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ABSTRACT

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Data from 94 Missouri reservoirs demonstrated a large interregional variation in total phosphorus (TP), total nitrogen (TN), algal chlorophyll (Chl), and suspended solids among the four physiographic provinces with numerous reservoirs. The interprovincial pattern for nutrients, algal biomass, and mineral turbidity was Ozark Highlands < Ozark Border : Glacial Plains < Osage Plains corresponding to an interregional gradient between forest and agriculture as the dominant land cover. On the basis of TP most Missouri reservoirs were eutrophic (61%) or mesotrophic (21%) with few hypereutrophic (7%) or oligotrophic (11%). Statewide, water clarity was low (median Secchi depth 1.0 m) and more strongly related to non-volatile suspended solids (NVSS, $R^2 = 0.80$) than algal Chl ($R^2 = 0.30$). Summer mean values showed a curvilinear relation between Chl and TP (\log_{10} transformed) reaching an asymptote above $\approx 50 \mu\text{g/L}$ TP/L — a range where most reservoirs have high NVSS and low TN:TP. Nitrogen limitation, light limitation, or binding of phosphorus by non-algal suspended material may explain reduced Chl:TP ratios in turbid reservoirs. Survey data, however, do not distinguish the roles of differing limiting nutrients and light limitation in reservoirs with $>10 \text{ mg NVSS/L}$. Conventional lake management scenarios based on phosphorus control seem appropriate for Missouri reservoirs of low to moderate turbidity.

Key Words: regional limnology, Missouri, reservoirs, nutrients, chlorophyll, transparency.

This paper overviews the regional limnology of Missouri reservoirs by documenting water chemistry, seston composition, and trophic state in 94 waterbodies considered representative of conditions within the state (Fig. 1). The analysis parallels comparative limnological studies conducted elsewhere (Deevey 1940, Moyle 1956, Jones and Bachmann 1978, Heiskary et al. 1987, Canfield and Hoyer 1988, Fulmer and Cook 1990) by examining regional patterns among reservoirs located in the major physiographic provinces of the state. The influence of the geographic setting on water chemistry and lake fertility is well known (Duarte and Kalff 1989) and a previous reservoir study demonstrated that ionic salinity and composition differ regionally within Missouri (Jones 1977). This study extends that assessment to a wider range of limnological variables, including measurements of plant nutrients, algal chlorophyll and suspended solids. As well, empirical analyses are presented that identify key variables controlling water clarity and describe algal biomass-nutrient relations for the state as a whole and for each physiographic province. This information allows us to assess nutrient limitation, compare the trophic status of Missouri reservoirs with waterbodies in nearby geographic regions, and evaluate the potential benefits of management practices for Missouri reservoirs.

Physiographic Provinces and Land Cover in Missouri

The physiographic provinces of Missouri have been described by Fenneman (1938) and Collier (1955), among others. We followed the approach of Thom and Wilson (1980) and divided the state into five provinces (Fig. 1). The Glaciated Plains Province corresponds to the northern third of the state and includes the Central Irregular Plains ecoregion described by Omernik (1987). Soils are formed from loess and glacial till from Pleistocene glaciation, and the bedrock is primarily limestone and shale (Stout and Hoffman 1973). The Osage Plains Province is an unglaciated area of limestone, sandstone and Pennsylvanian shale in west-central and south-west Missouri and it includes much of metropolitan Kansas City. The Ozark Highlands Province in south-central Missouri is an unglaciated region characterized by thin cherty soils and rough hills. The Ozark Border Province in central and east-central Missouri is an ecotonal region where the Ozark Highlands grades into the neighboring provinces. This province borders the Missouri and Mississippi rivers (Omernik 1987) and has productive soils and complex geology (Stout and Hoffman 1973). Metropolitan St. Louis is located in this province. The Mississippi Lowlands Province is a flat alluvial plain

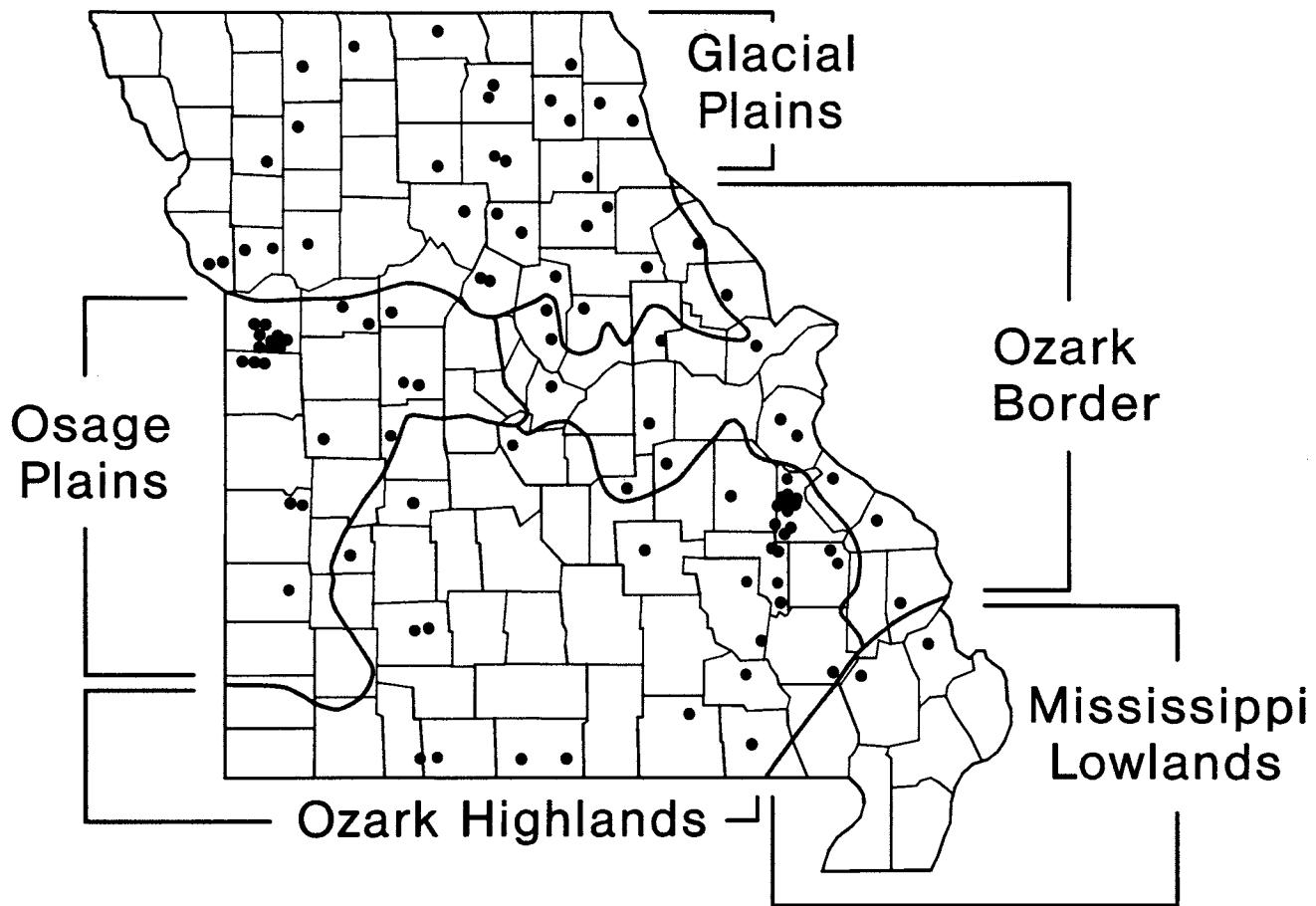


Figure 1. Physiographic map of Missouri showing the location of the reservoirs sampled in this study.

formed by past river activity with numerous wetlands, rivers and canals but few reservoirs.

Agriculture is the predominant land cover in Missouri (Table 1); among the provinces agriculture constitutes some 85% of land use in the Glaciated Plains, Osage Plains, and Mississippi Lowlands. Forest comprises some 59% of land cover in the Ozark Highlands and 42% in the Ozark Border Province. In the other provinces forest cover is 9-13% of the total.

There are a small number of karst and oxbow lakes in Missouri that were formed by natural processes, but the majority of lentic systems are man-made impoundments. These reservoirs were built for hydropower, flood control, recreation, and water supply. Reservoirs sampled in this study were selected to represent the range of reservoir types within the state and within each province. Reservoirs are not uniformly distributed among the provinces (Fig. 1). A reservoir in the Mississippi Lowlands was included to document its conditions (Table 2), but data from this province were excluded from the regional comparisons. We did not sample any of the small (<5 ha), privately owned impoundments that are common throughout the state.

Table 1. Land cover in Missouri expressed as a proportion (%) of the area in the states and each province in urban, agriculture, forest, or other categories. Data from U.S. Geological Survey (1983).

Physiographic Province	Urban	Agriculture	Forest	Other
Glacial Plains	1.2	84.9	13.0	0.8
Osage Plains	3.9	85.7	8.7	1.5
Ozark Border	4.7	51.8	41.6	1.9
Ozark Highlands	1.1	38.6	59.0	1.3
Mississippi Lowlands	1.8	86.5	9.2	2.5
Statewide Average	2.0	63.0	33.7	1.2

Table 2. Limnological parameters measured in Missouri reservoirs during 1978-1984. Values are lake means for the period of record and are presented by physiographic region.

Region, Lake, County	Years Sampled	Chlorophyll µg/L	Total Phosphorus µg/L	Total Nitrogen mg/L	Respiration mg/L/day	Volatile Solids mg/L	Non- Volatile Solids mg/L	Secchi Depth m
Great Plains (n = 32)								
Bethany (Harrison)	2	13	32	0.53	0.48	2.3	4.4	1.0
Bowling Green (Pike)	1	7	13	0.38	0.48	1.1	2.5	2.1
Brookfield (Linn)	3	7	19	0.64	0.48	1.5	3.0	1.9
Crystal (Ray)	1	62	80	0.68	—	—	—	0.5
Deer Ridge (Lewis)	3	17	47	1.95	0.96	4.4	5.8	0.8
Edina (Knox)	2	13	72	1.46	0.48	3.6	9.9	0.7
Ella Ewing (Scotland)	1	17	138	—	—	7.0	22.4	0.4
Fayette-Lower (Howard)	3	13	28	0.66	0.24	2.7	5.7	1.2
Fayette-Upper (Howard)	1	3	14	0.55	—	0.6	1.3	2.5
Forest (Adair)	5	6	26	0.59	0.24	1.3	4.4	1.3
Henry Sever (Knox)	3	8	25	0.51	0.48	1.9	2.5	1.5
Hunnewell (Shelby)	3	14	34	0.62	0.48	2.6	3.9	1.0
Little Dixie (Callaway)	7	14	44	0.59	1.20	2.5	4.2	1.0
Longbranch (Macon)	6	14	61	1.02	0.96	2.1	7.0	0.8
Macon (Macon)	1	19	81	—	—	4.9	16.3	0.4
Mark Twain (Monroe)	1	15	125	1.21	0.48	2.6	13.2	0.2
Monroe (Monroe)	1	16	53	—	—	3.9	11.8	0.4
Nehai Tonkayea (Chariton)	3	3	12	0.42	0.24	1.0	2.9	2.0
Paho (Mercer)	4	14	67	1.24	0.72	3.1	15.3	0.5
Pony Express (DeKalb)	4	27	66	0.75	1.44	3.2	6.3	0.9
Smithville (Clay)	3	19	43	0.74	0.96	2.3	4.4	1.1
Spring (Adair)	5	7	21	0.59	0.48	1.7	2.7	2.2
Sugar Creek (Randolph)	5	15	44	0.72	1.20	3.3	5.9	1.0
Thomas Hill (Randolph)	5	14	55	0.98	0.24	4.2	25.1	0.5
Thunderhead (Putnam)	2	10	34	0.86	0.24	1.6	8.9	0.9
Tri-City (Boone)	5	15	30	0.70	0.72	2.9	4.9	1.2
Vandalia (Andrain)	3	18	40	0.72	1.20	2.6	4.8	1.2
Viking (Daviess)	2	8	29	0.46	0.72	2.8	7.0	0.6
Wakonda (Lewis)	3	44	78	0.87	2.40	7.7	4.0	0.6
Watkins Mill (Clay)	1	17	54	0.41	0.72	3.3	8.2	0.6
Waucomis (Platte)	2	20	29	0.44	0.96	4.1	4.3	1.1
Weatherby (Platte)	1	4	11	0.30	—	—	—	3.1
Ozark Highlands (n = 25)								
Bull Shoals (Ozark)	2	4	9	0.21	0.24	1.5	1.9	3.6
Capri (St. Francois)	3	2	6	0.33	<0.1	0.5	1.4	3.7
Carmel (St. Francois)	3	2	8	0.36	0.48	0.5	1.2	3.0
Clearwater (Reynolds)	3	4	13	0.44	0.24	1.0	2.1	2.3
Fellows (Greene)	2	3	13	0.21	0.24	0.6	1.6	2.4
Fredricktown (Madison)	1	9	31	0.30	—	—	—	1.3
Lake of the Ozarks (Miller)	6	15	26	0.59	—	1.9	2.0	2.0
Logger's (Dent)	1	3	13	0.11	0.24	1.0	2.9	3.4
Lower Taum Sauk (Reynolds)	3	5	12	0.30	0.48	1.2	2.5	2.0
Marsailles (St. Francois)	3	2	9	0.33	0.24	0.6	2.1	3.0
McCormick (Oregon)	2	2	9	0.20	0.24	0.9	0.9	3.3
McDaniel (Greene)	1	14	54	0.55	—	—	—	0.6
Miller (Carter)	2	15	27	0.60	0.48	1.8	3.3	1.3
Norfolk (Ozark)	2	5	18	0.37	0.48	0.8	4.4	2.3
Pomme de Terre (Hickory)	4	14	21	0.36	0.96	1.9	1.7	1.8
Ripley (Ripley)	2	10	21	0.43	0.48	1.8	2.0	1.5
Stockton (Cedar)	4	5	10	0.39	0.72	0.8	1.3	3.6
Sonnen (Washington)	1	6	13	0.30	—	—	—	1.9
Table Rock (Stone)	5	4	9	0.36	0.48	0.6	0.9	4.1
Taneycomo (Taney)	3	6	28	0.59	1.20	1.4	4.4	1.8
Terre du Lac #4 (St. Francois)	1	1	14	0.53	—	0.8	3.5	1.3
Terre du Lac #5 (St. Francois)	1	2	9	0.47	—	0.7	3.0	1.7
Terre du Lac #6 (St. Francois)	1	1	6	0.47	—	0.6	1.7	2.3
Timberline (St. Francois)	2	2	6	0.22	0.24	0.3	0.9	2.7
Wappapello (Wayne)	3	23	38	0.55	0.72	3.4	5.2	1.0

Table 2. (continued)

Region, Lake, County	Years Sampled	Chlorophyll $\mu\text{g/L}$	Total Phosphorus $\mu\text{g/L}$	Total Nitrogen mg/L	Respiration mg/L/day	Volatile Solids mg/L	Non-Volatile Solids mg/L	Secchi Depth m
Ozark Border (n = 14)								
Ashland (Boone)	1	22	89	—	—	53	16.7	0.5
Binder (Cole)	3	32	59	0.85	1.44	4.4	3.7	0.8
Cedar (Boone)	1	47	89	—	—	7.8	20.5	0.6
Girardeau (Cape Girardeau)	3	36	45	0.85	0.72	6.9	3.9	1.0
Indian Hills (Crawford)	2	12	22	0.60	—	1.2	2.8	1.1
Lincoln (Lincoln)	2	5	17	0.37	0.72	1.2	3.6	2.3
Little Prairie (Phelps)	3	11	26	0.52	0.48	2.0	4.4	0.9
Peaceful Valley (Gasconade)	1	3	16	0.50	—	—	—	2.7
Perry (Perry)	2	29	48	0.59	1.92	4.5	2.9	0.9
Pinnacle (Montgomery)	1	28	38	0.80	—	—	—	1.0
Rocky Ridge (Ste. Genevieve)	1	16	35	0.30	—	—	—	1.5
St. Louis (St. Charles)	2	24	49	0.52	1.20	3.3	8.7	0.5
Tishomingo (Jefferson)	1	6	26	—	—	—	—	1.1
Wauwanoka (Jefferson)	2	6	17	0.30	0.48	1.3	2.1	2.3
Osage Plains (n = 22)								
Blind Pony (Saline)	4	26	72	0.79	1.20	3.2	12.0	0.7
Bodarc (Jackson)	2	46	117	0.84	1.92	5.0	10.1	0.5
Coot (Jackson)	2	15	71	0.45	0.72	3.0	18.3	0.2
Cottontail (Jackson)	2	29	187	1.30	0.72	7.9	43.8	0.2
Gopher (Jackson)	2	27	118	0.78	0.96	5.6	21.7	0.4
Harrisonville (Cass)	1	12	37	0.60	—	—	—	0.9
Higginsville (Lafayette)	2	19	68	0.74	0.96	2.3	12.1	0.8
Jacomo (Jackson)	2	23	29	0.48	1.20	2.7	2.6	1.0
Lamar (Barton)	1	14	41	0.70	—	—	—	0.8
Lotawana (Jackson)	2	20	35	0.48	0.96	2.1	6.3	1.1
Montrose (Henry)	5	55	104	0.93	1.68	6.8	25.9	0.3
Nell (Jackson)	2	25	106	0.60	0.96	5.0	22.1	0.3
Page (Lafayette)	2	16	48	0.84	0.24	2.3	14.8	1.0
Prairie Lee (Jackson)	2	27	70	1.07	0.72	7.6	39.0	0.7
Raintree (Cass)	2	6	87	0.86	0.48	8.5	55.8	0.8
Schell-Osage #1 (Vernon)	1	17	31	0.50	—	—	—	0.6
Schell-Osage #2 (Vernon)	1	47	94	1.22	—	—	—	0.3
Springfork (Pettis)	1	16	40	0.45	—	—	—	0.9
Tapawingo (Jackson)	2	13	35	0.52	0.72	1.4	4.9	1.3
Truman (Benton)	5	15	35	0.80	0.48	2.2	4.0	1.3
Westmoreland (Pettis)	1	27	61	0.50	—	—	—	0.7
Winnebago (Cass)	2	19	61	0.92	0.48	5.0	28.2	0.5
Mississippi Lowlands								
Tawapitty (Scott)	3	51	44	1.23	2.16	7.6	2.9	0.8

Methods

This paper is based on survey data collected by the University of Missouri during summers 1978-1984 (Fig. 1). Reservoirs were sampled on 1-10 occasions in each of 1-7 years. During each visit water samples were collected from the surface layer at 1-8 locations and transparency was measured with a Secchi disk. Samples were processed immediately or transported on ice to a laboratory. Analyses included measurement of algal chlorophyll (Chl), total phosphorus (TP), total nitrogen (TN), total suspended solids (TSS), volatile suspended solids (VSS), non-volatile suspended solids (NVSS), and

short-term biological oxygen demand (respiration). Some analyses were not conducted every year so the data set is not complete for each individual sample or lake. Details of analytical methods are given elsewhere (Hoyer and Jones 1983, Knowlton 1989, Knowlton and Jones 1989a, b).

Data are presented as seasonal means for water-bodies during individual years and as overall lake means. Seasonal means are based on the average of measurements from all sampling dates and sampling locations on a given reservoir during a given summer. The exceptions include widely separated sites on Lake of the Ozarks (Jones and Novak 1981), and lakes Truman, Pomme de Terre, Stockton, and Table Rock (Knowlton and Jones 1989b) which are

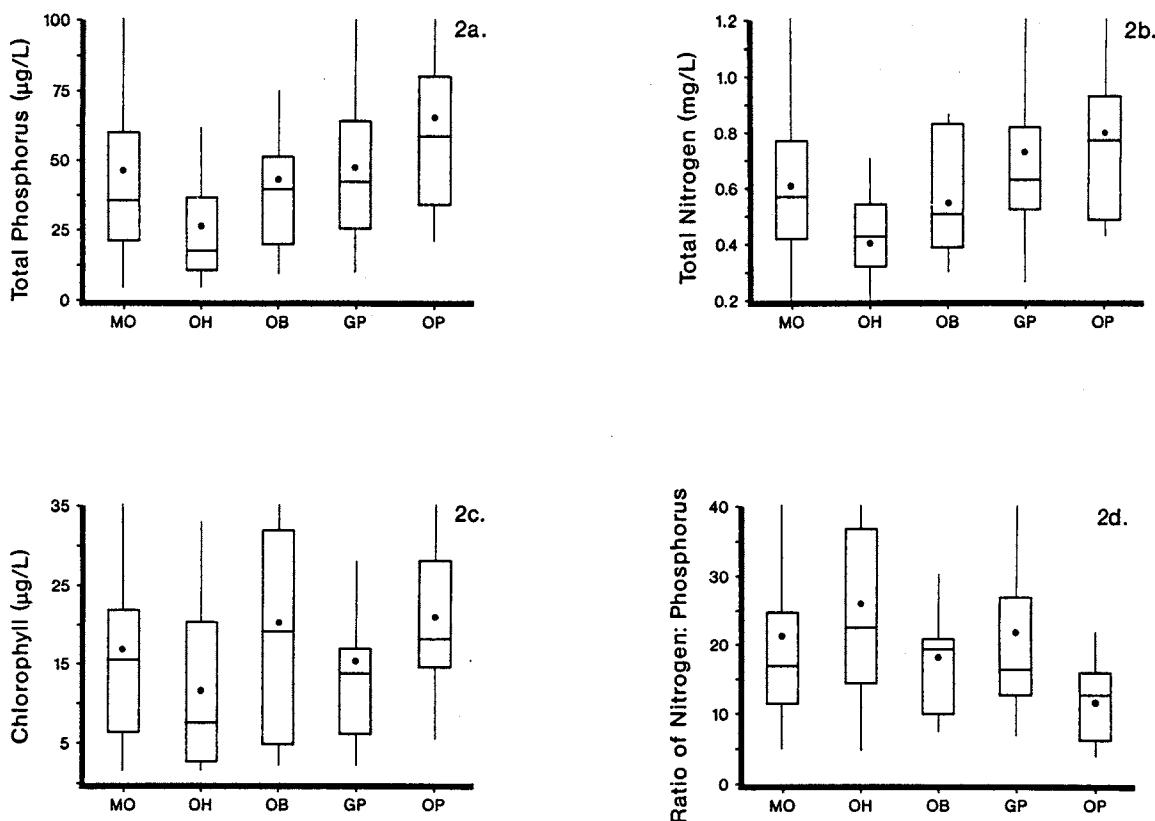


Figure 2. Box plots of total phosphorus, total nitrogen, algal chlorophyll, and ratio of total nitrogen:total phosphorus for all reservoirs sampled (MO), as well as reservoirs in the Ozark Highlands (OH), Ozark Border (OB), Glacial Plains (GP), and Osage Plains (OP) provinces. In the box plots the point represents the mean value, the line represents the median, the box represents the interquartile range, and the solid lines represent a distance 1.5 times the interquartile range. Outlying data points are not shown in these figures.

treated as distinct waterbodies because longitudinal gradients preclude using lake-wide averages to characterize conditions in these reservoirs. Seasonal means are used to calculate empirical relations for Missouri reservoirs. Lake means are the average of seasonal means for each reservoir and are used to describe general conditions in the state and within the various provinces. Lake means for the five reservoirs with pronounced longitudinal gradients are based solely on data from the sampling location near the dam.

We followed the approach of Knowlton (1989) to estimate the attenuation of photosynthetically active radiation (PAR) by non-algal substances (NALA, non-algal light attenuation) and dissolved substances. We assumed that absorbance of non-algal particles, averaged over the visible spectrum, is $0.023/\text{m}$ per mg/L NVSS. This coefficient was approximated from Kirk (1984) and unpublished Missouri data. We also assume the absorbance of dissolved colored materials is constant at $0.18/\text{m}$. This coefficient is derived from color values (Hazen

Table 3. Trophic state criteria based on chlorophyll, total P and total N modified from criteria proposed by Forsberg and Ryding (1980) and Canfield et al. (1983), and the percentage of reservoirs from this data set that fall within each of these designations.

Trophic State	Chlorophyll a		Total P		Total N	
	Criterion	% of reservoirs	Criterion	% of reservoirs	Criterion	% of reservoirs
		$\mu\text{g/L}$		$\mu\text{g/L}$		$\mu\text{g/L}$
Oligotrophic	≤ 3	10	≤ 10	11	≤ 300	13
Mesotrophic	$> 3 - 7$	20	$> 10 - 25$	21	$> 300 - 500$	26
Eutrophic	$> 7 - 40$	63	$> 25 - 100$	61	$> 500 - 1200$	53
Hypereutrophic	> 40	7	> 100	7	> 1200	8

method, APHA 1980) from 12 Missouri reservoirs assuming that one Platinum-Cobalt unit represents an absorption of 0.02/m (Hutchinson 1957, Kirk 1975). Together with the absorption of water itself (about 0.2/m for unaltered sunlight; Kirk 1985) this coefficient yields a background absorbance of 0.38/m. Thus, non-algal light attenuation is estimated as: NALA = 0.38 + 0.023 * NVSS. These estimates are conservative because they ignore light absorption by non-algal volatile suspended materials in the seston.

Results

Nutrients, Algal Chlorophyll and Trophic State

Among Missouri reservoirs TP concentrations ranged from 6 to 187 µg/L TP and TN ranged from 0.11 to 1.95 mg/L TN (Table 2). Median values were 35 µg/L TP and 0.57 mg/L TN (Fig. 2a and b). As a group, reservoirs in the Ozark Highlands had the lowest nutrient concentrations within the state (Fig. 2a and b); median values in this province were 13 µg/L TP and 0.36 mg/L TN and some 90% of these

waterbodies had values less than the statewide median for these two elements. Outside of the Ozark Highlands nitrogen concentrations were similar among reservoirs, averaging about 0.7 mg/L TN (Fig. 2b). Regional trends, however, were apparent for TP (Fig. 2a). On average, values in Osage Plains reservoirs were 70 µg/L TP, about 1.5 times larger than in the Glacial Plains and Ozark Border reservoirs (Fig. 2a).

Chl in Missouri reservoirs ranged from 1 to 62 µg/L with a median of 14 µg/L. Within this distribution the lowest values were most common among reservoirs in the Ozark Highlands (Fig. 2c); some 80% of waterbodies in this province had values smaller than the statewide median for Chl. Whereas in the Osage Plains >80% of the Chl values were larger than the statewide median. In the Glacial Plains the distribution of Chl was comparatively narrow — the median was similar to the statewide value but in most lakes concentrations were between 8 and 16 µg/L. Reservoirs in the Ozark Border Province showed a broad distribution in Chl (Fig. 2c).

Using modifications of the trophic state criteria proposed by Forsberg and Ryding (1980) and Canfield et al. (1983) some 80% of the reservoirs sampled were mesotrophic or eutrophic based on nutrient concentrations and algal biomass in the surface

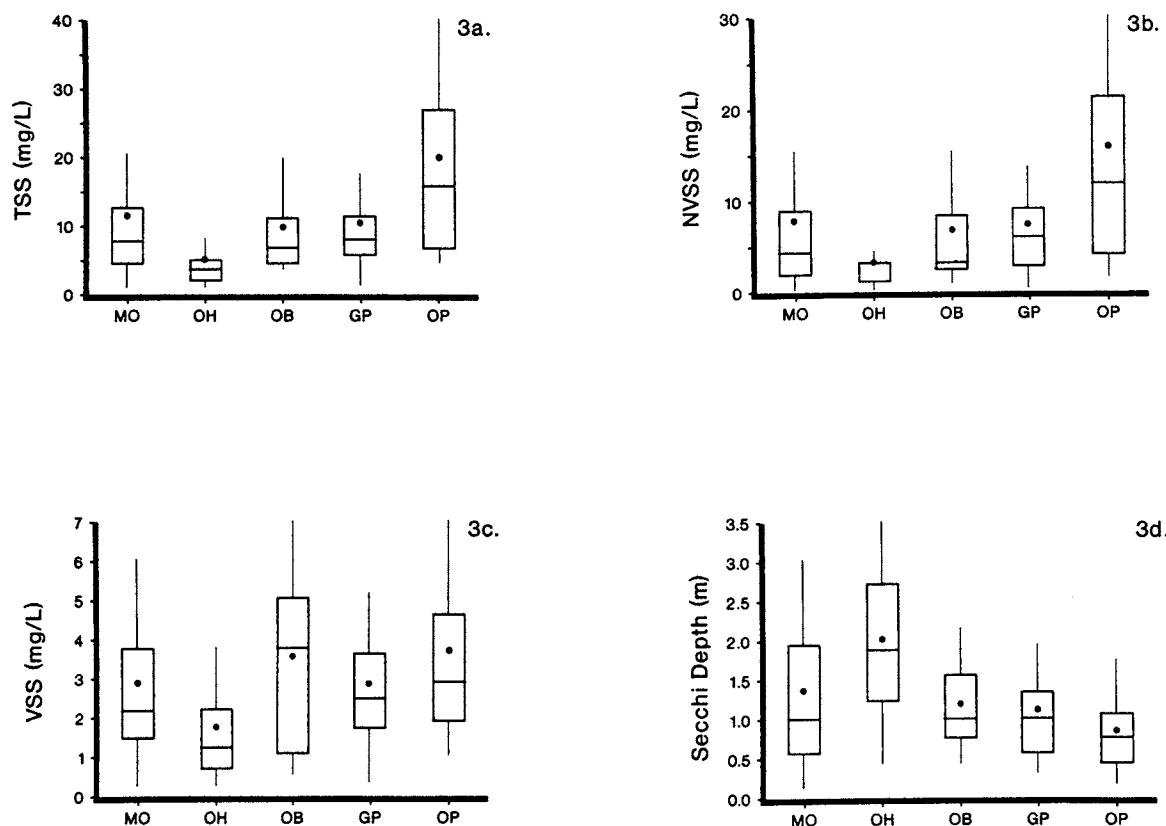


Figure 3. Box plots of total suspended solids (TSS), non-volatile suspended solids (NVSS), volatile suspended solids (VSS), and Secchi depth for all reservoirs sampled (MO), as well as reservoirs in the Ozark Highlands (OH), Ozark Border (OB), Glacial Plains (GP), and Osage Plains (OP) provinces.

water (Table 3). Oligotrophic and hypereutrophic reservoirs were present in about equal proportions; each category comprised $\leq 10\%$ of the total.

Within the state, reservoirs categorized as oligotrophic were located in the Ozark Highlands, along with about half the mesotrophic waterbodies (Table 4). The remaining mesotrophic reservoirs were located in the Ozark Border and Glacial Plains provinces. Eutrophic reservoirs were sampled in each province but the majority were found in the Glacial and Osage Plains provinces where all of the hypereutrophic reservoirs were located. Although this assessment is based on TP, the distribution was quite similar when based on TN or Chl.

Trophic state criteria for Missouri's reservoirs based on TN are slightly lower than criteria proposed by Forsberg and Ryding (1980) and much lower than OECD (1982) criteria. This adjustment was necessary because in many Missouri reservoirs TN was not abundant relative to TP. The median TN:TP ratio in the data set was 18 (Fig. 2d). Using trophic state criteria for TN proposed by Forsberg and Ryding (1980) or OECD (1982) would have greatly overestimated the number of oligotrophic waterbodies within the state because their lakes have higher TN:TP ratios than Missouri reservoirs.

This distribution of TN:TP suggests that both phosphorus and nitrogen limitation of phytoplankton would likely occur in Missouri reservoirs. In 28% of the reservoirs either nitrogen or phosphorus would be potentially limiting (TN:TP = 10-17, Forsberg and Ryding 1980). In 6% of the reservoirs this ratio was < 10 ; the point where nitrogen is thought to limit phytoplankton. And in the rest, phosphorus limitation could be expected (TN:TP > 17 , Forsberg and Ryding 1980). Among the provinces, values of TN:TP were largest in the least fertile reservoirs located in the Ozark Highlands, and smallest in the fertile lakes of the Osage Plains (Fig. 2d).

Our respiration measurements on surface waters were correlated with trophic state as measured by Chl, TP, and TN (\log_{10} transformation, $r = 0.77$, 0.59 and 0.43, respectively, $n = 68$). Based on TP

Table 4. Number of reservoirs classified as oligotrophic, mesotrophic, eutrophic and hypereutrophic on the basis of total phosphorus (Table 2) and their proportional distribution among the physiographic provinces.

Lake Trophic State	n	Physiographic Province			
		Ozark Highlands	Ozark Border	Glacial Plains	Osage Plains
Oligotrophic	10	100%	—	—	—
Mesotrophic	20	45%	20%	35%	—
Eutrophic ^a	57	10%	17%	40%	30%
Hypereutrophic	7	—	—	29%	71%

^aDoes not add to 100% because one reservoir is located in the Mississippi Lowlands.

Table 5. Regression equations of Secchi depth (SD, m) on the following independent variables (\log_{10} transformed): chlorophyll (Chl, $\mu\text{g/L}$), volatile suspended solids (VSS, mg/L) non-volatile suspended solids (NVSS, mg/L) and total suspended solids for reservoirs in Missouri using the seasonal mean data set (for observations including solids data).

Equation	R ²
(n = 232, Secchi range 0.1 - 5.3 m)	
LSD = 0.60 - 0.50 (LChl)	0.30
LSD = 0.33 - 0.88 (LVSS)	0.65
LSD = 0.48 - 0.71 (LNVSS)	0.80
LSD = 0.75 - 0.86 (LTSS)	0.87
LSD = 0.63 - 0.64 (LNVSS) - 0.17 (LChl)	0.83

criteria for trophic state, respiration values averaged 0.3 mg/L/day in oligotrophic reservoirs, 0.5 mg/L/day in mesotrophic reservoirs, 0.9 mg/L/day in eutrophic reservoirs, and 1.1 mg/L/day in hypereutrophic reservoirs. This pattern shows that microbial activity and oxidizable organic matter increase in Missouri reservoirs as a function of trophic state. The correlation between respiration and volatile suspended solids was $r = 0.62$ (\log_{10} transformation, $n = 68$).

Seston and Transparency

High concentrations of TSS and low transparency are major features of water quality in Missouri reservoirs. Statewide, the median TSS value was 7.4 mg/L and lake means ranged between 1.2 and 64.3 mg/L (Table 2). The median Secchi depth was 1.0 m (range 0.2-4.7 m, Table 2). Among the provinces, TSS values were smallest in the Ozark Highlands (Fig. 3a) where most values were between 2 and 4 mg/L. Whereas values were an order of magnitude greater in the Osage Plains reservoirs — typically between 10 and 30 mg/L (Fig. 3a). In the Glacial Plains and Ozark Border TSS values were intermediate, mostly between 8 and 15 mg/L (Fig. 3a). Inter-regional differences in transparency showed the opposite pattern (Fig. 3d).

Most Missouri reservoirs have relatively low concentrations of dissolved colored materials (≤ 15 Pt-Co Units, unpublished data) so transparency is largely controlled by the absorbance and scattering of light by seston (Kirk 1985). Variation in TSS explained 87% of the variation in Secchi depth (\log_{10} transformation, Table 5).

NVSS dominate the seston in most Missouri reservoirs and govern their transparency. On average, 68% of the TSS were NVSS (range 29-87%), and in waterbodies with > 15 mg/L TSS some 80% of the seston was non-volatile. Statewide, NVSS and TSS were highly correlated ($r = 0.97$, \log_{10} transformation) so that variation in NVSS explained nearly

as much variation in transparency as did TSS (80 versus 87%, Table 5). Hoyer and Jones (1983) and Knowlton and Jones (1989a) demonstrated the importance of NVSS on water clarity in midwest reservoirs; these findings are consistent with studies of other turbid lakes (Meijer et al. 1990, Koenings and Edmundson 1991).

In contrast with NVSS, VSS and algal biomass (as Chl) comprise small and variable fractions of the seston in Missouri reservoirs and have a minor influence on transparency. Assuming algal pigments comprise about 2% of phytoplankton dry weight (Healey and Hendzel 1980, Reynolds 1984) algal biomass in Missouri reservoirs constitutes about 10% of the TSS (range 0.4-64%) Volatile materials averaged 32% of TSS (range 13-71%). Chl showed moderate correlations with NVSS ($r = 0.44$) or TSS ($r = 0.57$) and accounted for only 30% of the variation in Secchi depth (Table 5). VSS explained 65% of the variation in Secchi depth but this was probably due to its strong correlation with NVSS ($r = 0.71$) and TSS ($r = 0.85$). Adding either Chl or VSS to a regression already containing NVSS resulted in only a minor improvement (e.g., Table 5).

Despite the pervasive influence of NVSS on the light regimens of many Missouri reservoirs, the Chl-Secchi relation by Jones and Bachmann (1978) provides reasonable estimates of transparency in waterbodies with <10 mg/L NVSS (Fig. 4). Mean Secchi depth for this group was accurately predicted by the Jones-Bachmann model and most observations were within the 95% confidence limits of the model. In one of these reservoirs, Lake Taneycomo (Table 2), Chl explained >80% of the temporal variation in Secchi depth during summer (Knowlton and

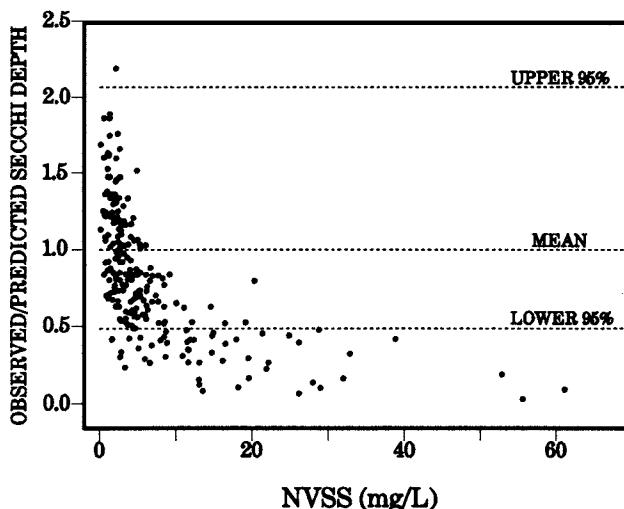


Figure 4. Effect of non-volatile suspended solids (NVSS) on the ratio of observed Secchi depth to Secchi depth predicted from chlorophyll after Jones and Bachmann (1978). Horizontal dashed lines indicate the mean and upper and lower 95% confidence limits on individual observation from the Jones and Bachmann model. Data shown are for seasonal means ($n = 232$).

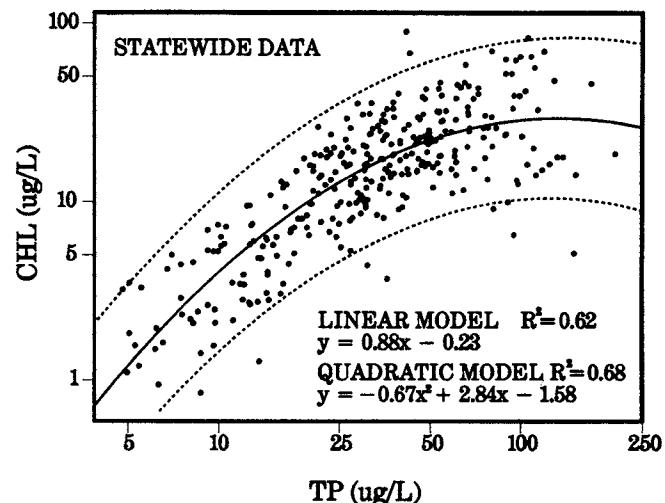


Figure 5. Relation between \log_{10} transformed concentrations of chlorophyll (Chl) and total phosphorus (TP) for Missouri reservoirs. Data shown are seasonal means ($n = 317$). The regression line and 95% confidence limits on individual observations are fitted for the quadratic model.

Jones 1990). In reservoirs with >10 mg/L NVSS the observed Secchi depths were about one-third of their predicted values and most of these observations were below the lower confidence limits of the Jones-Bachmann model (Fig. 4). In these waterbodies Secchi depth would not be a good measure of trophic state (Carlson 1977, Walker 1984).

For our seasonal means, estimates of non-algal light attenuation (NALA) varied about five-fold among the reservoirs; values ranged from 0.39 to 1.76/m with a median of 0.47/m. Availability of PAR for photosynthesis varies inversely with absorbance by non-algal materials in the water column (Bannister 1974). Given this fact, NALA data suggest that light potentially available for algal growth varies less among Missouri reservoirs than would be expected from Secchi transparency (a >20-fold range) and NVSS (a 200-fold range). This apparent discrepancy occurs because suspended materials, comprising the non-volatile fraction of the seston, scatter light far more strongly than they absorb it (Kirk 1985). Thus, NVSS strongly influence transparency and the visual appearance of lake water without having a proportional effect on light availability in the water column. Among the provinces, median estimates of NALA were smallest in the Ozark Highlands (0.43/m), largest in the Osage Plains (0.57/m), and intermediate in the Ozark Border and Glacial Plains provinces (0.47 and 0.50/m, respectively).

Chlorophyll-Nutrient Relations

\log_{10} transformed values of CHL (LChl) and TP (LTP) from Missouri reservoirs show a slight curvilinear relation (Fig. 5) with Chl approaching an asymptote above 50 $\mu\text{g/L}$ TP. On average, there

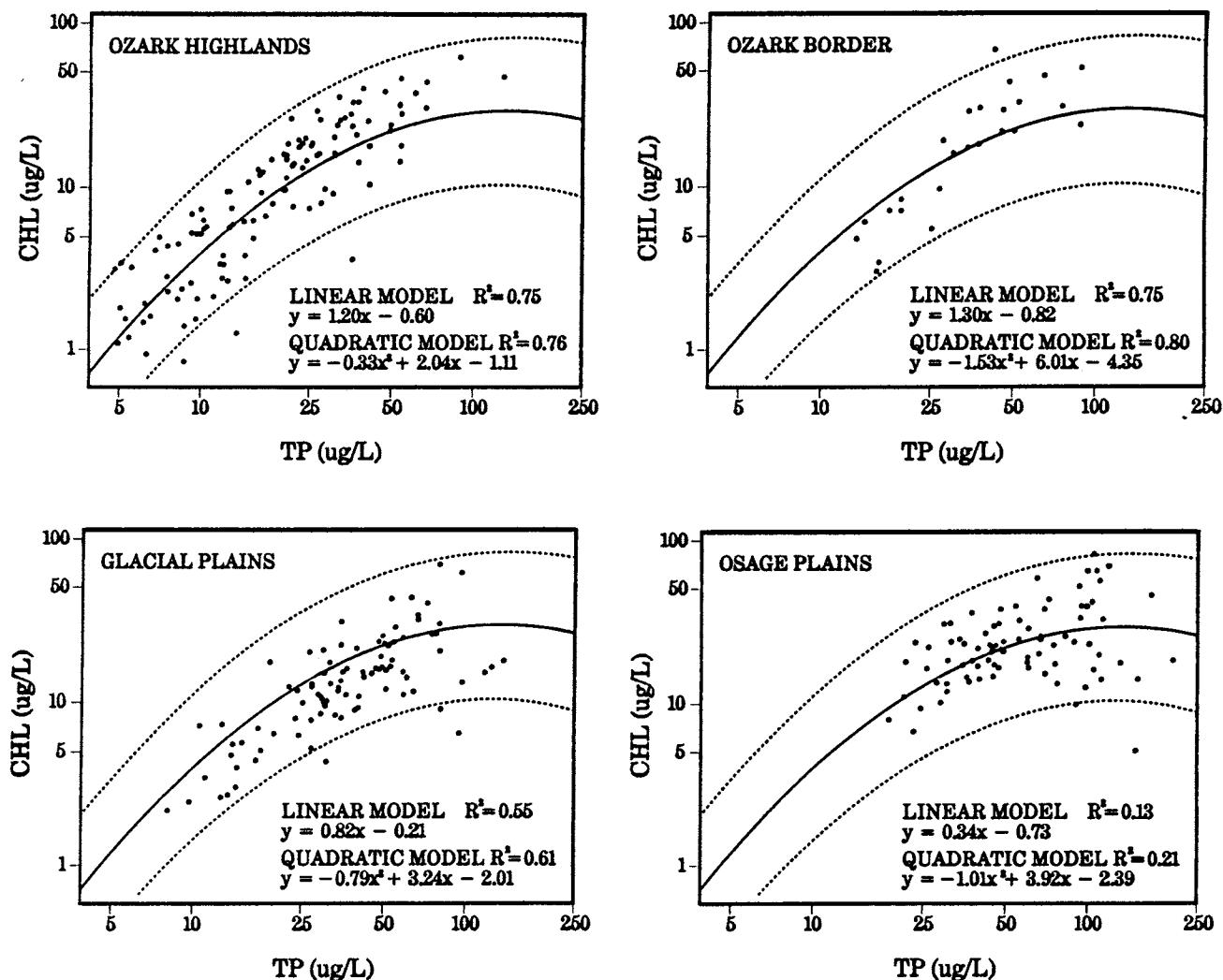


Figure 6. Relation between log₁₀ transformed concentrations of chlorophyll (Chl) and total phosphorus (TP) for reservoirs in the Ozark Highlands ($n = 115$), Ozark Border ($n = 25$), Glacial Plains ($n = 92$) and Osage Plains ($n = 82$) provinces. Data shown are seasonal means. The regression line and 95% confidence limits on individual observations are from the quadratic model for the statewide data set shown in Fig. 5.

is a 30% decline in the yield of Chl per unit of phosphorus among observations with $>50 \mu\text{g/L}$ TP compared to those with $<50 \mu\text{g/L}$ TP (mean Chl:TP = 0.35 versus 0.50). This pattern is consistent with studies showing that among lakes Chl does not rise linearly with phosphorus (Forsberg and Ryding 1980, Canfield 1983, Prairie et al. 1989, McCauley et al. 1989) but contrasts with Chl-TP models for many north-temperate lakes that show the yield of Chl per unit of phosphorus typically doubles or triples over this same range (Jones and Bachmann 1976, and others). Because of this curvilinearity a model including the square of LTP along with LTP fits the Missouri data set somewhat better ($R^2 = 0.68$, Fig. 5) than the linear one ($R^2 = 0.62$).

Data from the various provinces are positioned at different locations along this Chl-TP continuum (Fig. 6). Most observations from the Ozark Highlands (90%) and Ozark Border provinces (76%) are

situated in the linear portion of the relation ($<50 \mu\text{g/L}$ TP, Fig. 6) and span a nutrient range where algal biomass is considered responsive to TP (McCauley et al. 1989). The Chl-TP relations for both regions show a strong linear fit ($R^2 = 0.75$, Fig. 6). Whereas in the Osage Plains region about half the reservoirs lie in the asymptotic position of the Chl-TP relation ($>50 \mu\text{g/L}$ TP, Fig. 6) and Chl is weakly related to TP ($R^2 = 0.13$). For the Glacial Plains about one-third of the observations lie along the asymptote and the linear Chl-TP relation in this province is moderate ($R^2 = 0.55$). A quadratic term for TP was significant in all but the Ozark Highlands (Fig. 6).

The effect of LTP² in these equations suggests that factors regulating algal biomass change over the range encountered but does not identify the mechanism. Previous studies have attributed this reduced yield of Chl:TP to the effects of non-algal

seston (Jones and Novak 1981, Ferris and Tyler 1985, Hoyer and Jones 1983, Walker 1984). In Missouri reservoirs TP and NVSS are strongly correlated ($r = 0.80$, $n = 231$, \log_{10} transformation). In waterbodies with $>50 \mu\text{g/L}$ TP values of NVSS averaged 14.1 mg/L compared to 3.3 mg/L in the others. When \log_{10} NVSS is substituted for the quadratic term in the statewide or provincial Chl-TP models the fit matches the quadratic regression using phosphorus (Table 6). This magnitude of improvement is consistent with that achieved by Hoyer and Jones (1983), suggesting that light attenuation or other effects of non-algal seston reduce the Chl:TP value in many turbid reservoirs and account for much of the curvilinearity in the Missouri Chl-TP relation (Figs. 5 and 6).

A comparison of Chl values from Missouri reservoirs to values predicted using the phosphorus model for temperate lakes by Jones and Bachmann (1976) shows a hyperbolic relation over the range of NVSS values in our data set (Fig. 7). Most seasonal mean values with $<10 \text{ mg/L}$ NVSS fall within the confidence limits of Jones-Bachmann relation. Whereas most observations from reservoirs with $>10 \text{ mg/L}$ NVSS fall below the Jones-Bachmann regression line, and some 40% of the observations lie below the lower confidence limit (Fig. 7). This comparison suggests that in waterbodies with $>10 \text{ mg/L}$ NVSS the Chl:TP ratio is routinely less than expected for temperate lakes with similar TP values. This NVSS value could, therefore, serve as a tentative cutpoint to identify where the effects of NVSS seem to consistently dampen the relation between algal biomass and phosphorus. In this data set, 18% of the observations are above this threshold and exhibit reduced Chl:TP.

Despite low to moderate TN:TP ratios in many Missouri reservoirs (Fig. 2d) the relation between seasonal mean Chl and TN was weak, both in the statewide data set ($r = 0.49$, $n = 277$) and within each province ($r = 0.28$ to 0.59). TN also failed to enter in as a significant variable in any of the models that included TP, a quadratic term for TP or NVSS. Among these reservoirs, TN and TP are correlated ($r = 0.62$, \log_{10} transformation) but TP concentrations increase at a faster rate than TN. Because of this pattern low TN:TP ratios are generally found in reservoirs with high TP, like those in the Osage Plains (Fig. 2d). These are also the waterbodies that fall in the asymptotic range of the Chl-TP relation where limitation by light or other factors related to NVSS is most likely. In reservoirs with $\text{TN:TP} < 10$, NVSS averaged 15.5 mg/L ($n = 33$) compared with 4.8 mg/L for the others. Our TN:TP values suggest N-limitation occurs in Missouri reservoirs but given the negative correlation between NVSS and TN:TP in the data set ($r = -0.57$, $n = 192$, \log_{10} transformation) the role of N on algal chlorophyll may be confounded by suspended solids.

Discussion

Our results demonstrate that limnological characteristics of Missouri reservoirs differ among the major physiographic provinces. And we believe these differences are tied to regional variations in geology and land cover (Table 1). The major contrast within the state is between waterbodies in the Ozark Highlands and Osage Plains: as a group, reservoirs in the Ozark Highlands generally have

Table 6. Simple and multiple regression models of variation among \log_{10} transformed seasonal means of Chl excluding observations without NVSS data. Independent variables are abbreviated as: LTP = \log_{10} TP, LTP² = $(\log_{10}\text{TP})^2$, LNVSS = \log_{10} NVSS. Slopes labeled "ns" were not significant at 5% level. The Ozark Border Province is excluded because only 13 seasonal observations included NVSS.

	Independent Variables		Slopes		Intercept R ²	
Statewide (n=231)	LTP	0.797			-0.098	0.58
	LTP LTP ²	2.905	-0.715		-1.564	0.66
	LTP LNVSS	1.193	-0.414		-0.447	0.66
Glacial Plains (N=69)	LTP	0.744			-0.099	0.53
	LTP LTP ²	3.323	-0.838		-2.020	0.60
	LTP LNVSS	1.029	-0.306		-0.330	0.58
Ozark Highlands (n=83)	LTP	1.185			-0.548	0.76
	LTP LTP ²	2.171	-0.386ns		-1.141	0.77
	LTP LNVSS	1.343	-0.249		-0.663	0.77
Osage Plains (n=64)	LTP	0.248			0.881	0.07
	LTP LTP ²	3.323	-0.864		-1.807	0.14
	LTP LNVSS	0.657	-0.263		0.379	0.17

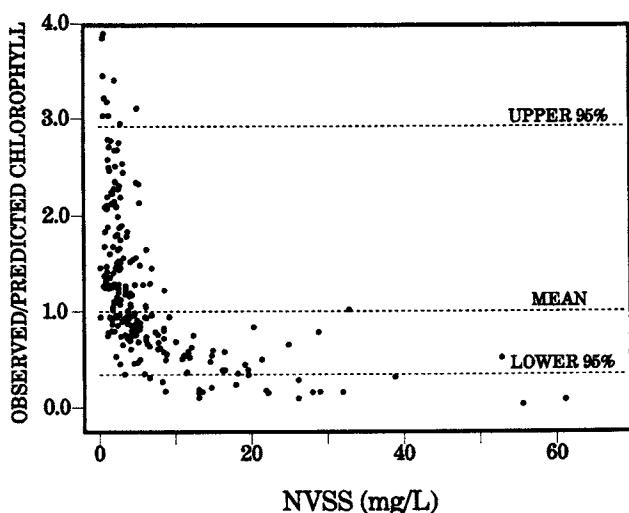


Figure 7. Effect of non-volatile suspended solids concentration (NVSS) on the ratio of observed chlorophyll concentration to chlorophyll concentration predicted from total phosphorus after Jones and Bachmann (1976). Horizontal dashed lines indicate the mean and upper and lower 95% confidence limits on individual observations from the Jones and Bachmann model. Data shown are for seasonal mean observations ($n = 231$).

lower algal Chl, nutrient content and suspended solids, and are more transparent than other Missouri reservoirs (Figs. 2 and 3). This dissected plateau is largely on carbonate rocks and the land cover is predominantly forest and pasture (Table 1). Stream data suggest that the annual sediment yield in this province is an order of magnitude lower than elsewhere in the state (MDNR 1979). Also, agricultural fertilizers are used less in this province than elsewhere (U. S. Bureau of the Census 1990). Omernik (1977) showed that stream nutrient concentrations within the Ozark Highlands, particularly phosphorus, are typically the lowest in the state. Smart et al. (1985) have demonstrated that within the Ozark Highlands streams draining forested catchments have low nutrient values relative to other land use practices. Predominance of forest land cover in the Ozark Highlands likely accounts for low nutrient loading and contributes to the low fertility of these reservoirs. In contrast, reservoirs in the Osage Plains have the highest content of algal Chl, nutrients and suspended solids in the state and they are also the least transparent (Fig. 3). This is an agricultural and urban region (Table 1) with high sediment loss (MDNR 1979). Reservoirs in the Glacial Plains and Ozark Border provinces have water quality intermediate between the extremes found in the Ozark Highlands and Osage Plains.

Collectively, Missouri reservoirs are similar to waterbodies throughout the ecoregions of the mid-continent area. Missouri reservoirs are predominantly mesotrophic and eutrophic (Tables 3 and 4) and based on Chl and TP values they are similar to waterbodies in Indiana (Spacie and Loeb 1990), North Central Hardwood Forests (Lillie and Mason

1983, Heiskary et al. 1987) and the Allegheny Plateau (Fulmer and Cooke 1990). Our study suggests that there are relatively few hypereutrophic reservoirs in Missouri (Tables 3 and 4) and none are as enriched or productive as waterbodies on the glacial lobe in Iowa or elsewhere on the Cornbelt Plains (Jones and Bachmann 1978, Heiskary et al. 1987, Lillie and Mason 1983, Fulmer and Cooke 1990). The oligotrophic and mesotrophic reservoirs in the Ozark Highlands have Chl and TP values similar to lakes in the Northern Lakes and Forests ecoregion (Lillie and Mason 1983, Heiskary et al. 1987).

This comparison, however, is made with caution because many Missouri reservoirs with low nutrients and algal biomass in the pelagic zone support extensive growths of aquatic macrophytes that contribute to lake fertility, but macrophytes are not considered in this classification system (Canfield et al. 1983). Other reservoirs considered oligotrophic on the basis of measurements of the epilimnion near the dam have fertile reaches located uplake, zones of oxygen depletion in the hypolimnion (Cole and Hannan 1990), and at least one waterbody supports a subsurface algal layer (Knowlton and Jones 1989a, b). In these respects, trophic state assessments of these impoundments do not exactly parallel the paradigm for natural lakes.

Nutrient measurements suggest that TN:TP ratios in Missouri reservoirs are lower than in many other temperate waterbodies (Fig. 2d, Forsberg and Ryding 1980, OECD 1982). Because of these proportionately low TN values we have adjusted conventional trophic state criterion for TN to classify Missouri reservoirs (Table 3). This approach is provisional and needs additional evaluation.

Few studies of regional limnology in the mid-continent have reported TN values but lake studies in Iowa (Jones and Bachmann 1978) and Wisconsin (Lillie and Mason 1983) suggest that in most waterbodies, nitrogen is abundant relative to phosphorus. The relative proportion of plant nutrients in many Missouri reservoirs is similar to reservoirs in the southeastern U.S. where nitrogen limitation is suspected (Kennedy and Gaugush 1988. Lohman et al. (1991) have demonstrated N limitation of periphyton in an Ozark stream and speculate that this condition is widespread throughout that province. Regional studies conducted elsewhere have experimentally demonstrated the importance of nitrogen to phytoplankton in reservoirs of low and moderate fertility (Morris and Lewis 1988, Dodds et al. 1989). The high proportion of Missouri reservoirs with TN:TP ratios <17 (about 45%, Fig. 3d) suggests that nitrogen may regulate algal biomass in many Missouri reservoirs, perhaps periodically (Prepas and Trimbee 1988) or contemporaneously with phosphorus (Dodds et al. 1989). In Missouri reservoirs, however, low TN:TP ratios usually co-occur with high NVSS and low transparency — conditions favoring light rather than nutrient limitation of

algal biomass. Also, TN:TP in turbid waterbodies may overestimate the importance of N because P binds to sediment particles; making it relatively less available for algal growth than N (Golterman and Kouwe 1980). Walker (1984) determined that not all forms of nitrogen in the TN measurement are related to algal Chl. Collectively, these factors may help explain why TN contributed little to our Chl regression models despite low average TN:TP in our reservoirs. And suggest that the value of TN:TP ratios as indicators of nutrient limitation in turbid lakes needs additional evaluation.

A predominant feature of water quality in Missouri reservoirs is the high concentration of TSS found mostly in reservoirs located outside of the Ozark Highlands (Fig. 3a). In most cases the majority of this material is NVSS. High concentrations of NVSS have been shown to have a major impact on water clarity by altering the quantity and quality of light in the water column (Kirk 1985) so that transparency is largely determined by non-algal constituents of the seston (Table 5) rather than by algal biomass and algal detritus (Jones and Bachmann 1978). NVSS alter Chl-nutrient relations through light limitations and, perhaps, reduced nutrient availability (Table 5, Jones and Novak 1981, Hoyer and Jones 1983, Walker 1984). By these mechanisms NVSS weakens the interrelations among nutrients, algal biomass and water clarity that are at the core of most lake management schemes (Dillon and Rigler 1975).

The effects of non-algal materials on Chl-TP relations and water clarity are likely continuous but not necessarily linear (Walker 1984). Our comparison of predicted (using Jones and Bachmann 1976) and observed Chl in the Missouri reservoirs shows a hyperbolic decrease across the NVSS range in our reservoirs (Fig. 7). This comparison suggests that in reservoirs with NVSS < 10 mg/L nutrient control of algal Chl most closely parallels the patterns demonstrated in temperate lakes with low concentrations of non-algal turbidity (Jones and Bachmann 1976). Therefore, we judge the influence of non-algal materials as being minimal on Chl production at a given nutrient level within this group. Some 40% of the reservoirs in this subset are located in the Ozark Highlands (Fig. 3) and previous studies have demonstrated the importance of nutrients in regulating algal blooms and water clarity in specific reservoirs in this province (Knowlton and Jones 1989b, 1990). Data from these reservoirs match the Chl-Secchi relation for temperate lakes (Fig. 4). Conventional lake management practices, centered around nutrient control, are best suited for these reservoirs.

The transition point of 10 mg/L NVSS separating reservoirs of low and moderate non-algal turbidity was selected by a comparison with conditions in temperate lakes (Jones and Bachmann 1976, 1978) and it needs additional evaluation. Our empirical analyses show that Chl-nutrient and Secchi-Chl relations become weaker in turbid reservoirs. These re-

servoirs were located mostly in the Osage and Glaciated Plains (Fig. 3). In these waterbodies transparency is a poor measure of trophic state because water clarity is not closely tied to algal biomass (Table 5; Walker 1984). Therefore, conventional practices directed at cutting watershed phosphorus loading to achieve reduced algal biomass and improve physical appearance (Dillon and Rigler 1975) of turbid reservoirs may not be beneficial without a concurrent reduction in sediment load from the catchment.

The response of individual lakes to an alteration in TP loading is uncertain (Smith and Shapiro 1981). Based on this comparison of seasonal mean values, we are confident that Missouri reservoirs with low NVSS will respond to changes in their nutrient supply in the same general pattern as other temperate lakes (Jones and Bachmann 1976, Smith and Shapiro 1981). We have less confidence, however, in predicting the response in turbid waterbodies. Light absorption by non-algal materials is related to the reduction in yield of algal biomass per unit of phosphorus. Unfortunately, our analysis cannot address whether phytoplankton under these conditions are entirely light limited, and would not respond to changes in nutrients, or whether algal biomass is co-limited by nutrients and light (Healey 1985, Guidford et al. 1987). If co-limitation is common, then nutrient abatement could reduce algal biomass.

Regression models in Table 6 assume that co-limitation is occurring. A given change in TP results in the same proportional change in Chl regardless of NVSS. For example, the statewide model with both TP and NVSS predicts that doubling TP will more than double Chl at any level of NVSS. This prediction may be correct, but our data are equally consistent with two alternative hypotheses: one explanation is that the algal community is light limited and Chl does not respond to TP past some threshold amount of NVSS; another interpretation is that the slope of the Chl-TP response curve declines as NVSS increases. These choices cannot be evaluated with regression analyses and require an experimental approach to distinguish them. Our multiple regressions, therefore, provide evidence of an effect of NVSS on the Chl-TP relation but have an uncertain potential for predictive use. Underlying functional relations must be determined before we can predict the effects of altering nutrient loads to turbid waterbodies.

While the overall effect of NVSS was to diminish the Chl:TP value, this was not always the case. Among the reservoirs with >10 mg/L NVSS some 10% of the Chl:TP values were >0.5, a ratio typical of clear northern lakes (Walker 1984). Most of these were shallow waterbodies (mean depth <3 m) where light induced reduction of algal biomass may not occur (Straskraba 1980). Among shallow, turbid lakes in Nepal, Jones et al. (1989) found NVSS did not reduce the mean square error in a Chl-nutrient

relation. Light availability varies with mixed depth (Talling 1971, Grobbelaar 1985) and others have tried to account for the effect of non-algal turbidity on Chl-nutrient relations by including a measure of euphotic depth or mixed depth (Verduin et al. 1978, Walker 1984). It was not possible to parallel these analyses, but thermal stratification can be transient in Missouri reservoirs and can affect the distribution and abundance of phytoplankton in the water column (Knowlton and Jones 1989a, 1990). Mixing patterns, therefore, contribute to the variable response of phytoplankton to phosphorus in turbid reservoirs and contribute to the variable response in Chl-TP relations within individual water-bodies.

Overall, this analysis is consistent with conclusions drawn by Duarte and Kalff (1989); the geographical setting influences lake chemistry and biology sufficiently that response of phytoplankton to phosphorus differs regionally. In Missouri, the Chl-TP relation is curvilinear primarily because of regional differences in TP and NVSS. These results suggest that accounting for NVSS can improve our ability to predict algal Chl in Missouri reservoirs and identify those most suited to management by nutrient control.

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