RELATIONSHIPS BETWEEN NET PRIMARY PRODUCTION, WATER TRANSPARENCY, CHLOROPHYLL A, AND TOTAL PHOSPHORUS IN OAK LAKE, BROOKINGS COUNTY, SOUTH DAKOTA

Lyntausa C. Kuehl and Nels H. Troelstrup, Jr.*
Department of Natural Resource Management
South Dakota State University
Brookings, SD 57007
*Corresponding author email: nels.troelstrup@sdstate.edu

ABSTRACT

Lake trophic state is of primary concern for water resource managers and is used as a measure of water quality and classification for beneficial uses. Secchi transparency, total phosphorus and chlorophyll a are surrogate measurements used in the calculation of trophic state indices (TSI) which classify waters as oligotrophic, mesotrophic, eutrophic or hypereutrophic. Yet the relationships between these surrogate measurements and direct measures of lake productivity vary regionally and may be influenced by external factors such as non-algal turbidity. Prairie pothole basins, common throughout eastern South Dakota and southwestern Minnesota, are shallow glacial lakes subject to frequent winds and sediment resuspension. Light-dark oxygen bottle methodology was employed to evaluate vertical planktonic production within an eastern South Dakota pothole basin. Secchi transparency, total phosphorus and planktonic chlorophyll a were also measured from each of three basin sites at biweekly intervals throughout the 2012 growing season. Secchi transparencies ranged between 0.13 and 0.25 meters, corresponding to an average TSI\textsubscript{SD} value of 84.4 (hypereutrophy). Total phosphorus concentrations ranged between 178 and 858 ug/L, corresponding to an average TSI\textsubscript{TP} of 86.7 (hypereutrophy). Chlorophyll a values corresponded to an average TSI\textsubscript{Chla} value of 69.4 (transitional between eutrophy and hypereutrophy) and vertical production profiles yielded areal net primary productivity values averaging 288.3 mg C\textperiodcentered m\textsuperscript{-2}\textperiodcentered d\textsuperscript{-1} (mesotrophy). Our results support the hypothesis that resuspended non-algal turbidity, not planktonic production, decreases water transparency and reduces potential net primary production. Chlorophyll a TSI values corresponded most closely with measurements of planktonic production and better represented the trophic state of this basin.

Keywords

areal primary production, trophic classification, shallow lake
INTRODUCTION

Lake trophic state is a measure of the productivity of a water body and is linked to beneficial use criteria (Carlson and Simpson 1996). Potential impacts of eutrophication include phytoplankton blooms, oxygen-depletion in deep waters, degradation of water supplies, and recreational use limitations (Carlson 1977; Chin 2006; Codd 2000; USEPA 1998; USEPA 2009b). Hypereutrophic conditions are often characterized by taste and odor issues, oxygen depletion, and the potential presence of cyanobacterial toxins as planktonic production accelerates and die-offs occur. Assessment of lake trophic state and deduction of factors influencing production are necessary before corrective measures can be applied (Wetzel 2001). Thus, it is important for water resource managers to monitor and control eutrophication (Chin 2006).

The trophic state of a lake describes its potential for primary production and ranges between oligotrophic and hypereutrophic (Carlson and Simpson 1996). An oligotrophic lake has low productivity (50 - 300 mg C·m⁻²·d⁻¹), clear water and low nutrient concentrations (Wetzel 2001) (Table 1). Mesotrophic lakes are moderately clear and productive (250 – 1,000 mg C·m⁻²·d⁻¹). A eutrophic lake is highly productive (> 1,000 mg C·m⁻²·d⁻¹) with low transparency and high planktonic algal densities and/or macrophyte growth. Finally, hypereutrophic lakes are very highly productive, with dense macrophytes and algae and very low transparency (Carlson and Simpson 1996).

Recent data for 124 South Dakota lakes showed that 0.01% were oligotrophic, 15% were mesotrophic, 51% were eutrophic, 34% were hypereutrophic, and 21% were unclassified (SDDENR 2012). The 2007 National Lakes Assessment program characterized trophic state based primarily on chlorophyll a values. Results indicate that of the 49,546 national lakes assessed, 13% were oligotrophic, 37% were mesotrophic, 30% were eutrophic, and 20% were hypereutrophic (USEPA 2009b).

Restoration and maintenance of the integrity of the nation’s waters by state and federal governments are regulated by the Clean Water Act (USEPA 1998). Subsequently, routine assessment of lakes is required to monitor condition and implement restoration actions. Financial resources are limited, however, preventing direct measurement of production by most monitoring agencies (USEPA 2002). Surrogate measurements, primarily water transparency, phosphorus, and chlorophyll a, are collected in place of direct measurements to evaluate lake productivity and assign trophic state (USEPA 2009a).

The Carlson Trophic State Index uses measurements of water transparency (Secchi transparency), total phosphorus, and/or chlorophyll a to assign lake trophic classes by applying the equations below (Carlson 1977; Carlson and Simpson 1996). The Trophic State Index (TSI) is a scale ranging from 0 to 100. TSI values falling within different index ranges are assigned to one of the following trophic classes: oligotrophy (TSI less than 30), mesotrophy (between 30 and 50), eutrophy (between 50 and 70), and hypereutrophy (greater than or equal to 70) (Carlson and Simpson 1996; USEPA 2009a) (Table 1).

\[
\text{TSI Total Phosphorus} = 14.42 \times \log_{10}(\text{TP} \ \mu\text{g/L}) + 4.15
\]

\[
\text{TSI Chlorophyll a} = 9.81 \times \log_{10}(\text{chlorophyll a} \ \mu\text{g/L}) + 30.6
\]

\[
\text{TSI Secchi transparency} = 60 - 14.41 \times \log_{10}(\text{Secchi transparency m})
\]
The most frequently measured surrogate variable for basin production utilizes a Secchi disc to measure water transparency (USEPA 1998; Likens and Wetzel 1991; Vollenweider 1969). The mean depth at which the disc disappears from view while being lowered into the water and at which it reappears when being raised is the transparency or Secchi depth (Likens and Wetzel 1991). This method of determining transparency is cost effective and simple, making it an ideal and common method for state agencies to rapidly evaluate trophic state (Vollenweider 1969; Wetzel 2001). In fact, many state agencies recruit members of lake associations and other volunteers for the collection of Secchi transparency data from otherwise unmonitored lake basins (USEPA 2002; USEPA 2009b).

Potential error can exist in the assessment of trophic conditions from Secchi transparency. Abiotic factors can influence water transparency and give a false indication of high productivity. For instance, in areas with moderate amounts of non-algal turbidity the Secchi disc is an inappropriate method of determining algal biomass for the classification of trophic state (Chin 2006; Wetzel 2001). Nutrient limitation or variations in transparency can also cause deviations in chlorophyll $a$ TSI values relative to those derived from total phosphorus or Secchi transparency (Carlson 1992).

Eastern South Dakota and southwestern Minnesota landscapes have high densities of glacial lakes. Many of these lakes are classified as hypereutrophic due to low transparency values. Yet many are also very shallow and easily mixed by frequent high winds. For example, Oak Lake, Brookings County, South Dakota, has an average depth of 1.2 m and a maximum depth of 2.0 m (Troelstrup 2009). The lake experiences high and often sustained winds, which produce waves that reach the basin bottom and resuspend sediments. Resuspended sediments may decrease transparency and inflate phosphorus values without a corresponding productivity increase (Carper and Bachmann 1984; Bachmann et al. 2000). Thus, high production could be falsely estimated through water transparency and total phosphorus measurements alone.

### Table 1. Trophic state classification ranges based on mean daily net primary production and TSI values derived from Secchi transparency, total phosphorus, or chlorophyll $a$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Oligotrophy</th>
<th>Mesotrophy</th>
<th>Eutrophy</th>
<th>Hypereutrophy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net Primary Production (mg C/m$^2$/d)$^1$</td>
<td>50 - 300</td>
<td>250 – 1000</td>
<td>&gt; 1000</td>
<td></td>
</tr>
<tr>
<td>Total Phosphorus (ug/L)$^1$</td>
<td>3.0 - 17.7</td>
<td>10.9 – 95.6</td>
<td>16 – 389</td>
<td>750 – 1200</td>
</tr>
<tr>
<td>Chlorophyll $a$ (ug/L)$^1$</td>
<td>0.3 – 4.5</td>
<td>3 – 11</td>
<td>3 – 78</td>
<td>100 – 150</td>
</tr>
<tr>
<td>Secchi Transparency Depth (m)$^1$</td>
<td>5.4 – 28.3</td>
<td>1.5 – 8.1</td>
<td>0.8 – 7.0</td>
<td>0.4 – 0.5</td>
</tr>
<tr>
<td>TSI (Secchi, TP, or Chlorophyll $a$)$^2$</td>
<td>&lt; 30</td>
<td>30</td>
<td>50 - 70</td>
<td>70 - 80</td>
</tr>
</tbody>
</table>

$^1$ Modified from Wetzel (2001)

$^2$ Modified from Carlson and Simpson (1996)
The issue then arises as to which approach or approaches best estimate productivity for shallow prairie lake basins. The objectives of this project were to (1) estimate mean daily plankton productivity vertically within a shallow pothole basin, (2) measure complementary Secchi transparency, total phosphorus and chlorophyll a concentrations, and calculate TSI values, (3) compare trophic state determined by direct production with TSI classifications and (4) examine the relationship between areal net primary productivity and water transparency.

METHODS

Site description—Areal planktonic net primary production was vertically profiled at Oak Lake, Brookings County, South Dakota, using the laboratory facilities and field equipment of the Oak Lake Field Station (Lat 40° 30’ 30.36”, Long -96° 31’ 52.98”) (Figure 1). Oak Lake is classified as hypereutrophic with a maximum depth of 2.0 m and an average depth of 1.2 m (SDDENR 2010; Troelstrup 2009). The watershed for this basin drains portions of the Northern Glaciated Plains ecoregion and falls within the headwaters of the Minnesota-Mississippi river system. Basin area is 163 ha and basin length is 3,081 m.

Figure 1. Oak Lake (Brookings County, South Dakota) and associated Oak Lake Field Station. The extent of the field station grounds is indicated in gray. Boundaries and basin monitoring sites where light/dark productivity and monitoring measurements were taken are indicated.
Three basin sites (north, middle, and south) are routinely monitored (1970 - present) and were thus chosen as sites for production measurement (Figure 1). The overlap in sampling and monitoring sites allowed assessment of correlations between production measurements and biophysical monitoring data.

**Measurement of production**—Biweekly measurements of plankton production were taken at each site throughout the period of May through August using the light/dark bottle method (Vollenweider 1969). Light and dark bottle pairs were filled and suspended at depths of 16 cm and at each 25 cm interval from the water surface to the basin floor at each site. One duplicate pair was suspended at 16 cm at one randomly chosen site each testing day as a recorded control. An initial set of dissolved oxygen (DO) concentration readings were recorded for each depth using a Biochemical Oxygen Demand (BOD) YSI DO probe (Yellow Springs Instruments 5905 BOD Probe, Yellow Springs, Ohio). Suspended bottles were collected after an incubation period of between 5 and 7 hr, and final DO concentrations were measured using the BOD YSI DO probe.

Initial and final oxygen concentrations from each bottle were used to estimate gross and net primary production and community respiration at depth (Lind 1985). Net primary production (NPP) was estimated by first dividing the change in dissolved oxygen by the incubation time and then multiplying that value by the number of hours in the photoperiod of each testing day (USNO 2012). The photoperiod was determined using sunrise and sunset times for Oak Lake as listed by the U.S. Naval Observatory after subtracting two hours for low sun angle at sunrise and sunset. Daily community respiration was estimated by extrapolating hourly oxygen change observed in dark bottles through a 24-hr period. Daily gross primary production (GPP) was determined by adding the estimated daily values for NPP and community respiration from a given site.

Net primary productivity values were integrated with depth by graphing production against depth. These plots were imported into graphical software (Plot Digitizer 2.5.1, Oracle Corporation, Redwood Shores, California) and the area under the curve digitized to calculate areal net primary productivity for each site on each sampling day. Daily NPP estimates were expressed in carbon units per square meter following the unit conversion of Lind (1985) which is 2.67 mg O$_2$ = 1 mg C. These values were used to analyze seasonal trends and the relationship between direct production and surrogate measurements. Relationships were evaluated using linear regression following log$_e$ transformation of all data.

**Surrogate parameters**—Oak Lake water quality and water depth were monitored every other week during the growing season at three basin sites (Figure 1). Measurements included dissolved oxygen, specific conductance, pH, and water temperature using an YSI Model 556. Sonar depth soundings were made at each basin site on each monitoring date. Secchi transparency was measured at each basin site (Lind 1985) and vertical profiles of photosynthetically active radiation (PAR) were measured at 25-cm intervals from the surface to the bottom at each site using a LICOR LI-1000 radiation sensor. Grab samples were collected below the surface, filtered, and chlorophyll a was extracted using 90% acetone. Planktonic chlorophyll a concentrations, corrected for phaeophytin, were measured spectrophotometrically (Clesceri et al. 1998). Total phosphorus
samples were collected from each site each testing day at a depth of 25 cm in 250 mL acid-washed polycarbonate bottles, acidified to a pH < 2, and refrigerated for preservation (Clesceri et al. 1998). Samples were sent to the South Dakota Department of Health for analysis of total phosphorus concentration. A blank sample of deionized water was similarly preserved and analyzed for approximately fifty percent of the sample dates as a quality control measure. Raw data for Secchi transparency, chlorophyll \(a\), and total phosphorus were converted to TSI values using the equations described previously and corresponding trophic classifications determined for comparison with direct measures of basin productivity.

RESULTS

Net primary production within the Oak Lake basin displayed significant seasonal variation among the three basin sites. Production generally increased at the Middle Basin (MB) and South Basin (SB) until mid-June, and decreased for the rest of the growing season. In contrast, production at the North Basin (NB) tended to increase across the season (Figure 2). NPP ranged from 0 to 810 mg C·m\(^{-2}\)·d\(^{-1}\) (\(\bar{x} = 245\) mg C·m\(^{-2}\)·d\(^{-1}\)), which classifies the basin as oligotrophic or mesotrophic (\(\bar{x} = \) oligo-mesotrophic). Secchi transparencies for Oak Lake ranged between 0.13 and 0.25 m, with corresponding TSI values of 89.40 and 79.98 (\(\bar{x}\) TSI\(_{SD}\) = 84.43, \(\sigma = \pm 2.7\)). Total phosphorus concentrations ranged between 178 and 858 \(\mu\)g/L and TSI\(_{TP}\) values ranged between 78.87 and 101.55 (\(\bar{x} = 86.72, \sigma = \pm 6.2\)). Chlorophyll \(a\) measurements ranged between 8.01 \(\mu\)g/L and 22.8

![Areal Net Primary Production Summer 2012](Image)

*Figure 2. Areal net primary productivity of Oak Lake (Brookings County) in mg C·m\(^{-2}\)·d\(^{-1}\) during the summer of 2012 (NB = North Basin, MB = Middle Basin, SD = South Basin). Production measured as the area under a curve from the surface to the production compensation point.*
ug/L. The corresponding TSI$_{Chla}$ values ranged between 51.01 and 83.52 ($\bar{x}$ = 69.43, $s = \pm 6.7$), respectively. Secchi transparency and total phosphorus strongly indicate hypereutrophy, while chlorophyll $a$ indicates eutrophy or hypereutrophy.

A significant positive linear relationship was observed between log-transformed NPP and Secchi transparency ($r^2 = 0.31$, $P < 0.01$) (Figure 3). Neither total phosphorus nor chlorophyll $a$ displayed a significant relationship with NPP ($P > 0.05$). Wind speed, light, and surface water temperature failed to explain additional variation in areal NPP. A multiple regression using log transformed Secchi transparency and log transformed total phosphorus again explained only 31% of the variation in NPP ($\log_{10}\text{NPP} = -5.26737 – 2.62585\log_{10}\text{SD} + 0.50260\log_{10}\text{TP}$, $P = 0.02$, $R^2 = 0.31$).

**DISCUSSION**

NPP in Oak Lake averaged 245 mg C·m$^{-2}$·d$^{-1}$ and ranged from 0 to 810 mg C·m$^{-2}$·d$^{-1}$. These values fall within or below the ranges reported for other shallow basins. For example, oligotrophic Lawrence Lake in Michigan yielded a mean daily productivity of 99 mg C·m$^{-2}$·d$^{-1}$ and ranged between 5 and 497 mg C·m$^{-2}$·d$^{-1}$ (Wetzel 2001). Shallow Sylvan Lake in Indiana is classified as eutrophic with a mean daily productivity of 1,564 mg C·m$^{-2}$·d$^{-1}$ and a range between 9 mg C·m$^{-2}$·d$^{-1}$ and 4,959 mg C·m$^{-2}$·d$^{-1}$. Lake Minnetonka in Minnesota, classified as mesotrophic, averages 820 mg C·m$^{-2}$·d$^{-1}$ in NPP. A study of Northern Great Plains saline lakes in North and South Dakota and Montana yielded a mean production rate of 125 mg C·m$^{-3}$·h$^{-1}$ in the summer with a range between 15
and 544 mg C·m⁻³·h⁻¹ (Salm et al. 2009). The production values for Oak Lake are reasonable, though on the lower end of the range reported in the literature for other lakes.

Direct production measurements indicate that Oak Lake ranges between oligotrophic and mesotrophic, with an average trophic state of oligo-mesotrophy. This is lower than the expected classification of mesotrophic or eutrophic. In contrast, individual surrogate indicators classify the basin as eutrophic or hyper-eutrophic, as originally hypothesized. Total phosphorus and Secchi transparency TSI values were similar, while chlorophyll a values were consistently lower. All three surrogate measures consistently overestimated actual net primary production (Figure 4). The discrepancy in the classifications is believed to be the result of non-algal turbidity, which has been shown to have some effect on the accuracy of surrogate measurements in assigning trophic state (Chin 2006, Wetzel 2001). Increases in non-algal turbidity increase phosphorus content and decrease water transparency without a corresponding increase in net primary productivity.

Seasonal trends in NPP follow the general pattern observed in other temperate lakes (Nõges et al. 2011; Sterner 2010; Wetzel 2001). Light and temperature are critical abiotic drivers of production (Brylinsky and Mann 1973; Goldman and Carpenter 1974; Wetzel 2001), even in shallow lakes experiencing wind driven sediment resuspension (Wielgat-Rychert et al. 2010). Studies have shown a positive correlation between water temperature and algal growth (Goldman and Carpenter 1974), and a similar relationship between light and photosynthesis.

![Figure 4. TSI values assigned by surrogate indicators on each testing day. The TSI scale has been marked with solid dark gray lines and labeled to indicate threshold values for trophic classifications (<30 = oligotrophic, 30-50 = mesotrophic, 50-70 = eutrophic, 70-80 = hypereutrophic). Mean NPP was determined to be 245 mg C m⁻² d⁻¹; the 95% confidence interval had a lower limit of 140 mg C m⁻² d⁻¹ and an upper limit of 349 mg C m⁻² d⁻¹. * marks the trophic classification assigned by NPP (oligo-mesotrophic).](image-url)
An increase in available light or water temperature results in increased growth or photosynthesis, and subsequently increased production. The extent of these relationships varies according to species. At higher temperatures respiration rates also increase (Wetzel 2001). Water temperature increased throughout the growing season while photoperiod increased until the end of June before decreasing throughout the remainder of the summer (USNO 2012). The general decrease in production after June is believed to be the result of respiration occurring over a greater range of depths in response to increased water temperature and decreased water depth brought on by drought conditions experienced during the 2012 growing season.

This study illustrates the difference between surface and depth-integrated measurements of production (Coloso et al. 2008; Kuehl and Troelstrup 2011). Surface measures (e.g. Secchi transparency and other methods) are the most common, but may underestimate the metabolism of the lake basin by not including the respiration-dominated zones of the water column. Production and respiration vary with depth; thus, depth-integrated measurements provide greater accuracy in estimating NPP (Coloso et al. 2008). Vertical production profiles of Oak Lake suggest that production occurs in a limited zone of the water column, typically within the top 0.5 meters. Such restriction of productivity is influenced by resuspended sediments, which decrease the amount of light available for photosynthesis. Greater non-algal turbidity results in decreased light penetration in the water column and subsequently a more restricted photic zone.

NPP displayed a significant linear relationship with Secchi transparency, however approximately 69% of the variation in NPP remained unexplained. This unexplained variation may have been the result of sampling error, circumstantial factors, and/or resuspended bottom sediments that decrease transparency without a corresponding increase in production. Some of the variation may have also been due to the influence of limiting nutrients apart from phosphorus, such as silicon, iron, or other trace elements (Hecky and Kilham 1988; Sterner et al. 2004). The positive relationship observed between production and transparency is consistent with that expected if transparency changes are not driven by primary production. No significant relationships were found between either total phosphorus or chlorophyll a and net primary production. This is interesting because one might expect a significant relationship between net primary production and chlorophyll pigment concentrations. Perhaps the lack of a significant relationship with chlorophyll a was due to light limitations on phytoplankton growth by suspended non-algal particulates (Robarts et al. 1992; Carlson 1992). No additional variation in NPP was explained by including Secchi transparency and total phosphorus. The majority of variation remains the result of factors undefined in this study. Thus, surrogate TSI measures were not found to be accurate indicators of lake trophic state. These measures or metrics tend to overestimate basin production. Further evidence for the influence of non-algal turbidity lies in the inter-relationship between the surrogate values of TSI [TSI(TP) = TSI(SD) > TSI(CHL)], which indicates that non-algal particulates or color dominate light attenuation (Osgood 1983; Carlson 1992).

Additional production studies are needed to evaluate temporal variation among multiple growing seasons and vertical variation in production within the
water column. Because many of the abiotic factors controlling production are likely to vary by basin, production studies are also needed on multiple shallow glacial prairie lakes to evaluate regional central tendencies and variation. These statistics might then be used within a biogeographic framework to establish production-based standards for future monitoring. Such a study may also assist in building improved uniform water analysis and monitoring on a national scale, identified as necessary by the National Lakes Assessment (USEPA 2009b). The results of this study also suggest commonly used surrogate measures of production are not accurate for characterizing shallow lakes in the region. Possible responses to this include regional calibration of surrogate values using direct measures of production. Alternatively, the technique of profile modeling, a technique utilizing light profiles, chlorophyll concentrations, and the diffuse attenuation coefficient, could possibly be applied (Nõges et al. 2011; Arst et al. 2008). This would enable the digital creation of vertical profiles of production without requiring extensive field sampling.

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