^2 = 0.77$, $p = 0.0002$, $n = 12$), we considered our GPP models appropriate for comparing benthic vs planktonic GPP dominance along a restoration gradient of water levels and clarity.

Benthic and planktonic GPP, modeled along a 3-m water-clarity gradient at full-pool (e.g., 2011), contemporary (2018), and low-pool (85-y minimum) water levels reflected the influence of water-column thickness and the effect of higher water clarity associated with decreasing phytoplankton biomass (Fig. 4A–C). At 2018 and full-pool water levels, the effect of increasing water clarity on BPP rates was suppressed (Fig. 4B), whereas modeled phytoplankton GPP remained roughly stable or increased by up to $\sim 25\%$ from 1 to 3 m of improved water clarity (Fig. 4A). The stabilization, rather than a continued increase, of phytoplankton GPP as water clarity improved at 2018 and full-pool water levels reflects the suppressing effect of resuspension on phytoplankton GPP in deeper water-column layers. At low-pool water levels, corresponding to reduced water-column thickness, phytoplankton responded negatively to the increasing water clarity, whereas BPP responded positively and plateaued at $\sim 100 \text{ g C m}^{-2} \text{y}^{-1}$ when $BP_{\text{max}} = 30 \text{ mg C m}^{-2} \text{h}^{-1}$ (Fig. 4A, B). The decline in phytoplankton with increasing water clarity resulted in up to a 40% decline in total GPP compared with 2018 GPP, but with BPP representing up to 30% of total lake GPP at the highest modeled water clarity (Fig. 4C). These models indicate that BPP is possible across the full lake area at low pool, but that to maintain BPP across >70% of the sediment surface area, water clarity must increase by at least 0.3 (at 2018 water levels) or 0.8 m (at full pool) from 2018 mean Secchi depths (0.2 m; Fig. 5).

Model estimates for phytoplankton and periphyton GPP for Provo Bay and Goshen Bay showed slightly different patterns than those of the whole-lake models. Annual phytoplankton and periphyton GPP increased with increasing water clarity in both bays at full pool (Figs S4A, B, S5A, B), resulting in net total productivity gains (Figs S4C, S5C) and relatively weak proportional increases in the BPP fraction of total productivity (maximum 13% BPP in Provo Bay at

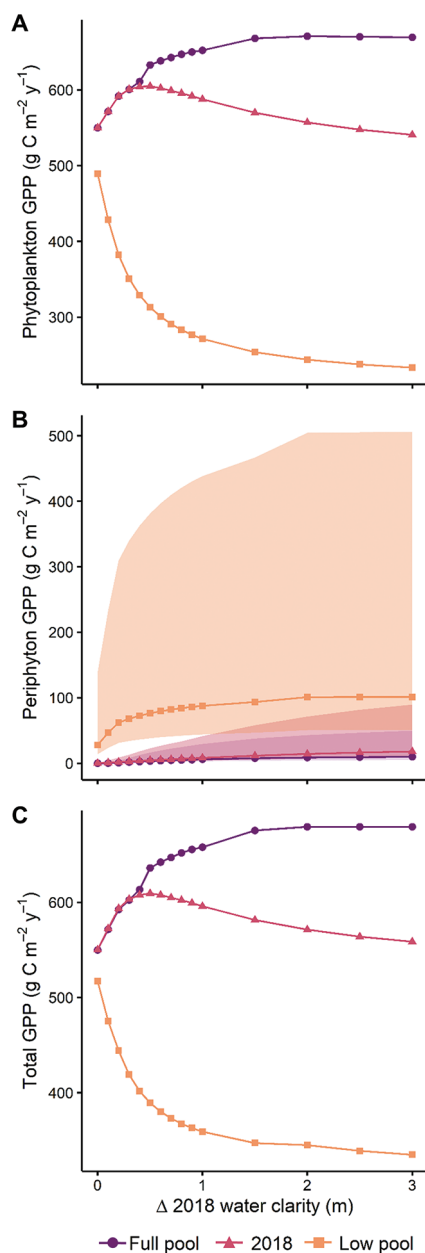


Figure 4. Phytoplankton gross primary production (GPP) (A), periphyton GPP, assuming light-saturated maximum rates of periphyton photosynthesis (BP_{\max}) of $30 \text{ mg C m}^{-2} \text{ h}^{-1}$ (B), and total GPP, assuming $BP_{\max} = 30 \text{ mg C m}^{-2} \text{ h}^{-1}$ (C) modeled at a whole-lake scale along a gradient of increasing water clarity in Utah Lake, Utah, USA. For panel B, CIs represent benthic GPP assuming BP_{\max} ranging from 15 to $150 \text{ mg C m}^{-2} \text{ h}^{-1}$. Modeled water levels include full-pool, contemporary (2018), and minimum water levels. Δ 2018 water clarity refers to Secchi depth, with 0 m representing mean monthly Secchi depth from 2018 (Table S1).

2018 water levels). However, the models indicated that the >70% threshold for BPP coverage was attainable with relatively minor water-clarity increases in both bays: Provo Bay required increases of 0 (2018 levels) to 0.2 m (full pool;

Fig. S6A), and Goshen Bay required increases of 0.1 (2018 water levels) to 0.3 m (full pool; Fig. S6B).

Macrophyte light compensation

Light levels ranged from 0.1 to $1950 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ at depths up to 3.8 m. The logistic relationship between depth and the probability of the light conditions being below the light compensation point varied depending on the threshold for light compensation chosen, but the CIs of the 3 models tested overlapped (Fig. 6). Assuming a light compensation point of $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$, the probability of a sample being below the light compensation point was 7% at 1-m depth, 30% at 2-m depth, and 71% at 3-m depth (Fig. S7). The depth at which there were equal odds of being above and below the compensation point was 2.49 m. Time of year affected the likelihood of conditions crossing the light compensation threshold, with May and June having higher light availability than later months (Fig. S7). Based on full-pool lake levels observed in 2019, 23% of the lake's surface area had greater odds of being above the light compensation point than below.

DISCUSSION

The overarching goal of this study was to determine how novel limnological theory and understanding could be used to benefit applied lake restoration initiatives, particularly in shallow, eutrophic lakes that appeared to be resistant to traditional remediation techniques. The framework presented here demonstrates that primary production modeling including benthic and planktonic producers can invoke regime shift theory dynamics, providing management agencies with detailed water clarity targets for restoring lakes. Below, we discuss how the application of this framework in a case study (Utah Lake) translates into specific strategies for ensuring that restoration efforts lead to a sustained shift in autotrophic structure. Subsequently, we discuss how this framework could be applied to a broader range of eutrophic lakes, including considerations of varying drivers of turbidity (e.g., phytoplankton compared with sediment resuspension) and prioritizing shallow and wind-sheltered bays when planning restoration efforts. Finally, we outline several broader implications associated with this work.

Recommendations for Utah Lake

Our models indicate that a transition to BPP dominance and, thus, a clear-water stable state, is possible in Utah Lake, with sustained water-clarity increases within ranges observed in recent years and across observed water level fluctuations. In recent decades, Utah Lake water levels have been at full pool in the late 1990s, late 2000s, and late 2010s, reflecting an approximate decadal periodicity. Although the models indicate that low-pool water levels would promote benthic dominance with minimal required increases

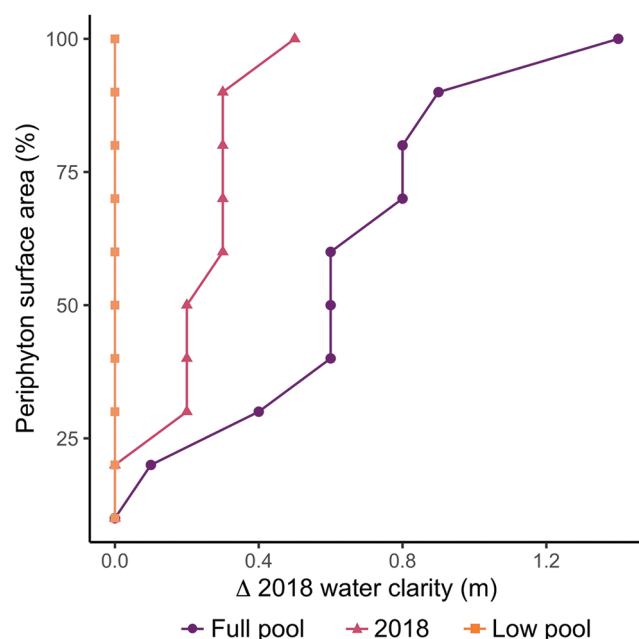


Figure 5. Percentage of total surface area of lake sediments supporting benthic gross primary production (assuming $BP_{\max} = 30 \text{ mg C m}^{-2} \text{ h}^{-1}$) modeled at a whole-lake scale along a gradient of increasing water clarity in Utah Lake, Utah, USA. Water levels modeled include full-pool, contemporary (2018), and minimum water levels. Δ 2018 water clarity refers to Secchi depth, with 0 m representing the mean monthly Secchi depth from 2018 (Table S1).

in water clarity, Utah Lake most recently approached low-pool water levels in 1989 and 1992, indicating these low water levels occur with less frequency. Therefore, we advise that Utah Lake restoration strategies focus on contemporary (2018) and full-pool lake levels, which provide a conservative estimate of sustained water-clarity requirements that BPP communities must be able to periodically tolerate to allow for a sustained shift in autotrophic structure.

Identifying the main driving factors of turbidity is necessary to ensure management efforts prove successful. We consider resuspension to be an important driving factor of turbidity in Utah Lake because of the relatively weak link between Chl *a* and Secchi depths ($r^2 = 0.05$, including many low Chl *a* concentration values associated with high turbidity conditions; Fig. S3), as well as the observed positive correlation between wind speed, sediment shear stress, and turbidity (Tetra Tech 2021). However, phytoplankton are still expected to be responsible for $\sim 1/4$ of the total turbidity in Utah Lake (Tetra Tech 2021). Reductions in phytoplankton biomass, the portion of turbidity controlled by nutrient reduction efforts, may thus be considered a catalyst for initial improvements in water clarity in the lake.

For initial gains in water clarity to be expanded and sustained, internal sediment stabilization feedback facilitated by greater BPP is likely necessary. Zhang et al. (2021) sug-

gested that 50% coverage of submerged macrophytes is optimal in shallow, eutrophic lakes; thus, we argue that a $>70\%$ sediment area threshold should be considered a conservative precondition for a sustained shift to BPP dominance in Utah Lake (following Hilt et al. 2006, Table 3 in Hilt and Gross 2008 and references therein). Calculated sediment shear stress in Utah Lake decreased by an order of magnitude with each doubling of water depth (Tetra Tech 2021). Considering conservative high-pool water levels, when sediment shear stress is minimized, $>70\%$ sediment surface area BPP coverage requires an increased water clarity of 0.8 m from 2018 levels or mean sustained Secchi depths of 1 m (Fig. 5).

Lake managers often apply trends in Chl *a* rather than Secchi depth as a restoration target (Dove and Chapra 2015), so we used the long-term Chl *a*–water clarity relationship for Utah Lake (Eq. 1, Fig. S3) to determine the relevant Chl *a* concentration associated with a given increase in water clarity. The relationship between Chl *a* concentrations and Secchi depths ($p < 0.0001$) suggests it is reasonable to assume that reductions in phytoplankton production (represented by Chl *a* concentrations) will result in improved water clarity. However, the high degree of variability in this relationship ($r^2 = 0.05$) highlights the fact that specific Chl *a* targets are associated with a relatively high degree of uncertainty because the lake’s water clarity is strongly controlled by sediment resuspension. Nevertheless, this relationship indicates that an appropriate restoration target for attaining a 0.8 m increase in water clarity is $\sim 20 \mu\text{g Chl } a/\text{L}$. If a Secchi depth increase of 0.8 m is applied to the 2019 light data set, all sampled locations on all dates

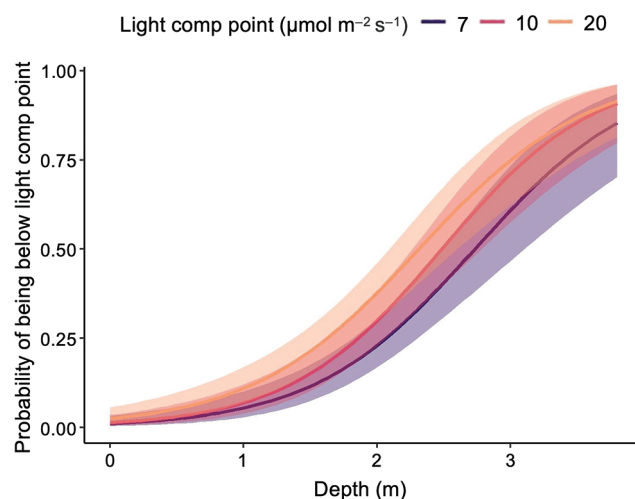


Figure 6. Logistic regression of depth and the probability of a given location of sediment surface being below the light compensation (comp) point for submerged macrophyte growth in present-day Utah Lake, Utah, USA. Curves represent a range of light compensation points for Utah Lake taxa, with 95% CIs for each curve indicated by shading.

would be above a macrophyte light compensation point of $10 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (range: 15.6–4248.5), demonstrating the capacity for submerged macrophyte restoration across the lake if clarity is improved.

Given the potential challenges associated with a whole-lake shift to a clear-water regime, an initial strategy for Utah Lake managers may be to prioritize remediating its shallow, wind-sheltered bays. Our models indicate that at full-pool water levels, Goshen Bay and Provo Bay would require increases in water clarity by 0.3 and 0.2 m, respectively (Fig. S6). Chlorophyll *a*–water clarity relationships (Eq. 1, Fig. S3) indicate that water clarity increases of that magnitude would require reductions of mean Chl *a* concentrations in these bays to ~25 and ~28 $\mu\text{g/L}$, respectively. Although we express a full range of variability for periphyton across a range of BP_{max} values and for macrophytes across a range of light compensation points, further sources of uncertainty exist (e.g., the uncertainties associated with the diel oxygen curve approach are widely addressed by Staehr et al. 2010 and reviewed in Brothers and Vadeboncoeur 2021) and may influence model-determined restoration target values and, thus, the success of restoration efforts. Despite such uncertainties, these results present lake managers with a specific target for restoration monitoring purposes that incorporates the role of BPP in maintaining restoration success.

We note that these models examine only the basic light requirements and lake morphometry dynamics of GPP and do not consider interactions with higher trophic levels, such as carp grazing on macrophytes, which likely play an important role in sustaining Utah Lake's turbid conditions (Miller and Crowl 2006). Our models indicate that at high-pool and contemporary water levels, whole-lake GPP would likely remain relatively stable or increase slightly with improved water clarity (Fig. 4C), providing potentially widespread benefits to the lake food web. Notably, an increase in primary production with improved water clarity does not necessarily imply higher algal biomass because more complex primary producer structures incorporating BPP can also support elevated levels of grazing and reduced algal biomass accumulation rates (Vadeboncoeur and Power 2017, Page et al. 2022). Large-scale efforts to remove Common Carp from Utah Lake aimed at reducing their impact on submerged macrophytes have already been underway for over a decade (Walsworth et al. 2020). Given both the direct grazing and indirect resuspension effects of carp on benthic GPP, the continued success of carp reduction measures is likely necessary for the successful and sustained re-establishment of BPP.

In addition to the effects of fish grazing on primary producers, it is also important to consider potential interactions between primary producers themselves. For instance, although both periphyton and submerged macrophytes have positive effects on water quality, periphyton can also have a direct negative shading effect on submerged macro-

phytes (Roberts et al. 2003). However, periphyton grazers, such as snails, can reduce this shading effect, and it has been argued that the presence of such macroinvertebrate grazers may ultimately make submerged macrophyte assemblages resilient to the effects of grazing by Common Carp (Hidding et al. 2016). Establishing a healthy submerged macrophyte assemblage and maintaining clear-water conditions in Utah Lake may ultimately reduce the necessary intensity of ongoing carp removal efforts. These complexities underscore that the minimum water-quality improvements described here may best be considered initial restoration targets subject to future adaptive management practices.

We propose a 2-tiered restoration approach for Utah Lake, combining nutrient abatement with additional management strategies, including continued biomanipulation, because the required increase in water clarity can likely only be partially met through nutrient mitigation (Jeppesen et al. 2005). We further suggest that restoration efforts focus initially on the shallow Provo and Goshen bays for 2 reasons. First, at the whole-lake scale, water level fluctuations and the role of sediment resuspension on water clarity may impede the effectiveness of nutrient reduction measures on submerged macrophyte recovery. In the wind-sheltered bays, nutrient mitigation effects on water clarity may be maximized, as suggested by Jin et al. (2022). Second, the BPP models indicated that the shallow bays were likely to support light conditions necessary for submerged macrophyte growth.

In addition to nutrient abatement and ongoing biomanipulation efforts, management strategies that may be beneficial for Utah Lake water clarity, especially in more wind-exposed areas of the lake, include large-scale enclosures and macrophyte transplantation (Chen et al. 2009, Lefcheck et al. 2018, Liu et al. 2018, Li et al. 2021, Guo et al. 2022). Submerged macrophytes do not always readily return on their own following nutrient reductions in lakes (Jeppesen et al. 2005), so active planting in key areas may be necessary. Restoration will also need to consider the life histories of different macrophyte species. For example, colonization depth may depend on macrophyte growth strategies. Some taxa grow taller to harvest light near the surface and may require only a short window of early summer transparency (Middelboe and Markager 1997; Fig. S7 orange dashed line), whereas others that grow near the bottom require consistent light conditions throughout the growing season (Fig. S7 purple and black dashed lines). Additional research would help improve the planning and optimizing of lake management strategies; however, our results indicate that a return to a clear-water regime in Utah Lake is viable.

Use of the framework for restoring eutrophic lakes

Through the restoration target framework (Fig. 1), lake managers can directly assess a trajectory for phytoplankton

and periphyton GPP, and the surface areas covered by BPP, with changing lake water levels and water clarity. To translate these data into actionable management strategies, and to answer the question of whether a given lake can realistically be returned to a clear-water regime, additional lake-specific characteristics should be assessed. Considerations include the timing and pattern of water level fluctuations and the predominant causes and controls of turbidity in a given lake.

The results of the phytoplankton and periphyton models provide lake managers with general guidelines, based on lake-specific routine monitoring data, that are broadly applicable to shallow lakes suffering from water-clarity degradation. Secchi depths and Chl *a* are 2 of the most frequently measured variables in lakes and will be commonly available to lake managers, along with lake location, daylength, and solar radiation information. In cases where data are not available, lake managers can use literature-derived values from a lake with comparable ecological conditions or can measure variables directly if timing and funding are sufficient. For example, lake-specific PI-curve parameters may not be available or easily obtained in all cases, but appropriate values can be obtained from the literature or measured directly (e.g., Dodds et al. 1999, Phillips 2020). However, additional consideration of the uncertainty associated with literature-derived values must be accounted for when interpreting results. For example, we accounted for such uncertainty by modeling periphyton GPP across a range of BP_{\max} values and by ensuring that the α value and I_k value in the phytoplankton GPP model resulted in GPP values that were consistent with both the measured annual and seasonal fluctuations of GPP (Fig. 3).

The timing and pattern of lake-level fluctuations can be a critical consideration for the potential recovery trajectory of a given lake because the periodicity of high vs low water-level periods may influence the establishment rates of native or desired macrophyte species (e.g., Hilt et al. 2006, Chao et al. 2022). Low water levels may promote BPP by reducing the water-column distance necessary for light to reach the sediment surface, but reduced water levels also introduce a critical risk of increasing turbidity because of sediment resuspension (Jeppesen et al. 2015), potentially limiting BPP recovery. This effect of increased turbidity at low water levels is especially apparent in eutrophic lakes (Lisi and Hein 2018). In contrast, although high water levels increase the water volume available for phytoplankton production, they may reduce wind-driven sediment resuspension because of increased water-column thickness and may increase water transparency (Lisi and Hein 2018). Therefore, high water-level years may provide beneficial opportunities for establishing BPP while maximizing the potential impact of nutrient reduction measures on controlling water clarity. If water clarity can be managed through continued nutrient abatement measures in subsequent years (i.e., years with decreasing water levels) to allow for a sustained shift to

BPP dominance, lake managers may be able to maintain a clear-water regime by capitalizing on the nutrient sequestration and sediment resuspension-reducing effects of a healthy BPP community (Hilt et al. 2017).

The framework presented here anticipates that management agencies may derive lake-specific relationships between Chl *a* and water clarity for use in determining restoration targets. Turbidity in eutrophic lakes is often controlled by a combination of wind-driven resuspension and phytoplankton biomass in the water column. An investigation of the relationship between water-column Chl *a* and concurrent Secchi depth measurements provides evidence of how strongly phytoplankton biomass controls turbidity, with a lower fit reflecting a stronger controlling role for resuspension. This relationship can be used to determine the target Chl *a* concentration associated with a change in water clarity and the likelihood that phytoplankton reductions will result in water-clarity increases. The relative importance of resuspension vs phytoplankton biomass can also play a role in determining a target fraction of macrophyte colonization on the lake bed because submerged macrophytes have the capacity to reduce resuspension by attenuating bed shear stress and stabilizing sediments (Wang et al. 2010). Ultimately, a strong relationship between Chl *a* and Secchi depth measurements indicates that turbidity is likely controlled by phytoplankton rather than sediment resuspension. The strength of this relationship may, thus, determine whether initial reductions in nutrient loading are sufficient to fully restore clear-water conditions in a lake or whether the aim should be to improve water clarity only enough to establish internal sediment stabilization feedbacks.

Broader implications

This study demonstrates how GPP modeling and regime shift theory may be used to improve restoration planning in shallow, eutrophic lakes, providing lake managers with ecologically relevant, lake-specific, water-clarity targets. Without accounting for the light requirements necessary for BPP to become established in lakes, external and internal nutrient loading reductions to lakes may potentially be insufficient at restoring stable clear-water conditions. Applying GPP modeling to Utah Lake revealed that a return to a clear-water state is possible with increases in water clarity that have been observed in recent years, especially in its wind-sheltered bays. The recommended reductions in Chl *a* and increases in water clarity may be achieved through a combination of management strategies, and the timing of these strategies may be planned to align with natural or controlled changes in lake water levels to maximize their chance for success. The use of the restoration framework presented here is broadly applicable to shallow, eutrophic lakes worldwide that have undergone regime shifts from a clear-water, BPP-dominated state to a turbid, phytoplankton-dominated state. Further research is necessary

to identify the appropriate combination of lake management strategies that will lead to the improvements in water clarity necessary for BPP establishment. Nevertheless, strategies that incorporate GPP modeling may allow management agencies to maintain long-term improvements in water clarity and quality by utilizing the ecosystem services provided by clear-water regimes, thus minimizing the resources necessary for lake management.

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Author contributions: LK, JB, and SB conceived the ideas and designed the study. SD, MJP, and KRS contributed to study concept and design. Data were analyzed by LK, SB, KRS, and MJP. LK and SB led the writing of the manuscript, though all coauthors contributed to the manuscript writing. SB and JB contributed to funding the study. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability statement: All analyses were made using data from the Utah Lake Data Explorer (UDEQ 2019).

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