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Limnological characteristics of Lake of the Ozarks (Missouri, USA): long-term assessment following formation of a reservoir series

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ABSTRACT

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Impoundment of Truman Lake in 1980 on the Osage River, above Lake of the Ozarks (LOTO), created a reservoir series. This analysis details the changes and processes over the ensuing 35 yr (1980–2014) in this large impoundment dominated by a longitudinal gradient along the mainstem. Temporal variation was determined by hydrology; seasonal mean total phosphorus (TP) ranged between 12 and 58 µg/L at the near-dam location, and hydrologic flushing during summer explained 82% of this variation. After dam closure, mineral suspended solids, attributed to channel scouring of erodible materials in the tailwater reach, declined over time, with a 50% reduction near the dam. Concurrently, organic suspended solids increased by 1 to 4%/yr in mid-reach locations, which indicates greater autotrophic production. Compared with other Missouri reservoirs, algal chlorophyll (Chl) averaged 1.6 times the value predicted from TP. Ratios of Chl:TP have increased over past decades concurrent with an increase in organic suspended solids and expansion of the ultraplankton (<11 µm) fraction of total Chl. Warm and dry conditions are associated with an increase in Chl in the ultra fraction, suggesting climate influence. A comparison with data collected prior to the closure of Truman Dam (1976–1979) provides incontrovertible evidence that light transmission has improved, and both Chl and Chl:TP have increased in LOTO. Formation of a reservoir series resulted in immediate and long-term changes in this major impoundment.

KEYWORDS

Algal chlorophyll; mineral turbidity; organic suspended solids; reservoir series; reservoirs; seasonal variation; ultraplankton

Lake of the Ozarks (LOTO; Fig. 1) was impounded by the closure of Bagnell Dam on the Osage River in 1931. This hydropower structure supplemented regional electrification and over recent decades has become a destination for aquatic recreation, which increased the local population and expanded shoreline development. Impoundment of the Osage River behind Truman Dam formed Truman Lake, creating a reservoir series (Jones and Kaiser 1988). Limnological study of LOTO, initiated in 1976, showed that characteristics were dominated by a longitudinal gradient between the turbid, nutrient-rich riverine reach in the headwaters, a transition zone, and a lacustrine section near Bagnell Dam (Jones and Novak 1981). Following impoundment of Truman Lake upstream, conditions for algal growth were more favorable because of lower turbidity; phosphorus decreased while algal chlorophyll increased (Jones and Kaiser 1988). Seasonal sampling during 1989–1993 quantified the role of hydrology on inorganic suspended solids and nutrients and demonstrated periods of light and nutrient limitation on algal biomass (Perkins and Jones 2000).

This article details limnological conditions in LOTO during midsummer 1980 to 2014. The analysis addresses changes in temporal and spatial patterns that characterize processes in large impoundments, following impoundment of Truman Lake (Kimmel and Groeger 1984, Jones and Kaiser 1988). We also draw comparisons with the larger body of information on Missouri reservoirs (Jones et al. 2008a, Jones et al. 2020). Most characterizations of Missouri reservoirs are space-for-time analyses based on among-system

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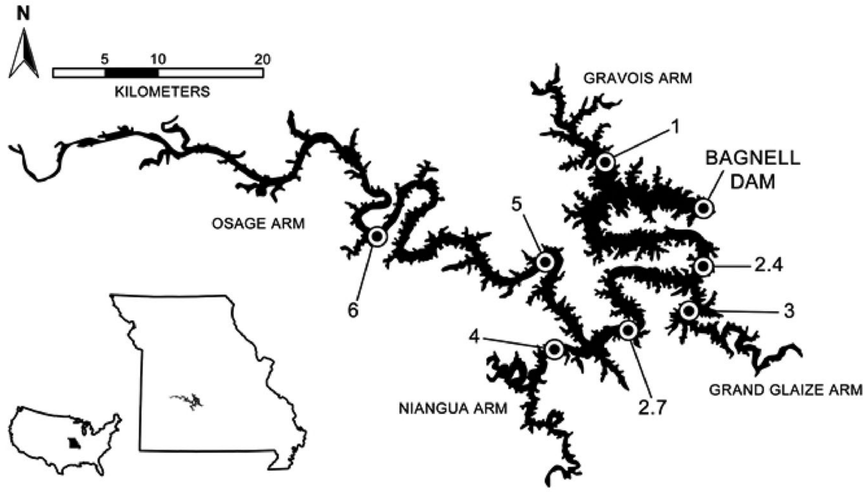

Figure 1. Map of Lake of the Ozarks showing location within the state and country and sampling sites.

comparisons (Pickett 1989, Jones et al. 2020). This long-term dataset, however, allows for analyses of multiple sites (space) over 35 seasons (time) in a single system. Edmondson (1969, 127) stated, "Some lakes are being studied in a way that they may well provide valuable information in the future if these lakes become changed." Information from LOTO makes up one of those datasets.

Site description and methods

Bagnell Dam is located in the Ozark Highlands physiographic section of Missouri, but the watershed includes the agricultural Osage Plains (Jones et al. 2008a). Characteristics of Lake of the Ozarks (LOTO) and Truman Lake have been detailed previously (Jones and Novak 1981, Jones and Kaiser 1988, Perkins and Jones 2000, Jones et al. 2008a). Briefly, LOTO has a surface area of 240 km^2, a volume of 2.37×10^9 m^3, and had an average flushing rate of 4.2/yr during the study, ranging from 0.7/yr in 2006 to 8.8/yr in both 1985 and 1993. It is one of the largest and most rapidly flushed impoundments in the state (Jones et al. 2008a). Land cover in the watershed in 2010 was approximately 44% grassland/pasture, 32% forest, 15% crop, and about 3% each in water, wetlands, and urban area. Between 1980 and 2010 the population doubled in some of the largest incorporated municipalities adjacent to the shoreline (Camdenton, Osage Beach, Lake Ozark, and Sunrise Beach), and increased by 175% between 1990 and 2010 in a recreational development (Village of the Four Seasons, located near the dam); these census data illustrate expanded recreation and regional growth during the study period.

Truman Lake (surface area = 225 km^2) includes 2 major impoundments in its watershed: Stockton Lake (100 km^2) and Pomme de Terre (32 km^2). Land cover in the Truman Lake watershed in 2010 was approximately 48% grassland/pasture, 24% forest, 19% crop, 4% wetland, and ~2% in both water and urban area. Discharge is controlled by a weir that directs oxic surface water (approximately 5 m depth) through hydropower turbines or over a spillway to LOTO. These impoundments differ in elevation by 14 m. Data from a near-dam site in Truman Lake were collected in a statewide monitoring program (Jones et al. 2008a, Jones et al. 2020) and are included for reference.

Data were collected at the 6 sites on LOTO identified by Jones and Novak (1981) and the additional 2 sites established in 1984 (Jones and Kaiser 1988) to better describe the longitudinal gradient along the former Osage River channel (the mainstem) below the riverine and transition sites (Fig. 1, sites 6 and 5, respectively). Methods are detailed in previous publications (Jones and Novak 1981, Jones and Kaiser 1988, Jones et al. 2008a, Watanabe et al. 2009) and include total phosphorus (TP, μg/L), total nitrogen (TN, μg/L, initiated in 1983), algal chlorophyll (Chl, μg/L, uncorrected), nephalemetric turbidity (NTU), nonvolatile suspended solids (NVSS, mg/L), volatile suspended solids (VSS, mg/L), total suspended solids (TSS, mg/L, sum of NVSS and VSS), filterable suspended solids (fTSS, mg/L, particles passing through TSS filters measured in 1999 and continuously after 2004; Knowlton and Jones 2000), and nonalgal suspended solids (NAS, mg/L, sum of NVSS and fTSS). Net separation of algal Chl was done using mesh screens into ultraplankton (<11 µm, starting in 1994), nanoplankton (<35 µm, starting in 1999), and >35 µm (by subtraction from total Chl; Graham and Jones 2007, Jones et al. 2008a). These proportions of total Chl were expressed as ultraChl, nanoChl, and Chl > 35 in the text. Colored dissolved organic matter (CDOM) was estimated by the absorption coefficient at 440 nm of water filtered through the TSS filter (starting in 2004; Watanabe et al. 2009). Nonchlorophyll light attenuation (NCLA, 1/m) was calculated using empirical equations from Jones and Hubbart (2011) and Secchi transparency (m). Water residence time was calculated using discharge data gauged below Bagnell Dam (USGS Gauge 06926000, on the Osage River) and the total volume released during the summer months of each year was divided by the average lake volume to arrive at monthly volume-equivalent discharge during the 1980 to 2014 period of study. Monthly totals were used individually combined across the summer months to assess the influence of hydrology on reservoir water quality. Water levels in LOTO are nearly stable during summer, to accommodate recreational activities. A seasonal hydrologic analysis was conducted by Perkins and Jones (2000) and referenced in this summary. Weather data were compiled from the National Weather Service location at Kaiser, MO, Lee C. Fine Memorial Airport, near Bagnell Dam. The Palmer Drought Severity Index (PDSI; NOAA 2019) from region 3 in Missouri was used to characterize dry (negative values) and wet conditions (positive values) over the study period. Values were averaged (arithmetic) over June, July, and August of each year and ranged from −11.4 to +13.4, with a median of 3.4 ($n = 35$).

Certain analyses are based on individual measurements ($n = 1092$ samples), but most assessments are based on seasonal means from individual sites ($n = 272$ for most trophic state parameters and solids, $n = 254$ for TN); these were calculated as the geometric mean of 4 samplings during July and August over the period of record (occasionally 3 collections). Samples from each location were composites of surface water from about 0.25 m depth. Data analyses, including correlation, regression (simple and stepwise), residual analysis, and one-way analysis of variance (ANOVA), were performed, often on $\log_{10}$-tranformed data using SPSS (v.27). Regression included overall coefficients of determination (r^2) and partial r^2 values for significant parameters. Significance was set at a P value of ≤0.01. Regression was used to identify variables accounting for variation and not for prediction; in such cases the models were not shown (MNS). Locally weighted regression (Lowess fit in SPSS) was used to show general patterns. Nutrients, turbidity, and residence time in the riverine and transition locations in large reservoirs (sites 6 and 5 in LOTO) are known to differ from increasingly lacustrine down-reservoir locations. Accordingly, one or both up-reservoir sites were excluded from several analyses (Jones and Novak 1981, Jones and Kaiser 1988). Residual analysis to adjust for the influence of seasonal hydrology, after Jones and Kaiser (1988), was used because it provided a clear illustration of temporal patterns.

Results and discussion

Longitudinal gradients and trophic state

Data collected across 35 summers following closure of Truman Dam show that longitudinal gradients along the mainstem of LOTO were similar to patterns initially documented after creation of this reservoir series (Table 1; Jones and Kaiser 1988). On average, TP declined by 69% between the riverine site and Bagnell Dam (to 20 µg/L), with half this decrease occurring in the ~33 km between the upper 2 sites on the Osage channel (Fig. 1, Table 1). Mean TN decreased by 26% along the mainstem (to 475 µg/L), resulting in more than doubling the TN:TP ratio (from 10 to 24, Table 1). Chl declined by nearly half (to 11.2 µg/L), with a similar decline in VSS (Table 1).

Table 1. Mean values of limnological parameters at sampling sites on Lake of the Ozarks during 1980 to 2014 (1984 to 2014 at sites 2.4 and 2.7).

Site	Distance Km	Total P, µg/L	Total N, µg/L	TN:TP	Chlorophyll, µg/L	Chl:TP	Nonvolatile solids, mg/L	Volatile solids, mg/L	Filterable solids (fTSS), mg/L	Secchi depth, m	Nonchlorophyll light attenuation (NCLA), 1/m	Colored dissolved organic matter (CDOM), 1/m
1	0.1	20	475	24	10.6	0.52	0.7	1.8	0.5	2.1	0.10	27.7
2	10	20	460	24	11.2	0.57	0.8	1.9	0.5	2.0	0.13	25.2
2.4	28	26	520	20	14.0	0.54	1.0	2.0	0.4	1.8	0.14	31.0
3	30	24	495	21	13.5	0.56	1.0	2.2	0.4	1.8	0.15	28.2
2.7	46	32	560	17	16.9	0.53	1.3	2.5	0.5	1.4	0.23	33.3
4	50	31	530	17	17.6	0.57	1.4	2.6	0.4	1.4	0.22	31.0
5	62	42	605	14	18.2	0.43	2.5	2.8	0.4	1.1	0.42	39.2
6	95	65	645	10	20.0	0.31	10.5	3.8	0.2	0.5	1.41	50.0
Truman	–	34	675	19	17.0	0.49	2.6	2.6	0.3	1.2	0.33	41.2

Total nitrogen was measured 32 seasons. Fiterable suspended solids (fTSS) was measured 12 seasons. Colored dissolved organic matter (CDOM) was measured 11 seasons. Truman reservoir was sampled 29 seasons during 1980 to 2014 (Jun through Aug, no collections during 1984 to 1988).

Concurrently, NVSS declined by an order of magnitude (10.6 to 0.7 mg/L, Table 1) while fTSS doubled. Similarly, NCLA declined by an order of magnitude, with 70% occurring between the uppermost sites. Secchi transparency increased more than 4-fold along the mainstem (to an average of 2.1 m, Table 1). CDOM varied by a factor of 2 among sites, with averages showing a longitudinal decrease (Table 1).

Spatial variation is largely a function of sedimentation and dilution as flow passes through this large reservoir (Jones and Novak 1981, Jones and Kaiser 1988). Surface collections from a near-dam site on Truman Lake during June through August (1980 to 2014, Table 1) are our best index of water quality from the major inflow. Concentrations of TP and Chl in Truman Lake approximate values at mid-reach site 2.7 (Table 1). Values of TP at the riverine site (site 6) averaged about double the inflow concentration and NVSS showed an increase of more than 3 times (Table 1). Collectively, increases relative to measurements in Truman Lake reflect the scour of unconsolidated particulates from the former river channel (Petts and Gurnell 2005), which is now a tailwater area in upper LOTO. Increases in TP and NVSS in this reach, but not a similar influence on TN, were found by Jones and Kaiser (1988). Reactive P adsorbed to sediments is a source of increased TP in the riverine reach (Zhou et al. 2005, Yuan and Jones 2019).

Measurements from the major arms (Gravois, site 1, Grand Glaize, site 3, and Niangua, site 4, Fig. 1) fit the general longitudinal pattern. For some parameters, long-term averages differ slightly from the nearby station on the Osage channel, presumably reflecting local watershed influences and flow patterns. Overall, however, conditions within these arms are most similar to proximate locations on the mainstem, particularly among sites nearest Bagnell Dam, which was the case in early studies (Jones and Novak 1981, Jones and Kaiser 1988). The Niangua arm (site 4) had higher nutrients and Chl and less transparency than the others; this arm receives municipal wastewater from a large community, and periodically is influenced by flow from the upper mainstem (Table 1, Fig. 1; Jones and Kaiser 1988).

Consistent with previous classifications (Jones and Novak 1981, Jones and Kaiser 1988, Perkins and Jones 2000), average nutrient concentrations at sites within 30 km of Bagnell Dam were typical of mesotrophic conditions in Missouri reservoirs (Table 1, criteria of Jones et al. 2008a), with eutrophic values in the upper locations. Mesotrophic conditions typify reservoirs in the Ozark Highlands, which includes the Bagnell Dam site (Jones et al. 2008a). Truman Lake data indicate eutrophic conditions prevail (Table 1); much of the watershed is located in the Osage Plains, where reservoir nutrients, on average, are double the values in the Ozark Highlands (Jones et al. 2008a).

Temporal variation

Temporal variation in water quality is a distinctive feature of Missouri reservoirs (Knowlton and Jones 2006a, 2006b). During the 35 yr study, the minimum seasonal mean for TP, TN, VSS, and Secchi at the 8 sampling sites averaged half, or less, of the long-term mean at a given site (geometric mean of 35 seasons), with minimum Chl at 0.32 and NVSS at 0.15 times the overall mean (Table 2). Seasonal maximums were typically 1.6 to 2 times the long-term mean, with the most extreme for Chl, TP, and NVSS at 3.6 to 6 times the overall mean. Among individual samples from the 8 sites ($n = 130$ to 140), maximum values averaged 105 times the minimum for NVSS and 30 times for Chl; for other variables, the difference was <10 (Table 2). This analysis is the most complete long-term comparison of temporal variation in a Missouri reservoir; it is consistent with statewide analyses (Knowlton and Jones 2006a, 2006b), and underscores extreme temporal variation in Chl, TP, and NVSS relative to TN. The outcome was similar when data from the upper 2 sites were excluded.

Hydrology is a key variable accounting for temporal variation in reservoir water quality (Knowlton and Jones 1989, Straskraba 1999, Perkins and Jones 2000, Jones et al. 2008b) and directly influences the magnitude of longitudinal gradient in a given season. As illustrated using TP, the relative positions of the lacustrine, transition, and riverine zones vary with the

Table 2. Frequency distributions of the seasonal mean values of water quality metrics at the 8 sampling sites divided by the overall mean for that site ($n=35$ and $n=31$).

Parameter	Minimum/mean	10%	25%	75%	90%	Maximum/mean	Individual samples, maximum/mean
Total P	0.52	69	82	119	145	3.3	7
Total N	0.45	71	91	115	129	1.7	5
Chlorophyll	0.32	61	79	127	149	2.6	30
NVSS	0.15	51	71	148	211	6.0	105
VSS	0.50	69	85	121	137	2.1	10
Secchi	0.41	73	87	117	135	1.6	6

For individual samples ($n=130$ to 140 per site) the maximum value was divided by the mean value.

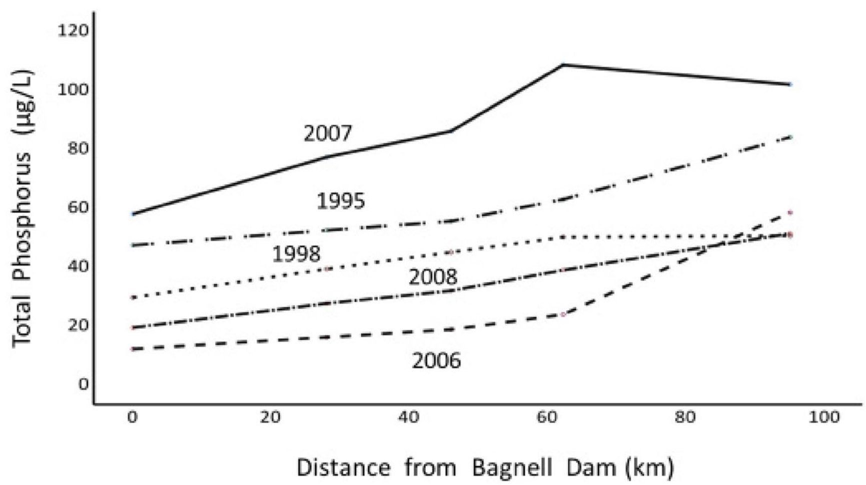

Figure 2. Seasonal mean total phosphorus (µg/L) depicting the longitudinal gradient among sampling sites along the mainstem (former Osage River channel) under contrasting flow conditions.

magnitude of throughflow (Fig. 2). In years with low to modest flow, lacustrine conditions associated with the near-dam location extend up the Osage arm, while riverine conditions dominate the upper reach during maximum flow. Summer throughflow contributes to temporal variation at individual sampling sites in LOTO (Table 2) and other impoundments (Knowlton and Jones 2006a); variation documented in LOTO highlights the necessity of using data from multiple seasons to characterize reservoir trophic state (Knowlton and Jones 2006a, 2006b, Jones et al. 2020).

During the 35 yr study, seasonal mean TP varied from 12 to 58 µg/L at Bagnell Dam (Fig. 1, Site 2, overall mean 20 µg/L TP), which encompasses about half of the entire range of long-term mean TP in reservoirs statewide (Jones et al. 2020). Volume-equivalent discharge during 1980–2014 in July ranged from 0.03 to 1.5 times the average volume of the impoundment. This flow estimate accounted for 82% of temporal variation in TP at the near-dam site (Fig. 3a). At mid-reach site 2.4 on the main channel (Fig. 1), discharge in July–August accounted for 87% of TP variation (from 0.06 to 2.1, Fig. 3b), and from 71 to 84% in sites 2.7 to 5 (Fig. 1). Meanwhile, in the Gravois Arm, located off the main channel, discharge during June through August (from 0.14 to 3.1, Fig. 3c) explained 83% of variation. These differences illustrate temporal flow patterns along the mainstem and major arms in this large impoundment. These 3 discharge categories were strongly correlated ($r=0.83$ to 0.93, $n=35$) and were also correlated with the summer PDSI value ($r=0.69$ to 0.76, flow was log transformed, $n=35$). In contrast, only 35% of variation in TP was explained by July–August discharge at the riverine site. These findings support previous observations that TP is lowest in dry years and responsive to flow (Jones and Kaiser 1988, Perkins and Jones 2000). Overall, hydrology explained less temporal variation in TN than TP at the sampling locations (r^2 from 0.26 to 0.52) and was not significant at the riverine site (site 6). Consequently, the ratio of TN:TP declined with discharge volume at all sites.

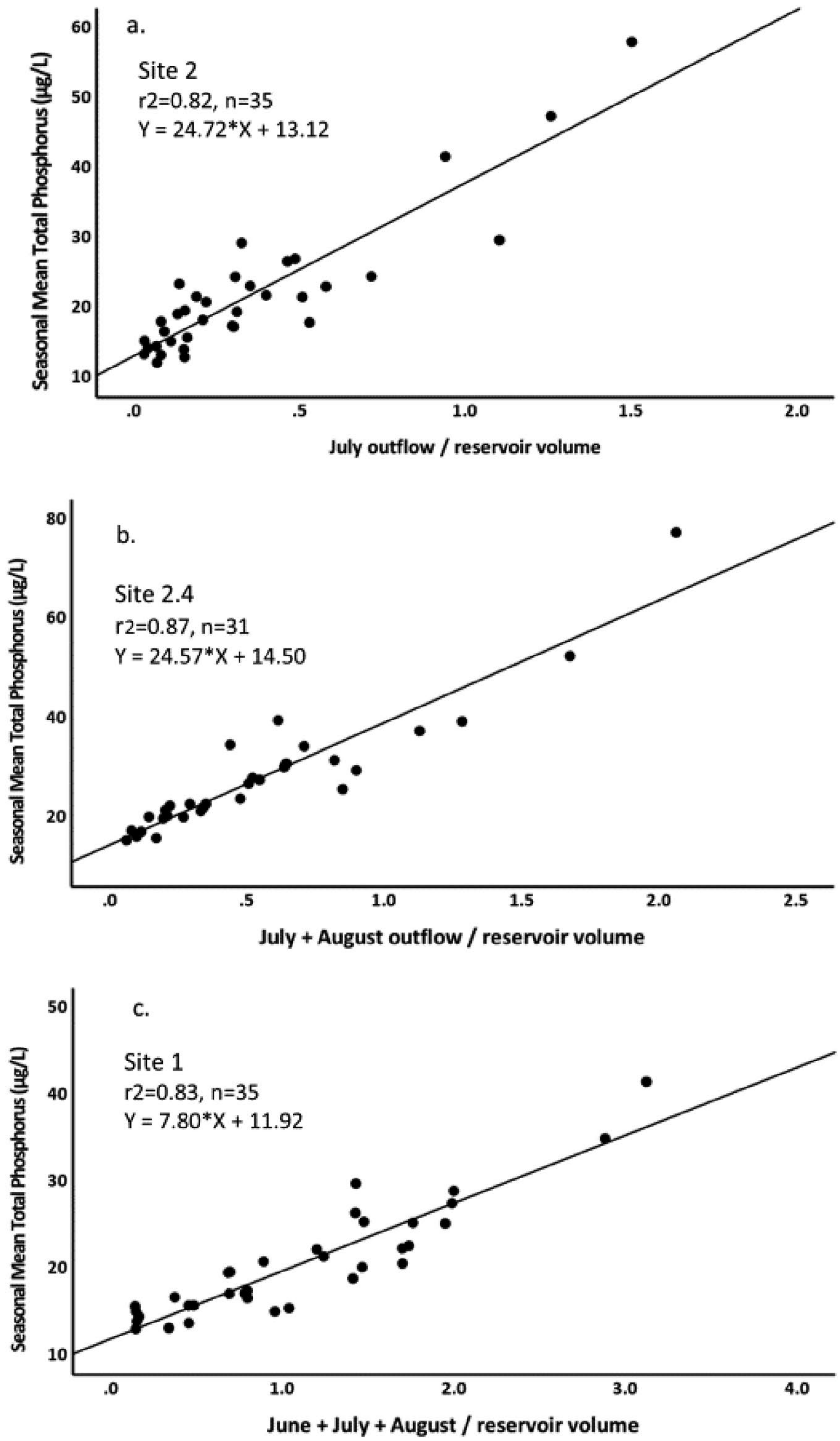

Figure 3. Seasonal mean total phosphorus (µg/L) regressed on summer outflow divided by reservoir volume to illustrate temporal changes with hydrology. Locations are near the dam (site 2, panel a), in the mid-reach (site 2.4, panel b), and the Gravois Arm (site 1, panel c).

After adjusting for temporal differences in flow (using residuals, after Jones and Kaiser 1988), there was not a significant trend between measured and predicted TP or TN and year of collection after the reservoir series was created (35 yr). This residual analysis indicates that once hydrology was accounted for, neither nutrient showed a temporal change at these sampling locations during midsummer that stood out from other sources of variation, despite population growth and expanded shoreline development.

Exceptions were TN in the Gravois and Niangua arms, where hydrology explained 26 to 36% of temporal variation and year of collection (time), entered as a second variable, increasing explained variation to 39 to 46% (positive coefficients, $0.03 > P > 0.02$, $n = 32$, MNS). Noteworthy is that the residuals from these 2 sites were strongly correlated ($r = 0.79$), and residuals from both sampling locations plotted against year of collection had similar slopes, which equated to a temporal increase of ~24% in mean TN in both arms over the period of record. Both arms receive wastewater discharge, treated to remove organic materials, and the increase in TN is consistent with population growth. These locations are not often influenced by throughflow along the mainstem, which largely determines nutrient concentrations in much of the impoundment. This finding, however, adds to our understanding of the influence of municipal effluents on reservoir nutrients (Knowlton and Jones 1989, 1990, Obrecht et al. 2005).

There was a distinct temporal decline in NVSS during the study. For each location between the transition zone and dam, hydrology accounted for 30 to 61% of variation in NVSS in regression analysis. In each case, year entered as a significant second variable, with a negative coefficient, which increased explained variation to between 47 and 77%. After adjusting for volume-equivalent discharge (after Jones and Kaiser 1988), NVSS showed a strong temporal trend with positive residuals between 1980 and 1993 (larger NVSS than expected based on hydrology); subsequently, residuals declined to near or below zero at all sites between the transition and near-dam locations, including the major arms (Fig. 4a–c). A categorical variable delineating these 2 periods (1980–1993 and ≥1994) was significant in regression analysis and, along with hydrology, removed the temporal trend in residuals. Discharge during July, July and August, and June through August did not significantly differ between the 2 periods ($P = 0.46$, $n = 14$ and 21, respectively), nor was there a temporal trend within either period. NVSS declined, on average, by 38%, with a

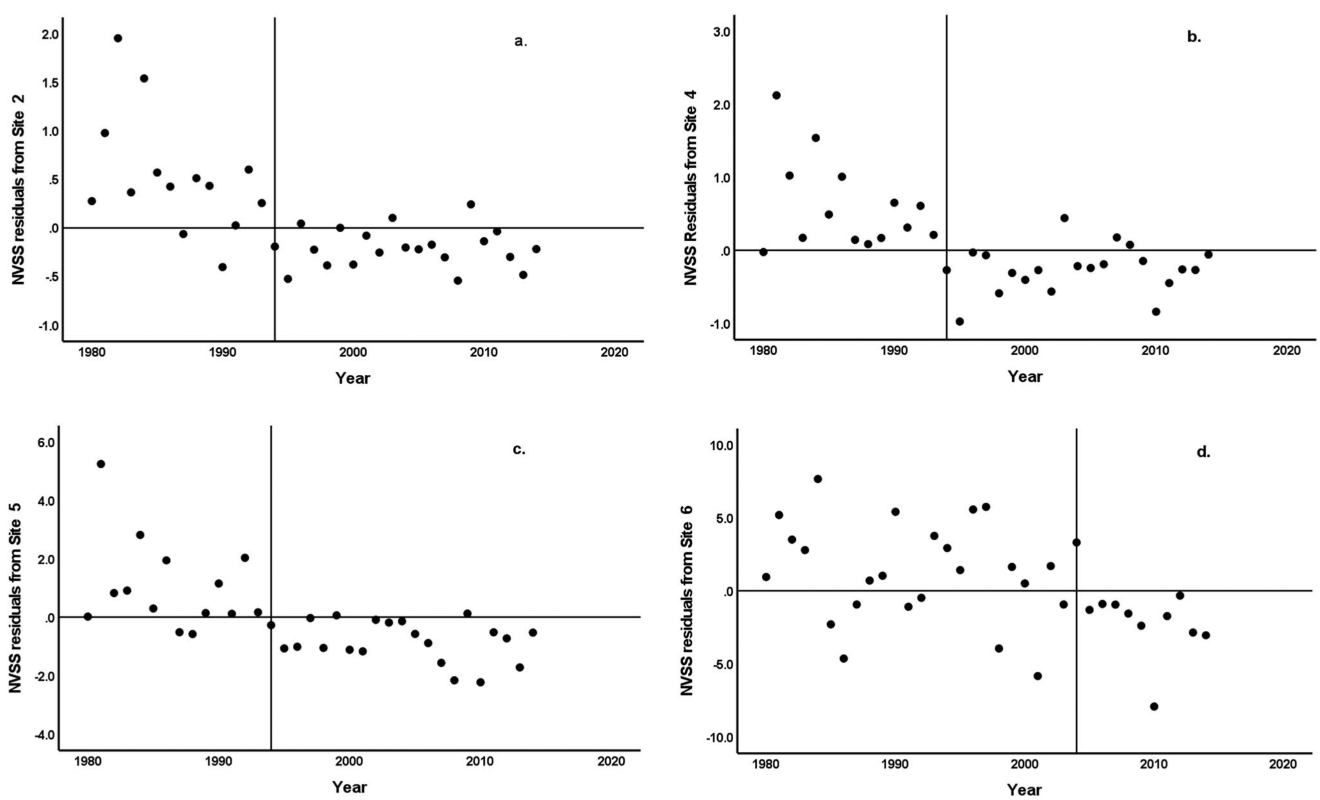

Figure 4. Residual values (observed–predicted) for nonvolatile suspended solids (NVSS, mg/L) adjusted for hydrology depicting a decrease ≥1994 at sites below the transition zone (panels a to c) and after 2004 at the riverine location (panel d).

decrease of 50% at the near-dam location (Fig. 3a). This decline resulted in LOTO supporting some of the smallest NVSS values in reservoirs within the state (Jones et al. 2020).

In Truman Lake, NVSS averaged 2.6 mg/L (Table 1), with no change over the period of collection. Channel scouring in the tailwater was suggested by Jones and Kaiser (1988) as the mechanism elevating NVSS values in the riverine reach (Table 1). These data suggest that it took some 14 yr to transport and subsequently sediment the most erodible materials from the upper Osage channel (between Site 6 and Truman Dam, Fig. 1). Channel scouring and fluvial metamorphosis in tailwater reaches following dam closure are well documented in other systems (Petts and Gurnell 2005), and these data fit the general pattern.

NVSS residuals from the riverine site showed values dropping to below zero after 2004 (Fig. 4d); a categorical variable using this breakpoint was significant in a regression analysis specific to this site, showing NVSS declined by 20% relative to pre 2004. These data suggest that elevated channel erosion in the tailwater zone, above the riverine site, continued for about a decade after a decline in sediment transport was detected at down-reservoir locations. Noteworthy is that NVSS measurements during midsummer 1979 averaged 29 mg/L at the riverine site and 12 mg/L in the transition zone (Jones and Novak 1981). These measurements reflect inflow from the Osage River prior to the impoundment and sedimentation processes in Truman Lake, and exceed post 1980 averages by severalfold (Table 1).

At sites below the riverine zone, July–August discharge explained from 28 to 57% (median 51%) of temporal variation in TSS (the sum of NVSS and VSS). TSS did not, however, show a temporal pattern during the study. Values were not significantly related with year of collection at individual locations, nor did values significantly differ after NVSS declined in 1994 ($P = 0.12$ to 0.91, log-transformed, ANOVA).

VSS, the organic fraction of TSS, is influenced by both algal biomass and edaphic factors (Jones and Knowlton 2005a). After adjusting for flow (after Jones and Kaiser 1988), VSS showed a significant 1 to 4% increase over the period of study at sites between 30 and 62 km from Bagnell Dam (sites 2.7 to 5). At the 2 sites nearest Bagnell Dam (sites 1 and 2), mid-reach location 2.4, and the riverine zone the increase was not significant ($P > 0.10$). This change in VSS at these central locations suggests autotrophic processes have increased since creation of the reservoir series, which is consistent with the early findings of Jones and Kaiser (1988). Given that NVSS declined during the study (Fig. 3), without a significant change in TSS, the ratio of NVSS:VSS at sites below the riverine zone declined by about half, from 0.79 to 0.40, after 1994.

Secchi transparency

Secchi transparency in Missouri reservoirs is largely determined by TSS (Jones et al. 2008a, Jones et al. 2020). In LOTO there is considerable temporal and spatial variation among seasonal means (Tables 1 and 2), with 91% of this variation explained by TSS ($n = 272$, log-transformed, MNS). Between the 2 fractions of TSS, NVSS accounted for 79% of variation, and VSS entered subsequently increased the explained variation to 87% ($n = 272$, log-transformed MNS), indicating mineral suspended solids mostly determined transparency across sites and time. This finding is consistent with the statewide pattern, and when predicted using the cross-system Secchi–TSS relationship (equation in Jones et al. 2008a, Fig. 13a), calculated values were nearly identical to those observed in LOTO (median difference = −0.02 m, interquartile range = −0.13 to 0.09 m, $n = 272$).

Consistent with cross-system patterns in Missouri reservoirs (Jones et al. 2008a), Secchi depth has a strong negative correlation with TP ($r = -0.89$, log-transformed, $n = 272$), which reflects the strong positive correlation between TP and TSS ($r = 0.88$, log-transformed, $n = 272$) and both fractions of TSS in the dataset ($r = 0.70$ with VSS and 0.86 with NVSS, log-transformed, $n = 272$).

Excluding the 2 least transparent sites from the analysis (sites 5 and 6), NVSS accounted for 43% of variation in Secchi during 1980 to 1993, with VSS entering to explain 60% of overall variation ($n = 76$, log transformed, negative coefficients, MNS). In contrast, after 1994, VSS explained 68% of variation in Secchi among the sites and increased to 80% with NVSS as the second variable ($n = 126$, log-transformed, negative coefficients, MNS). This temporal shift in the principal fraction of TSS explaining water clarity reflects the change in TSS composition over time, with lower mineral turbidity and increased organic particulates.

While Chl is known as a strong correlate of water clarity (Jones et al. 2008a), it explained only 41% of variation in Secchi depth across all sites during 1980 to 1993 ($n = 90$, log-transformed, MNS), which increased to 68% after 1994 ($n = 147$, log-transformed, MNS). The results were similar when the transition and riverine sites were excluded from the analysis. Contributing to this temporal increase is that the correlation between Chl and VSS increased from 0.42 to 0.69 after 1994 ($n = 90$ and 147, respectively, log-transformed). Greater correspondence between Chl and VSS is consistent with an increase in autotrophic processes during the study.

Nonchlorophyll light attenuation

Non-Chl light attenuation (NCLA) in Missouri reservoirs is estimated from an empirical calculation of deviation from maximum Secchi depth at a given Chl value (Jones and Hubbart 2011). Statewide, the median value was 0.596/m (248 reservoir means; JR Jones, University of Missouri, unpubl.). In comparison, most NCLA values in LOTO are in the lower third of this distribution, with values at locations within 30 km of Bagnell Dam among the lowest 5% (Table 1). Deviations from maximum transmission in the analysis are accounted for by NVSS and fTSS, with residual variation attributed to size fractionation of the algal community and color (Watanabe et al. 2009, Jones and Hubbart 2011).

Among seasonal means (all sites), NCLA in LOTO was strongly correlated with NVSS ($r = 0.93$, $n = 272$) and NAS ($r = 0.96$, $n = 96$), and less so with CDOM ($r = 0.68$, $n = 88$) and fTSS ($r = 0.39$, $n = 96$). Among the algal fractions, correlations were positive with %Chl > 35 µm ($r = 0.35$, $n = 152$) and negative with both ultraChl ($r = -0.34$, $n = 200$) and nanoChl ($r = -0.35$, $n = 152$) fractions. Based on the strength of these associations, NCLA serves as a surrogate measurement of the various factors that influence light attenuation in the water column (Jones and Knowlton 2005a, Jones et al. 2008b, Jones and Hubbart 2011).

Among seasonal means where NAS, NVSS, fTSS, CDOM, Chl, and Chl size fractions were measured (omitting sites 5 and 6), 69% of variation in NCLA was accounted for by NAS^2 (positive coefficient), followed by Chl > 35 (negative coefficient, overall $r^2 = 0.74$, $n = 66$, MNS). The implication is that mineral suspended solids largely determine light attenuation in LOTO and that NAS^2 explained most variation, supporting the nonlinearity between light transmission and suspended solids. The negative coefficient between NCLA and Chl > 35 is consistent with large algae scattering less light than small cells (Edmondson 1980). The analysis was nearly as strong with the ultraChl as the second explanatory variable, which had a positive coefficient (MNS). In the transition (site 5) and riverine (site 6) sites, where light was most strongly attenuated (Table 1), variation in NCLA was explained by NAS^2 ($r^2 = 0.66$ and 0.82, respectively, $n = 11$). Measurements of CDOM were correlated with NCLA ($r = 0.68$, $n = 88$, all sites), but values did not explain residual variation in NCLA in LOTO, which is consistent with analyses showing that color explains little variation in light attenuation in Missouri reservoirs (Jones et al. 2008a, Watanabe et al. 2009).

Chlorophyll

During the 35 yr study, the average Chl:TP ratio increased from ~0.3 at the riverine site (site 6) to ~0.4 at the transition zone (site 5), with values ≥0.5 at sites down reservoir (Table 1). This longitudinal pattern is consistent with long-established gradients in large reservoirs (Jones and Novak 1981, Kimmel and Groeger 1984, Jones and Kaiser 1988). It reflects the combined influences of increasing hydraulic residence time along the mainstem and major arms, greater transparency, and additional local inputs. Some 25% of seasonal mean ratios were between 0.6 and 1.0, which exceeds most values statewide. Ratios of Chl:TP ~0.4 are typical of summer conditions in Missouri reservoirs (Jones and Knowlton 2005b, Jones and Hubbart 2011). Sampling LOTO during midsummer contributes to this finding (Jones and Knowlton 2005b). Lake phytoplankton introduced from Truman Lake would also be a factor relative to reservoirs not in a series (Soballe and Bachmann 1984). The average Chl:TP in Truman Lake was slightly below the averages in much of LOTO (Table 1). Among sites below the transition zone, Chl averaged 1.6 times the value predicted from TP using the cross-system equation for Missouri reservoirs (from Jones et al. 2008a, Fig. 7, interquartile range 1.5 to 1.9, $n = 202$ seasonal means), which further demonstrates comparatively high Chl:TP ratios in this impoundment.

Most Chl was contained in small algae; on average 89% was measured in nanoplankton (<35 µm, $n = 575$ individual samples), of which 86% was ultraplankton (<11 µm, $n = 575$, or 77% of total Chl), while ~11% of Chl was >35 µm and ~12% was in the 11–35 µm fraction. Size fractionation of Chl began in 1990 ($n = 25$ yr) and the distribution was similar to that found in reservoirs statewide (Jones et al. 2008a, Jones et al. 2020).

Below the transition zone (sites 1 through 4, Fig. 1), ultraChl averaged from 73 to 78% of Chl and differences among stations were not significant ($P > 0.10$, log-transformed, ANOVA, $n = 150$), with annual averages ranging from 60% to 86%. Chl and ultraChl were not significantly correlated among these seasonal means ($P > 0.10$, $n = 150$). In stepwise regression TP explained 66% of variation in Chl, which increased to 77% with inclusion of ultraChl and TN:TP (log-transformed, positive coefficients, partial r^2 = 0.067 and 0.045, respectively, $n = 150$, MNS). Year entered the model to explain an additional 1% of residual variation (positive coefficient).

This analysis was our first inclusion of size fractionation of the algal community to assess variation in Chl:TP. Characteristics of small phytoplankton likely contribute to an increase in Chl:TP, which include a decrease in intracellular Chl as algal cell size increases (Agustí 1991), high Chl:C ratios in small algae (Yacobi and Zohary 2010), and efficient light utilization by small algae (Teubner et al. 2001). Bioassays during one summer showed nitrogen limitation at the near-dam location (Perkins and Jones 2000), and some 45% of individual samples from these 6 sites had TN:TP ratios between 10 and 20 ($n = 765$), which indicates potential N-limitation (Forsberg and Ryding 1980). Entry of TN:TP into the model is consistent with findings in reservoirs statewide (Jones et al. 2008a). Light limitation from NVSS can reduce Chl:TP ratios in Missouri reservoirs, but values were considerably below the value where light limitation replaces nutrient limitation (5 mg/L, Knowlton and Jones 2000); this variable did not enter as significant.

Chl:TP increased across this time period (Fig. 5a), with year of collection accounting for 15% of variation, which ranged from 24% (site 1) to 10% (site 2.4), with 14 to 18% explained at the other sites. Some 23% of temporal and spatial variation in Chl:TP was explained by ultraChl among these 6 sites (Fig. 5b). There is considerable scatter in the pattern; however, across the upper boundary of the distribution Chl:TP values increased with ultraChl, and Chl:TP > 0.7 was associated with ultraChl values of 80%. Among individual sites the explanation varied from 27 to 36% at 3 sites (sites 1, 2, and 2.7) and between 10 to 20% at the other locations (sites 2.4, 3, and 4). Data from each location fit within the overall pattern.

Noteworthy is that 32% of the variance in ultraChl was described by 3 variables. First, volume-equivalent discharge during May–August (partial r^2 = 0.192, discharge range 0.4 to 4.2/yr, median = 1.4/yr) entered with a negative coefficient. Second, year of collection (partial r^2 = 0.091) entered with a positive coefficient, suggesting a temporal increase. Third, the average maximum air temperature in August entered with a positive coefficient to explain modest residual variation (partial r^2= 0.034, range 27.1 to 34.6 C, median = 31.0 C, $n = 150$, MNS). These metrics suggest that warm, dry conditions favor an increase in ultraChl in LOTO. This finding is supported by a negative correlation between ultraChl and the summer PDSI ($r = -0.46$, $n = 150$), which indicates Chl:TP ratios would likely increase under such conditions. Collectively, this analysis suggests an increase in the autotrophic process over the past 25 yr as measured by Chl:TP, which is tied to the ultra fraction of the

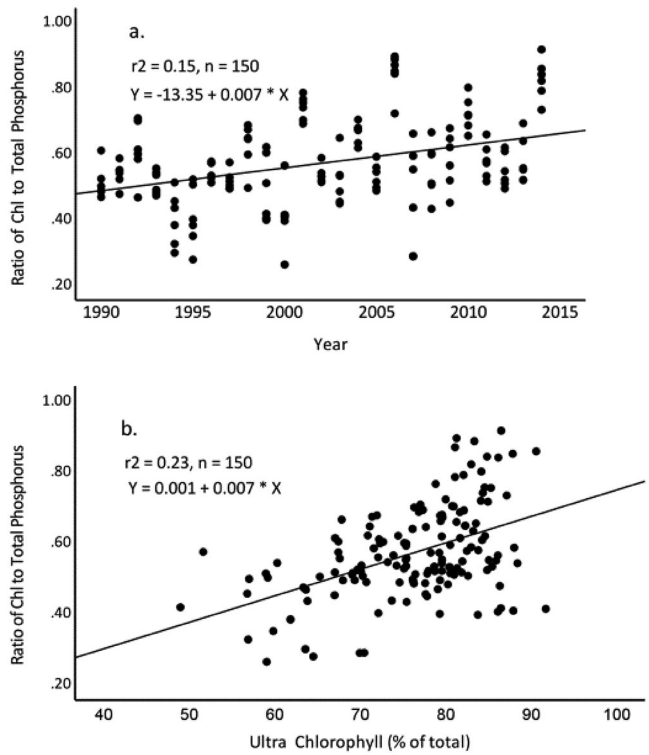

Figure 5. Regression of the ratio of chlorophyll to total phosphorus at sampling sites below the transition zone (sites 1 through 4) from 1990 through 2014 against year of collection in panel a and against the ultra chlorophyll fraction (% of total) in panel b.

phytoplankton. This finding adds to the growing body of information on the impact of climate, specifically warm and dry periods, on algal biomass in lakes and reservoirs (Binding et al. 2011, Vogt et al. 2015, Paterson et al. 2017).

Further evidence of a temporal increase in Chl:TP in LOTO comes from samples collected by citizen volunteers at various locations throughout the impoundment during the summers of 1994 to 2014 (Fig. 6). Two locations in the mainstem and the Gravois Arm were sampled routinely during this period, and a LOESS line across the average shows a general increase over time, with most seasonal means after 2000 exceeding a Chl:TP ratio of 0.6, with values below 0.4 previously (Fig. 6a; $n = 173$ samples). Seventeen sites located along the mainstem and 3 major arms were sampled between 1994 and 2014 (none continuously, $n = 386$ samples); the temporal pattern in the seasonal average suggests a similar increase in Chl:TP (Fig. 6b). These data, collected independently from our long-term study, support the conclusion of an increase in autotrophic processes in LOTO.

The reservoir series—before and after

Jones and Kaiser (1988) found Chl increased by 25% concomitant with a near-proportional decrease in TP, with changes most pronounced at up-reservoir locations along the Osage channel following creation of the reservoir series. A graphical comparison of before (1976–1979) and after (≥1980) impoundment of Truman Lake supports that initial finding (contrast not adjusted for hydrology; Fig. 7). Overall, TP declined throughout LOTO (Fig. 7a) because external loading from the Osage River has been reduced by reservoir processes, such as nutrient uptake by algae and sedimentation of inorganic materials, now occurring in Truman Lake. Concurrent with lower TP, Chl, and the Chl:TP ratio have increased at all locations, with the largest changes at up-reservoir sites (Fig. 7b and c). Light transmission in the water column has improved. Nephalemetric turbidity (NTU) has sharply declined along the Osage channel, by 82% at the transition site to 57% at the near-dam location (Fig. 7d), with smaller declines in the major

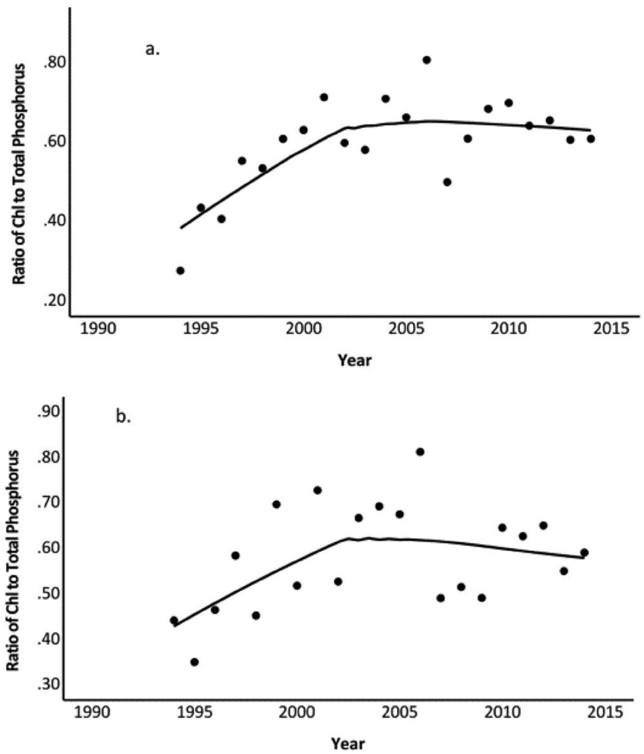

Figure 6. Ratio of chlorophyll to total phosphorus in samples collected by citizen volunteers. Panel a includes data from 3 locations sampled routinely during summers 1994 through 2014. Panel b includes data from 17 sites located throughout the reservoir sampled during various durations within the 1994 through 2014 period. In all cases data were averaged across sites within years and a locally weighted regression line (Lowess) shows the temporal trend.

arms. NTU is strongly correlated with NVSS in the ≥1980 dataset ($r = 0.92$, $n = 206$ seasonal means), so serves as a surrogate estimate of inorganic suspended solids. These contrasts illustrate the broad changes in LOTO following impoundment of Truman Lake. Alkalinity, a conservative water quality metric, averaged 98 mg/L prior to impoundment and 99 mg/L subsequently, which suggests no change in major ion content over time.

Conclusion

This 35 yr dataset from multiple sites on LOTO details the patterns and changes during midsummer following impoundment of Truman Lake. Creating this reservoir series in 1980 immediately reduced mineral suspended solids and increased algal biomass (Jones and Kaiser 1988), with additional changes occurring over decades and further changes underway. Longitudinal gradients and temporal variation characterize this large, mainstem impoundment. Temporal variation matches that found in impoundments statewide, and the analysis quantifies the role of hydrology on longitudinal gradients in this rapidly flushed impoundment, which is illustrated by the nearly 5-fold difference in midsummer TP at the near-dam location. Following creation of the reservoir series, changes in TN and TP were not detected in the mainstem (after adjusting for hydrology), which can be attributed to rapid flushing from a large watershed and by lacustrine processes in Truman Lake. The exception to this pattern was the increased TN levels in 2 major arms, likely in response to increased municipal discharge.

The significant decline in NVSS after more than a decade following impoundment of Truman Lake, and a decade longer at the riverine site, is consistent with fluvial processes in tailwaters following dam closure. Scour of unconsolidated materials between the tailwaters and the riverine site has moderated but continues to elevate suspended solids relative to the inflow from Truman Lake, with reduced influence down-reservoir. Lower NVSS coincided with VSS gradually increasing by 1 to 4%/yr in mid-reservoir sampling locations on the Osage channel and several

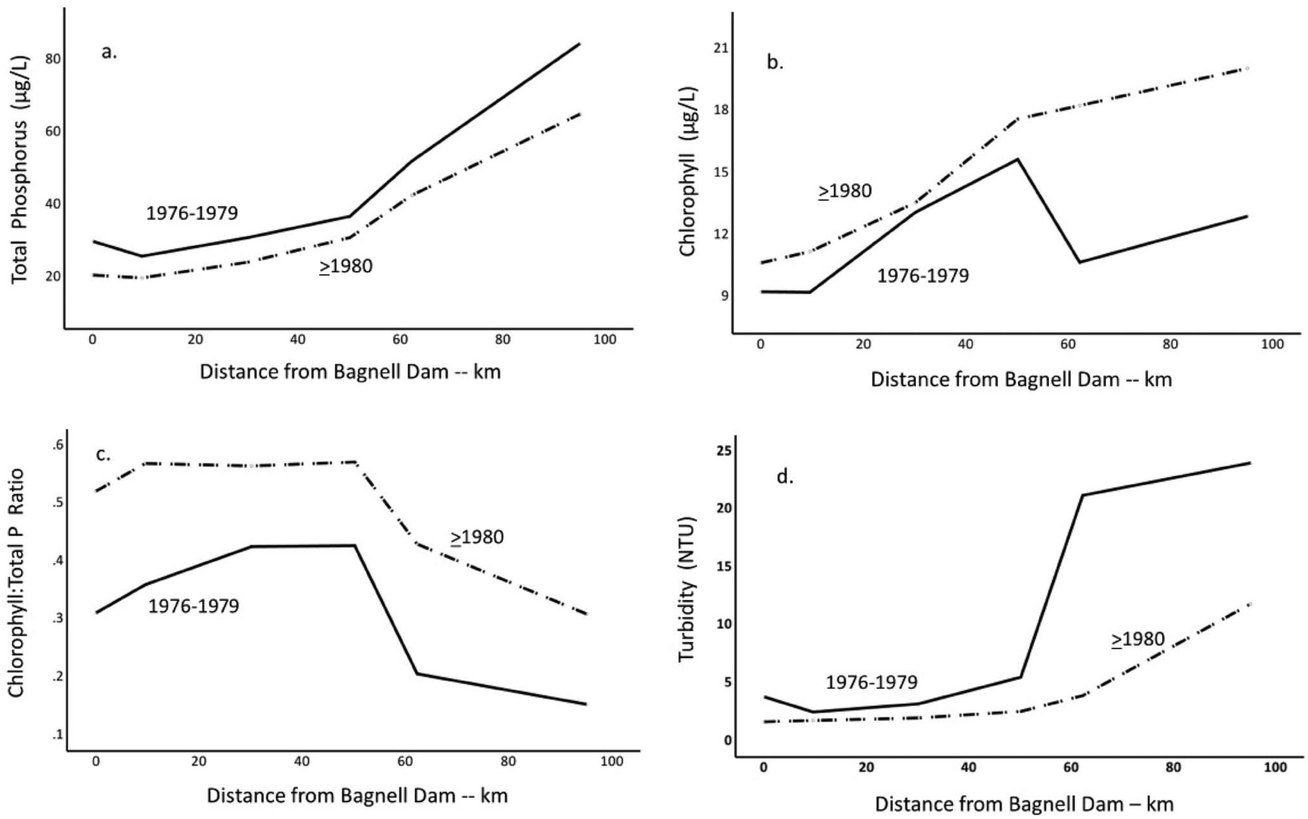

Figure 7. A graphical comparison of total phosphorus (µg/L, panel a), chlorophyll (µg/L, panel b), chlorophyll to total phosphorus ratio (panel c), and nephelometric turbidity (panel d) at sampling sites along the Osage channel before (1976–1979) and after (≥1980) the impoundment of Truman Lake, forming a reservoir series.

major arms, indicating greater autochthonous production. These data support initial indications of Jones and Kaiser (1988) that conditions for algal growth are currently more favorable relative to when direct river flow entered the Osage channel. Secchi transparencies match the pattern with TSS statewide. Increases in the Chl:TP ratio and VSS over the past 2 decades suggest organic production has increased in LOTO. An increase in ultra fraction within the algal community coincides with these changes; this pattern should be evaluated in other impoundments and extended to include biomass measurements of the phytoplankton. These monitoring data suggest that both ultraChl and the Chl:TP ratio will increase under warm, dry conditions, indicating an influence of climate. Temporal changes in LOTO are apparent in a straightforward comparison of post-1980 data with our initial information and illustrate that modifications have occurred throughout the impoundment but are most pronounced at up-reservoir locations because inflow is from a reservoir rather than a river.

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