

Nutrients, seston, and transparency of Missouri reservoirs and oxbow lakes: An analysis of regional limnology

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Abstract

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A long-term (1978–2007) summer monitoring study of 167 Missouri reservoirs and floodplain lakes shows wide ranges in the trophic state variables total phosphorus (TP; 6–395 µg/L for reservoir means), total nitrogen (TN; 200–3290 µg/L), chlorophyll (Chl; 1–223 µg/L) and Secchi depth (0.15–4.3 m). There are strong regional contrasts between eutrophic-hypereutrophic water bodies in the predominantly agricultural Osage Plains, Glaciated Plains and Big Rivers sections and the mostly oligotrophic-mesotrophic reservoirs in the largely forested Ozark Highlands. The ecotonal Ozark Border was intermediate. Missouri reservoirs had slightly less TN relative to TP than predicted by global models, but TN:TP (median = 18.4) is typical of North American lakes and was about five-fold lower in the most enriched reservoirs compared to the least enriched ones. Concentrations of seston, measured as total suspended solids (TSS), volatile suspended solids (VSS), nonvolatile suspended solids (NVSS), filterable (small) suspended solids (fTSS) and the sum of all fractions (Σ TSS), were strongly correlated with TP, TN, and Secchi depth. The proportion of mineral seston (NVSS, fTSS) increased with TSS and was the dominant fraction in most reservoirs, especially in the agricultural regions. Phytoplankton was dominated by small forms (<11 µm), and Cyanophyta were the most common algae comprising a median 46% of phytoplankton biovolume. Chlorophyll-nutrient regressions showed a dominant effect of TP ($r^2 = 0.83$ for reservoir means) with a lesser, negative effect of mineral seston (NAS or fTSS, partial $r^2 \sim 0.05$). Secchi depth was more strongly controlled by mineral seston than by phytoplankton such that Secchi was a better predictor of nutrients (especially TP) than algal biomass. Frequency of algal blooms (Chl >10 µg/L) and Secchi <1 m increased sigmoidally with TP and TN with midrange nutrient concentrations (TP 20–50 µg/L, TN 400–700 µg/L) showing the greatest response to change. Trophic state criteria appropriate for Missouri reservoirs are similar to other north temperate lakes except for Secchi depth for which cutpoints are much lower because of nonalgal turbidity.

Key words: chlorophyll, Missouri, nutrients, oxbow lakes, regional limnology, reservoirs, seston, transparency

The geographic position of Missouri, in the mid-section of the conterminous United States, is located within the ecotonal zone at the intersection of the prairies and broad-leaved forests (Bailey *et al.* 1994). Reservoir impoundments are the principal lentic habitat in this region of the country (Thorn-ton *et al.* 1990). Most are recent additions to the landscape; about 90% of all Missouri reservoirs have been constructed over the past 50 years, and many are less than half that age. They vary in size from large reservoirs that serve as flood control and hydropower structures to small impoundments that provide municipal water, recreation and fish and wildlife propagation. There are also locally important karst, scour,

and oxbow lakes formed by natural processes (Knowlton and Jones 1997).

This paper updates an earlier summary of Missouri reservoir limnology (Jones and Knowlton 1993) by documenting nutrient content, seston composition, water clarity and trophic state in 167 water bodies considered representative of conditions within the major physiographic sections of the state. The analysis parallels regional lake studies conducted elsewhere in the mid-continent (Iowa: Jones and Bachmann 1978, Hatch 2003; Indiana: Spacie and Loeb 1990; Minnesota: Moyle 1956, Heiskary *et al.* 1987; Ohio: Fulmer and Cook 1990; Wisconsin: Lillie and Mason 1983) and emphasizes the

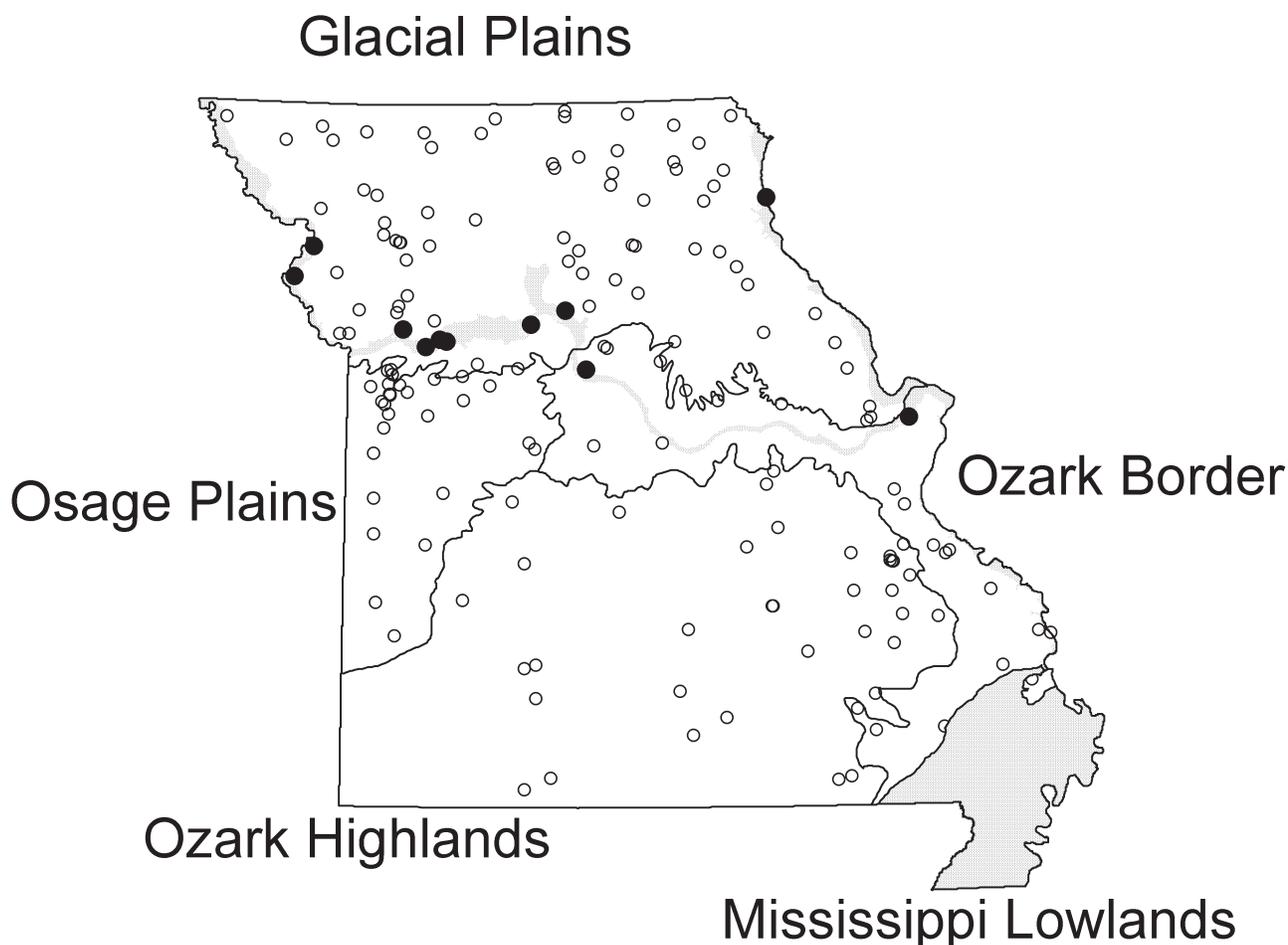


Figure 1.-Physiographic sections of Missouri and waterbodies included in this study. Open circles indicate reservoirs; filled circles indicate oxbow and scour lakes in the Big Rivers section which, along the Mississippi Lowlands is shaded to indicate alluvial topography.

influence of the geographic setting on water chemistry and phytoplankton (Duarte and Kalff 1989). In addition, empirical analyses are presented that identify key variables controlling algal biomass and water clarity within these water bodies. In this comprehensive synthesis we include data from oxbow and scour lakes in the Big Rivers physiographic section, not considered in the earlier summary. These water bodies are mostly natural floodplain lakes adjacent to the Mississippi and Missouri rivers, but without direct river connection. This assessment characterizes the current condition of lentic resources in Missouri and describes regional patterns. Information on regional limnology is of particular importance because of current interest in identifying the limiting nutrient and setting nutrient criteria consistent with indigenous conditions within the biogeographic regions of the country (Gibson *et al.* 2000).

Missouri ecological sections and land cover

The natural regions of Missouri have been described based on various environmental characteristics. Most recently, Nigh and Schroeder (2002) classified the distinct biogeographic regions of the state into four sections based on geomorphology, potential vegetation and major soil groups (Fig. 1): Ozark Highlands, Central Dissected Till Plains (referred to herein as the Glacial Plains), Osage Plains, and the Mississippi Alluvial Basin (the Mississippi Lowlands in Thom and Wilson 1980). This approach is generally consistent with the statewide classification system used previously (Jones and Knowlton 1993) wherein biogeographic units were referred to as provinces rather than sections. In this regional analysis we recognize the Ozark Border, an ecotonal area where the Ozark Highlands grades into neighboring sections (Thom and Wilson 1980), as a section rather than a subsection, which is the approach of Nigh and Schroeder (2002). This

Table 1.—Median land cover by physiographic section. Watershed data for floodplain lakes in the Big Rivers Section were not available.

Cover Type	Physiographic Section			
	Ozark Highlands	Ozark Border	Glacial Plains	Osage Plains
Crop	<1%	4%	26%	25%
Forest	51%	59%	15%	14%
Grass	27%	25%	34%	38%
Urban	3%	2%	3%	6%

analysis also recognizes the Big Rivers sections along the Missouri and Mississippi rivers (Thom and Wilson 1980), which contain naturally formed oxbow and scour lakes, classified by Nigh and Schroeder (2002) as river alluvial plain subsections.

Missouri has a continental climate with distinct seasons and a strong climatic gradient from the northwestern corner to the southeast corner of the state. Mean annual temperature and precipitation range from 11 °C and 86 cm in the northwest to 14 °C and 127 cm in the southeast (Nigh and Schroeder 2002).

Carbonate rocks, dolomites, and limestones dominate the Ozark Highlands with local areas of igneous rock and sandstone. Western and northern Missouri is composed mostly of limestone and shale formations. Weathered glacial till in northern Missouri is mostly a silty clay or clay with loess materials occurring locally. Residuum derived from bedrock forms much of the land surface south of the Missouri River, and in the plains of west-central Missouri the residuum is clay. Alluvium forms surficial material along the major rivers and is mostly silt or sandy silt (Nigh and Schroeder 2002).

Missouri is positioned centrally between the western grasslands and eastern forests. Northern Missouri was largely cleared for cropland during settlement, but over time cultivation of marginal farmland has been subsequently abandoned. Land cover currently is a mixture of cropland in low gradients and better soils, pasture on irregular areas and eroded soils, and second-growth forest on steeper slopes and rough land (Table 1). Land use history is similar in the Osage Plains, but less cropland has been converted to grass and timber. Cropland and pasture are more common in the western Ozarks than the more forested eastern Ozarks because the land is less dissected and soils somewhat better. Bottomlands in the Big Rivers section are highly productive croplands (Nigh and Schroeder 2002).

Reservoirs sampled in this study were selected to represent the range of conditions within the state and each section.

Delineations of the sections have shifted slightly since the previous summary (Jones and Knowlton 1993) and 14 reservoirs have shifted to different sections in this analysis. Most notably, Tywappity Reservoir (Table 2), formerly in the Mississippi Lowlands (Jones and Knowlton 1993) is located in an area of loess-covered hills (Crowley's Ridge) now designated as part of the Ozark Border (Nigh and Schroeder 2002). Some 300,000 ponds and small impoundments, mostly private, constructed throughout Missouri are not represented in this regional analysis.

Methods

This paper is based on monitoring data collected by the University of Missouri during summers 1978–2007. Typically, reservoirs (Fig. 1) were sampled on three or four occasions during May–August from a composited collection from the surface layer (0.25–0.5 m) at a site near the dam. Individual reservoirs are represented in the data set by collections ranging from 4 to 27 summer seasons; two-thirds of the systems were represented by collections from ≥ 8 seasons (mean = 11 seasons, median = 10 seasons). An analysis of temporal variation determined that collections in at least four summer seasons are needed to represent average conditions in a typical Missouri reservoir (Knowlton and Jones 2006a).

Transparency was measured with a standard 20-cm Secchi disk. Samples were transported on ice to a field laboratory and processed by standard methodology (Knowlton and Jones 1995). Analyses included measurements of algal chlorophyll (Chl; uncorrected for degradation products) with an additional estimate of pheophytin (Pheo), total phosphorus (TP), total nitrogen (TN), total suspended solids (TSS), volatile suspended solids (VSS), nonvolatile suspended solids (NVSS) and conductivity. Filterable suspended solids (fTSS; particles passing through the filters used in TSS analysis) were estimated nephelometrically (Knowlton and Jones 2000). Nonalgal suspended solids (NAS) were estimated as the sum of NVSS and fTSS. In some years Chl was measured on filtrates of water passed through 35- μm (nanoplankton) or 11- μm (ultraplankton) mesh Nitex® screens to assess algal size distribution. In 2002, absorption at 440 nm was measured on samples filtered through 0.2- μm membrane filters to estimate color of dissolved substances (Watanabe 2004). In 2000, surface samples from 60 reservoirs, preserved with Lugol's iodine, were composited over the four summer collections for microscopic determination of algal biomass with identification to genus. In 2003, samples from 63 reservoirs during mid-summer (2–30 July), preserved with glutaraldehyde, were similarly identified (Ann St. Amand, pers. comm.). This preservation allowed enumeration of picoplankton not counted in 2000. Lakes in the Big Rivers Section were not sampled for algal identification.

Table 2—Limnological parameters measured in 167 Missouri reservoirs during 1978-2007. Values are reservoir means for the period of record and are presented by ecological sections.

Section, Reservoir, (County)	Years Sampled	Chlorophyll	Total P µg/L	Total N	Volatile	Non-	Secchi Depth m	Conduc- tivity µS
					Solids	Volatile		
					mg/L			
Ozark Highlands (n=34)								
Austin (Texas)	11	6.8	20	555	2.4	1.0	1.5	110
Bismark (St. Francois)	8	6.2	21	380	1.2	0.8	1.7	122
Capri (St. Francois)	22	1.3	6	285	0.7	0.6	4.3	262
Carmel (St. Francois)	14	1.6	8	320	0.7	1.1	2.6	222
Clearwater (Wayne)	22	4.6	13	225	1.2	1.8	1.8	189
Council Bluff (Iron)	19	2.0	7	225	0.8	0.6	3.2	134
Crane (Iron)	7	4.1	13	240	1.5	2.3	1.2	52
Fellows (Greene)	20	4.1	12	325	1.2	0.9	2.6	220
Fourche Creek (Ripley)	12	2.1	9	235	1.0	0.7	3.1	301
Indian Hills (Crawford)	15	13.4	32	600	2.5	2.9	0.9	100
Killamey (Iron)	8	25.3	56	565	4.3	3.1	0.8	178
Lake of the Ozarks-Dam (Miller)	27	11.2	23	535	1.9	1.2	1.9	258
Little Prairie (Phelps)	22	7.6	26	470	1.6	3.0	1.0	84
Loggers (Shannon)	8	2.6	9	195	0.9	0.6	3.1	182
Lower Taum Sauk (Reynolds)	13	3.6	12	210	1.1	1.7	1.9	124
Marseilles (St. Francois)	13	1.6	9	330	0.8	0.8	3.4	248
McDaniel (Greene)	19	15.1	32	460	3.0	1.6	1.2	261
Miller Community (Carter)	12	6.9	20	500	2.3	1.3	1.4	47
Monsanto (St. Francois)	10	2.0	9	375	0.9	1.4	2.0	231
Noblet (Douglas)	8	2.0	11	210	0.8	0.6	2.6	280
Peaceful Valley (Gasconade)	14	16.1	30	730	3.3	1.5	1.3	161
Pomme de Terre (Hickory)	23	12.9	24	505	2.4	1.1	1.8	248
Ripley (Ripley)	10	10.9	24	600	2.7	0.8	1.5	48
Roby (Texas)	8	3.0	14	425	1.2	0.8	1.9	78
Shayne (Washington)	18	1.1	6	255	0.7	1.4	2.8	232
Sims Valley (Howell)	10	11.5	24	475	3.0	1.5	1.1	63
Springfield (Greene)	6	10.5	59	950	2.8	5.4	0.8	323
Stockton (Cedar)	23	5.7	11	385	1.2	1.0	2.9	245
Sunnen (Washington)	14	2.9	12	275	0.9	1.2	2.4	199
Table Rock (Taney)	23	4.1	9	365	1.2	0.7	3.3	198
Taneycomo (Taney)	9	2.5	21	705	0.8	1.3	2.6	213
Turner (Dent)	8	9.2	17	485	1.8	0.9	1.6	75
Wappapello (Wayne)	22	19.7	36	490	3.8	3.5	0.8	139
Ziske (Dent)	9	13.8	25	580	2.5	1.0	1.4	69
Mean	14.3	7.3	19	425	1.7	1.5	2.0	173
Median	13.0	5.2	16	405	1.2	1.2	1.9	186
Ozark Border (n = 22)								
Ann (Ste. Genevieve)	11	15.7	39	620	2.8	1.3	1.3	249
Bella Vista (Cape Girardeau)	8	8.1	23	515	2.0	1.8	1.3	149
Binder (Cole)	21	22.7	52	775	3.8	2.8	0.9	289
Boutin (Cape Girardeau)	8	6.6	21	560	1.8	1.4	1.6	66
D.C.Rogers (Howard)*	14	7.0	29	525	2.1	3.6	1.2	223
Fayette (Howard)*	9	13.7	39	765	3.3	3.8	0.9	181
Fredricktown City (Madison)	11	26.2	59	675	4.7	4.2	0.7	208
Girardeau (Cape Girardeau)	11	31.5	51	790	5.1	2.1	0.8	94
Glover (Callaway)	7	15.3	58	850	4.2	2.8	1.0	242
Goose Creek (Ste. Genevieve)	11	3.0	12	385	1.0	1.5	2.1	213
Manito (Moniteau)	8	12.8	90	960	2.2	4.1	0.6	84
Northwoods (Gasconade)	13	3.8	21	440	1.3	2.6	1.1	78
Perry County (Perry)	10	35.7	67	890	5.7	2.6	0.8	204
Pinewoods (Carter)	6	15.3	33	735	3.8	0.9	1.3	35
Pinnacle (Montgomery)	7	4.7	19	490	1.4	1.5	1.8	193
Rocky Fork (Boone)	8	5.7	21	540	1.7	1.4	1.8	669

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Table 2-Continued

Section, Reservoir, (County)	Years Sampled	Chlorophyll	Total P µg/L	Total N	Volatile	Non-	Secchi Depth m	Conduc- tivity µS
					Solids	Volatile		
					mg/L			
Timberline (St. Francois)	14	1.5	7	275	0.6	0.6	4.0	241
Tishomingo (Jefferson)	12	4.2	20	480	1.1	1.4	1.7	242
TriCity (Boone)	15	14.6	43	795	3.4	5.0	0.8	103
Tywappity (Scott)	9	33.0	47	1060	5.7	2.1	0.8	62
Wanda Lee (Ste. Genevieve)*	10	15.7	46	600	3.3	2.2	1.1	238
Wauwanoka (Jefferson)	13	2.5	12	375	0.8	1.1	2.7	280
Mean	10.7	13.6	37	640	2.8	2.3	1.4	197
Median	10.5	13.3	36	610	2.5	2.1	1.2	206
Glacial Plains (n = 73)								
Allaman (Clinton)	6	11.6	39	655	3.5	2.7	1.1	269
Baring Country Club (Knox)	9	14.1	27	915	3.5	2.7	1.2	242
Belcher Branch (Buchanan)	6	14.6	35	565	2.3	3.1	1.1	250
Bethany (Harrison)	14	8.0	29	655	2.2	3.2	1.2	216
Bilby Ranch (Nodaway)	9	33.7	51	1005	5.3	2.5	0.9	226
Blind Pony (Saline)	17	25.1	75	1150	4.2	5.1	0.6	197
Bowling Green (Pike)	20	6.2	21	500	1.6	1.3	1.9	217
Brookfield (Linn)	21	7.4	22	610	2.0	3.5	1.2	190
Busch 37 (St. Charles)	4	8.0	26	505	1.9	2.6	1.2	110
Cameron #1 (DeKalb)	7	37.0	178	1445	6.9	15.7	0.4	253
Cameron #2 (DeKalb)	7	23.5	53	785	4.5	5.0	0.7	282
Charity (Atchison)	4	14.8	39	615	3.0	2.0	1.3	417
Deer Ridge (Lewis)	22	12.2	38	740	2.8	2.7	1.0	128
Edina City (Knox)	12	18.4	64	1230	4.3	6.2	0.6	199
Ella Ewing (Scotland)	9	22.2	79	1295	4.9	5.6	0.5	170
Elmwood (Sullivan)	10	17.6	52	770	3.1	4.0	0.7	199
Forest (Adair)	24	4.5	22	415	1.3	3.2	1.3	263
Fox Valley (Clark)	8	6.6	18	590	1.5	0.7	2.3	153
Green City (Sullivan)	8	24.2	71	1025	4.6	5.4	0.6	147
Grindstone (DeKalb)	6	26.7	141	2195	5.6	8.9	0.4	242
Hamilton City (Caldwell)	12	13.5	55	955	3.5	4.5	0.8	219
Harrison County (Harrison)	9	41.2	59	1090	5.6	2.5	0.8	190
Hazel Creek (Adair)	14	7.3	27	595	1.9	3.3	1.2	217
Henry Sever (Knox)	22	14.3	44	930	2.8	3.3	0.9	130
Higginsville (Lafayette)	21	20.6	83	1055	3.9	7.9	0.6	296
Hunnewell (Shelby)	22	16.4	41	775	2.9	3.1	0.9	111
Indian Creek (Livingston)	5	11.3	23	625	2.3	1.0	1.6	199
King (DeKalb)	6	18.7	189	1525	6.4	23.9	0.2	207
Kraut Run (St. Charles)	19	57.7	96	1090	8.9	5.9	0.4	190
LaBelle (Lewis)	6	47.8	60	1350	7.7	2.1	0.7	184
Lake St. Louis (St. Charles)	8	18.2	63	910	4.1	9.9	0.5	235
Lancaster (Schuyler)	5	32.7	70	955	6.4	3.3	0.7	198
LaPlata (Macon)	5	13.4	26	785	3.1	2.4	1.1	166
Lawson City (Ray)	4	22.3	33	935	4.9	2.9	0.9	202
Limpp (Gentry)	4	63.6	105	1430	10.3	9.4	0.4	270
Lincoln (Lincoln)	21	4.3	16	405	1.4	1.4	2.1	205
Little Dixie (Callaway)	26	16.9	55	740	3.0	4.7	0.7	118
Long Branch (Macon)	25	11.7	45	885	2.3	5.3	0.7	174
Macon (Macon)	13	22.2	51	865	4.1	4.2	0.7	195
Maple Leaf (Lafayette)	7	18.7	38	825	3.0	2.3	1.1	227
Marie (Mercer)	11	3.6	14	445	1.3	1.4	2.6	185
Mark Twain (Ralls)	20	14.6	54	1195	2.3	3.0	0.9	193
Maysville (DeKalb)	12	38.7	162	1275	6.1	5.3	0.6	257
Memphis City (Scotland)	11	37.4	75	1205	7.1	6.9	0.5	209
Moberly (Randolph)*	14	18.4	49	740	3.5	5.3	0.8	248

Table 2-Continued

Section, Reservoir, (County)	Years Sampled	Chlorophyll	Total P µg/L	Total N	Volatile Solids mg/L	Non-Volatile Solids	Secchi Depth m	Conductivity µS
Monroe City (Monroe)	13	28.1	77	1105	5.6	9.1	0.5	174
Monzingo (Nodaway)	9	20.5	31	855	3.5	1.8	1.3	228
NehaiTonkayea (Chariton)	14	2.5	14	400	1.0	2.3	1.8	177
New Marceline (Chariton)	11	28.8	83	1030	5.0	3.9	0.7	148
New Milan (Sullivan)	10	11.0	38	670	2.6	3.4	1.0	196
Nodaway County (Nodaway)	9	21.4	44	970	4.0	5.1	0.8	228
Old Marceline (Linn)	4	31.4	83	1115	4.5	3.5	0.7	149
Paho (Mercer)	16	11.8	50	905	2.8	6.5	0.6	163
Pape (Lafayette)	14	21.1	67	980	3.9	8.0	0.6	222
Pony Express (DeKalb)	15	27.4	64	965	4.2	4.7	0.7	175
Ray County (Ray)	4	114.3	152	1920	13.8	3.8	0.4	151
Savannah City (Andrew)	4	17.3	38	765	3.1	2.7	1.2	358
Shelbina (Shelby)	10	30.8	96	1060	5.7	6.5	0.5	203
Smithville (Clay)	22	15.3	34	780	2.6	3.7	1.0	246
Spring (Adair)	14	6.4	26	520	1.7	3.0	1.3	229
Sterling Price (Chariton)	9	53.6	93	1415	8.9	3.7	0.5	168
Thomas Hill (Randolph)	18	12.8	46	760	2.6	8.6	0.6	290
Thunderhead (Putnam)	14	13.3	44	915	2.8	6.0	0.7	216
Unionville (Putnam)	12	32.7	93	1185	5.2	6.5	0.6	278
Vandalia (Audrain)	15	22.4	58	905	3.9	3.1	0.9	156
Viking (Daviess)	20	8.1	25	500	1.8	3.2	1.2	237
Watkins Mill (Clay)	20	16.4	39	610	3.1	4.0	0.8	243
Waukomis (Platte)	10	11.4	25	545	2.3	2.2	1.4	343
Weatherby Lake (Platte)	5	4.1	16	385	1.6	2.0	2.0	277
Whiteside (Lincoln)	4	6.1	19	640	1.4	0.4	2.4	120
Williams (Clay)	9	22.3	68	880	5.1	7.8	0.6	316
Willow Brook (DeKalb)	5	35.8	75	1095	6.1	5.7	0.6	235
Worth County (Worth)	4	29.9	62	1240	5.8	2.6	0.7	178
Mean	11.8	21.6	57	910	4.0	4.6	0.9	212
Median	10.0	18.2	50	905	3.5	3.5	0.8	205
Osage Plains (n = 27)								
Amarugia Highlands (Cass)	8	10.2	45	670	2.4	3.8	0.7	155
Atkinson (St. Clair)	19	31.0	69	985	5.0	8.9	0.5	159
Blue Springs (Jackson)	4	16.1	35	570	2.9	3.4	1.1	286
Bushwacker (Vernon)	5	12.6	28	625	2.2	2.0	1.2	113
Butler City (Bates)	5	35.0	68	885	5.2	4.6	0.7	245
Cottontail (Jackson)	4	12.6	149	1050	6.6	35.9	0.2	175
Gopher (Jackson)	4	14.9	94	715	4.0	14.4	0.3	181
Harmony Mission (Bates)	8	19.3	44	815	3.2	2.0	1.0	160
Harrisonville (Cass)	10	15.7	47	845	3.4	4.9	0.8	253
Hazel Hill (Johnson)	8	33.7	49	990	5.1	3.3	0.7	197
Holden City (Johnson)	7	15.5	40	930	3.0	5.1	0.7	160
Jacomo (Jackson)	10	16.6	30	545	2.6	2.4	1.2	301
Lamar City (Barton)	12	39.9	73	950	6.2	1.7	0.7	154
Lone Jack (Jackson)	4	13.8	27	640	2.9	1.0	1.7	189
Longview (Jackson)	8	10.6	32	670	2.5	6.1	0.8	293
Lotawana (Jackson)	11	15.0	31	620	2.6	2.5	1.3	318
Montrose (Henry)	15	56.3	152	1125	9.2	33.2	0.3	470
Nell (Jackson)	4	12.9	78	690	3.7	13.4	0.3	159
North Lake (Cass)	19	35.9	97	995	5.3	4.5	0.7	221
Odessa (Lafayette)	4	21.4	38	855	3.9	1.9	1.2	195
Prairie Lee (Jackson)	9	20.9	50	900	4.4	6.4	0.7	315
Raintree (Cass)	21	10.6	50	835	2.9	7.6	0.5	230
Spring Fork (Pettis)	13	42.6	139	1070	5.9	4.8	0.6	157

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Table 2-Continued

Section, Reservoir, (County)	Years Sampled	Chlorophyll	Total P µg/L	Total N	Volatile Solids mg/L	Non- Volatile Solids	Secchi Depth m	Conduc- tivity µS
Tapawingo (Jackson)	10	21.8	33	740	4.5	2.2	1.2	299
Truman (Benton)	24	14.9	37	745	2.4	3.2	1.1	263
Westmoreland (Pettis)	7	5.8	21	600	1.7	0.6	1.9	128
Winnebago (Cass)	12	17.5	44	810	3.2	4.5	0.7	236
Mean	9.8	21.2	59	810	4.0	6.8	0.8	223
Median	8.0	16.1	45	815	3.4	4.5	0.7	197
Big Rivers (n = 11)								
Contrary (Buchanan)	5	223.4	392	3290	30.9	16.9	0.2	433
Cooley (Clay)	4	51.4	260	1755	11.0	29.9	0.3	316
Creve Couer (St. Louis)	7	50.3	148	1020	9.4	20.4	0.3	388
Dalton Cutoff (Chariton)	4	97.3	395	2410	21.4	59.1	0.2	237
NC-8 (Howard)	4	26.5	88	720	5.4	13.5	0.4	314
NC-16 (Ray)	4	25.5	61	630	4.5	8.7	0.6	556
NC-17 (Ray)	4	24.8	64	700	4.8	12.0	0.5	414
Sugar (Buchanan)	5	161.3	332	2430	22.4	36.3	0.2	400
Sunshine (Ray)	4	99.9	348	1990	20.5	73.9	0.2	434
Teteseau (Saline)	4	78.9	225	1330	11.3	25.1	0.3	691
Wakonda (Lewis)	9	41.6	81	1060	7.1	3.1	0.7	280
Mean	4.9	80.1	218	1575	13.5	27.2	0.4	406
Median	4.0	51.4	225	1330	11.0	20.4	0.3	400
Statewide (n = 167)								
Mean	11.4	21.4	58	805	4.0	5.5	1.2	217
Median	10.0	15.0	39	740	3.0	3.1	0.9	208

** Name changed since publication of Jones and Knowlton (1993). DC Rogers formerly Fayette Lower, Fayette formerly Fayette Upper, Moberly formerly Sugar Creek, and Wanda Lee formerly Rocky Ridge.”

Certain analyses are based on individual measurements from samples collected over the period of record. Most assessments, however, are based on reservoir means calculated as the geometric mean averaged within each summer of record and then averaged across all seasonal means for each of the 167 water bodies in the data set (Fig. 1). Land-use data describing reservoir catchments are based on 30-m imagery from the LANDSAT thematic mapper developed by the Missouri Resource Assessment Partnership (James Harlan, pers. comm.). Land cover was not compiled for oxbows and scour ponds in the Big Rivers Section because watershed boundaries are poorly defined in river floodplains. For parsimony, we refer to lentic systems in this analysis as reservoirs while recognizing that oxbows and scour ponds are not impoundments. Data analyses including correlation and regression (simple, multiple, and stepwise) and one-way analysis of variance (ANOVA) were performed using log₁₀-transformed data. Regression results include coefficients of determination (r²) and root mean squared error (RMSE) as measurements of goodness of fit. Statistical analyses were conducted using SPSS (v.13) and SAS (v.9.1).

Results

Nutrients

In this large data set from Missouri reservoirs, mean values of TP ranged from 6 to 395 µg/L and TN ranged from 200 to 3290 µg/L (Table 2). Median values were 39 µg/L TP and 740 µg/L TN, and the inter-quartile ranges for these two elements were 23–67 µg/L TP and 520–970 µg/L TN. In multiple regression analyses, the simple metrics of latitude and longitude, identifying reservoir location within the state, account for about a quarter of cross-system variation in TP_{log} and a third of TN_{log} variation. Statewide, both nutrients increase in reservoir systems along a gradient toward the north and west (Fig. 1 and 2). These trends parallel the pattern of land cover (Table 1). Cropland increases along this axis (r² = 0.26, Big Rivers excluded), whereas forest cover declines (r² = 0.50). Grass cover increases toward the west in Missouri without a significant north-south gradient.

As a group, reservoirs in the Ozark Highlands had the lowest nutrient levels within the state (Table 2; Fig. 2a and 2b);

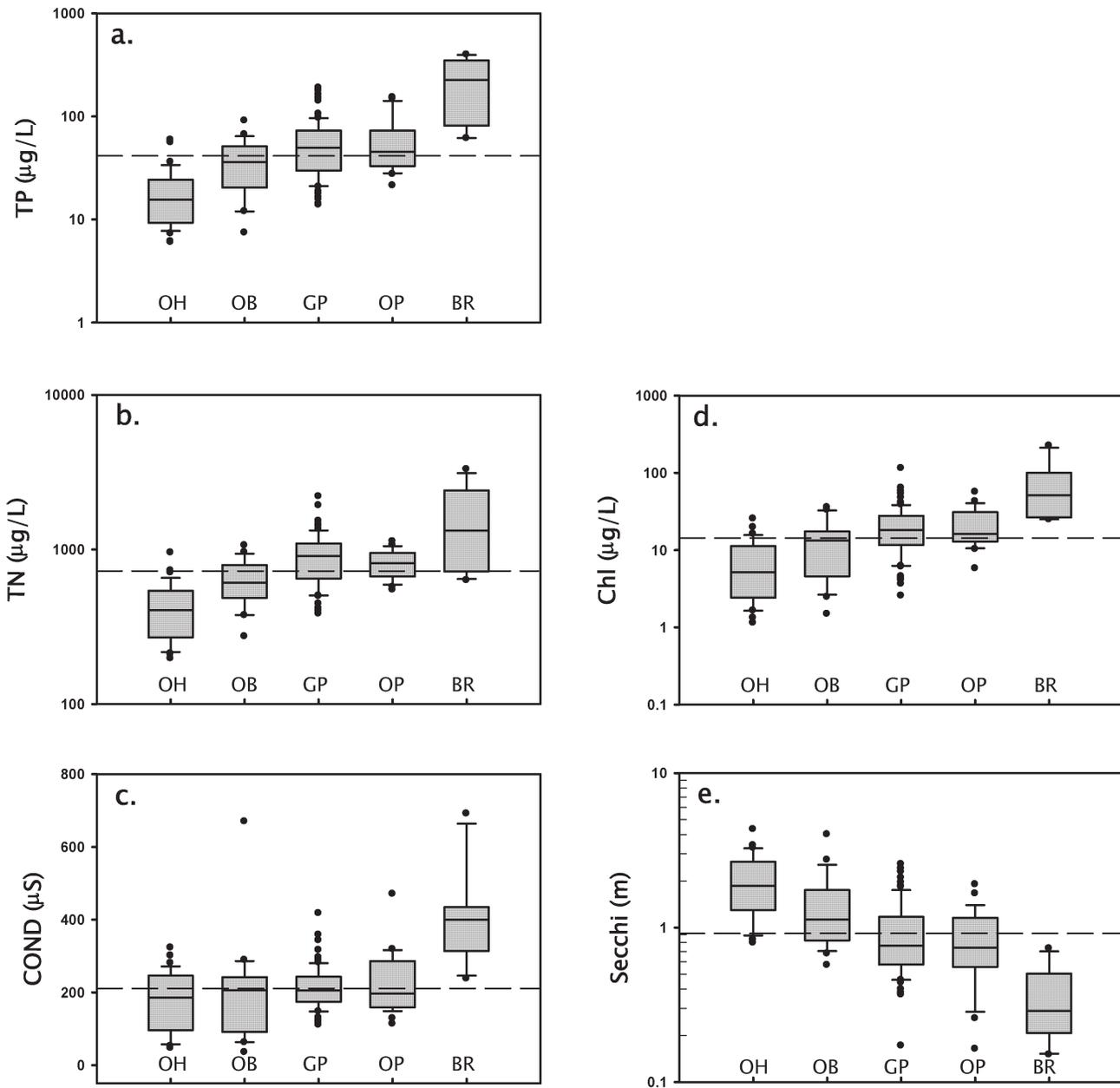


Figure 2.-Distributions, by section, of reservoir mean values of TP, TN, conductivity, Chl, and Secchi depth. Boxes span the 25th to 75th percentiles with a central line marking the median. “Whiskers” above and below boxes mark the 10th and 90th percentiles, and dots mark individual outliers. Horizontal dashed lines are statewide medians.

median values were 16 $\mu\text{g/L}$ TP and 405 $\mu\text{g/L}$ TN, with >90% of the values less than the statewide median for these nutrients. The largest nutrient concentrations were among oxbow and scour lakes in the Big Rivers section (Fig. 2a and 2b), wherein median values were 225 $\mu\text{g/L}$ TP and 1330 $\mu\text{g/L}$ TN. Most nutrient values in the Big Rivers section exceeded the statewide median for both elements (Table 2). For reservoirs in the ecotonal Ozark Border section, the median values were somewhat less than statewide medians

(Fig. 2a and 2b). Nutrients were more variable among Glacial Plains reservoirs than in the Osage Plains, but median values were similar in these two prairie sections; among all Plains reservoirs >63% of mean values exceeded the statewide medians for nutrients.

As demonstrated in other regional studies and in global data sets (Downing and McCauley 1992, Nürnberg 1996), TN_{\log} was positively related to TP_{\log} among reservoir mean values

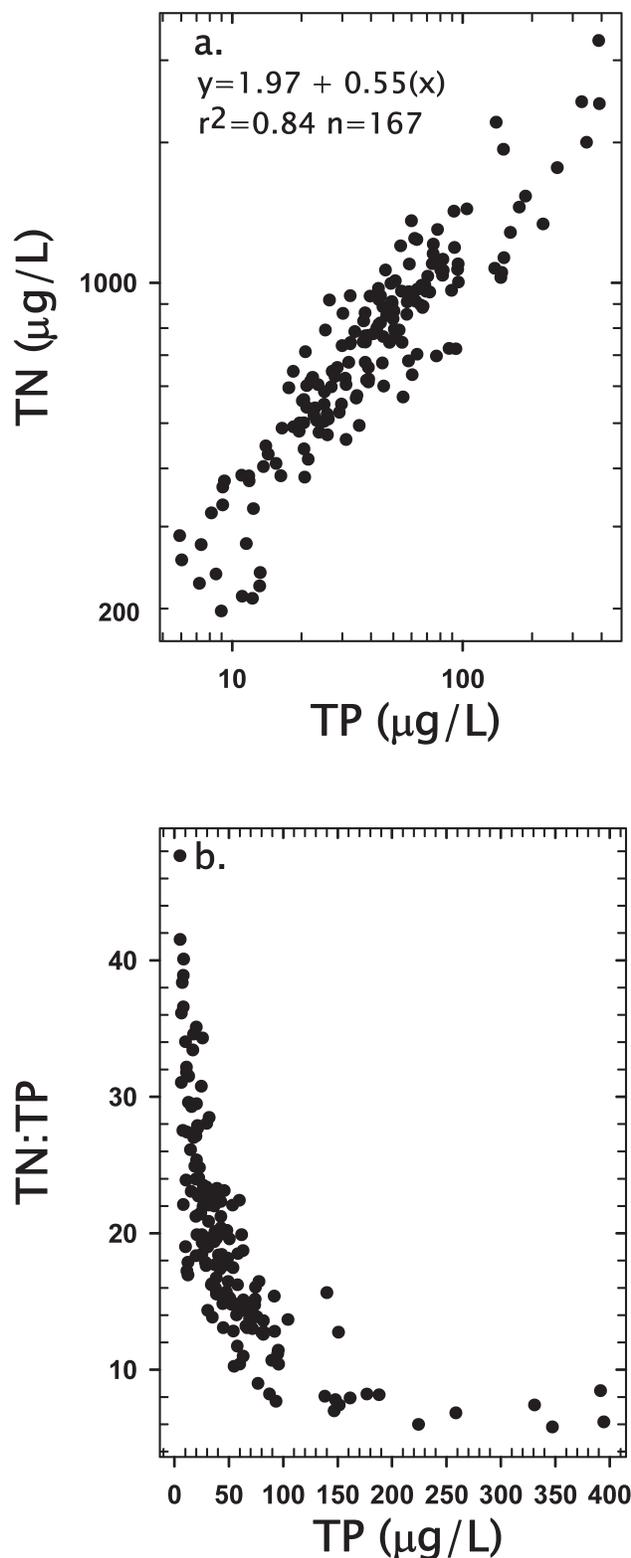


Figure 3.-Relation of TN and TN:TP to TP for reservoir mean data sets.

(Fig. 3a; $r^2 = 0.84$). The slope of the relationship is ~ 0.5 , indicating the increase in P is greatly accelerated relative to increases in N. Because of this pattern the TN:TP ratio in Missouri reservoirs declines sharply with TP (Fig. 3b). The overall median TN:TP ratio was 18.4 for reservoir means, but median values varied from 37.9 among reservoirs with $<10 \mu\text{g/L}$ TP, to 25.6 with TP 10–25 $\mu\text{g/L}$, to 16.7 with TP 25–100 $\mu\text{g/L}$, and 7.5 where TP $>100 \mu\text{g/L}$. Among individual samples ($n = 6856$) about half the TN:TP ratios were <20 and some 10% were <10 .

Jones and Knowlton (1993) suggested TN values were low in Missouri reservoirs relative to other temperate lakes, resulting in low TN:TP ratios. The equation relating TN to TP concentrations for North American lakes by Nürnberg (1996; $\text{TN}_{\log} = 1.99 + 0.538(\text{TP}_{\log})$) predicts TN values virtually identical to the observed measurements (mean of observed to predicted = 1.06, median = 1.00, $n = 6856$). Nürnberg's TN equation for lakes located world wide (1996; $\text{TN}_{\log} = 2.1 + 0.492(\text{TP}_{\log})$), however, predicts slightly larger TN values than measured in Missouri reservoirs (mean of observed to predicted = 0.97, median = 0.91, $n = 6856$). Among Missouri reservoirs the median shortfall in TN was some 60 $\mu\text{g/L}$ when compared with Nürnberg's world equation, which equates to 16% of observed TN for reservoirs with TP $\leq 25 \mu\text{g/L}$ and only 6% among reservoirs with 25–100 $\mu\text{g/L}$ TP. This comparison broadly suggests TN is slightly depressed in Missouri reservoirs, particularly among the least productive systems. The two TN-TP equations of Nürnberg predict median TN:TP ratios of 18.7 (North America) and 20.4 (World) for the overall data set, both estimates are similar to observed medians of 18.8 for unaveraged data and 18.4 for reservoir means.

Conductivity

Conductivity varied nearly 20-fold across the data set (35–691 μS ; Fig. 2c) with the largest values in the Big Rivers lakes and values mostly between 100 and 250 μS in the other sections. Unlike many lake districts, cross-system correlations between conductivity and plant nutrients were modest within the Missouri data set ($r = 0.36$ for TP and 0.24 for TN, $n = 167$) and were not statistically significant ($p > 0.05$) when the Big Rivers lakes ($n = 11$) were omitted.

Seston composition

Mineral seston ($\text{NAS} = \text{NVSS} + \text{fTSS}$) is a feature of water quality in many Missouri reservoirs (Knowlton and Jones 2000, Jones and Knowlton 1993, 2005a). Statewide, the median NVSS value, a measure of particulates retained on a glass fiber filter, was 3.1 mg/L, and reservoir means ranged between 0.4 and 73.9 mg/L (Table 2). Among the sections, NVSS was least in the Ozark Highlands (Fig. 4a) where most values were between 1 and 3 mg/L. In contrast, values

were an order of magnitude larger among Big River lakes where measurements were typically >14 mg/L. Except for a few turbid reservoirs in both Plains sections, most (~80%) remaining reservoirs had NVSS between 2 and 6 mg/L (Fig. 4a), which is two to five times the concentration of a typical reservoir in the Ozark Highlands.

Nonvolatile suspended solids averaged 66% of total mineral seston in our samples (NVSS/NAS; Fig. 5a; median 69%, $n = 4982$), and the inter-quartile range of the proportion was 55–80%. Based on this distribution fTSS, the filterable (small) fraction of NAS, accounted for >30% of the weight of mineral seston in half of our samples. Half of fTSS measurements were >1 mg/L, and 25% were >2 mg/L. Among reservoir means, the median fTSS was 1.2 mg/L (Fig. 4b; range 0.4–19.3 mg/L); across sections, median values increased by more than three-fold between the Ozark Highlands (0.7 mg/L) and Big Rivers (2.6 mg/L). The two metrics NVSS_{log} and fTSS_{log} were strongly correlated ($r = 0.80$, as reservoir means), and both were strongly correlated with NAS_{log} ($r = 0.98$ for NVSS_{log} and 0.89 for fTSS_{log}). Likewise, these measures of mineral seston are strongly correlated with TP_{log} (Fig. 6; $r \geq 0.70$); by comparison, correlations with TN_{log} were consistently weaker (Fig. 6). Among individual samples, NAS_{log} was negatively correlated with TN:TP_{log} ($r = -0.64$) indicating mineral seston is associated with enriched, low TN:TP systems.

Among reservoir means, about half the material composing TSS was in the NVSS fraction (median and mean = ~51%, inter-quartile range = 41–60%, $n = 167$), and there was a general increase in the proportion of NVSS (%) with increasing TSS_{log} ($r = 0.40$). Within the geographic sections, %NVSS ranged from an average of 45% in the Ozark Highlands to 63% in the Big Rivers.

Volatile seston (VSS_{log}) was strongly correlated with TSS_{log} ($r = 0.92$, $n = 167$) and NVSS_{log} ($r = 0.80$, $n = 167$) and showed the same inter-sectional pattern as NVSS (Fig. 4c). Statewide median VSS was 3.0 mg/L but ranged from 1.2 mg/L in the Ozark Highlands to 11.0 mg/L among lakes in the Big Rivers (Fig. 4c). In the Ozark Border and Plains sections VSS was typically two to three times values in the Ozark Highlands. Both VSS_{log} and TSS_{log} were strongly correlated with TP_{log} and less so with TN_{log} (Fig. 6; $r \geq 0.94$ for TP and ≥ 0.86 for TN); TSS and the sum of TSS and fTSS (Σ TSS; our estimate of all particles in the seston; Fig. 6) were also strongly correlated with both nutrients.

Algal chlorophyll and taxa

Reservoir mean Chl values in Missouri ranged from 1 to 223 $\mu\text{g/L}$ with a median of 15 $\mu\text{g/L}$ (Table 2) and an inter-quartile range of 7 to 25 $\mu\text{g/L}$. Across this distribution, low values were most common in the Ozark Highlands where the median

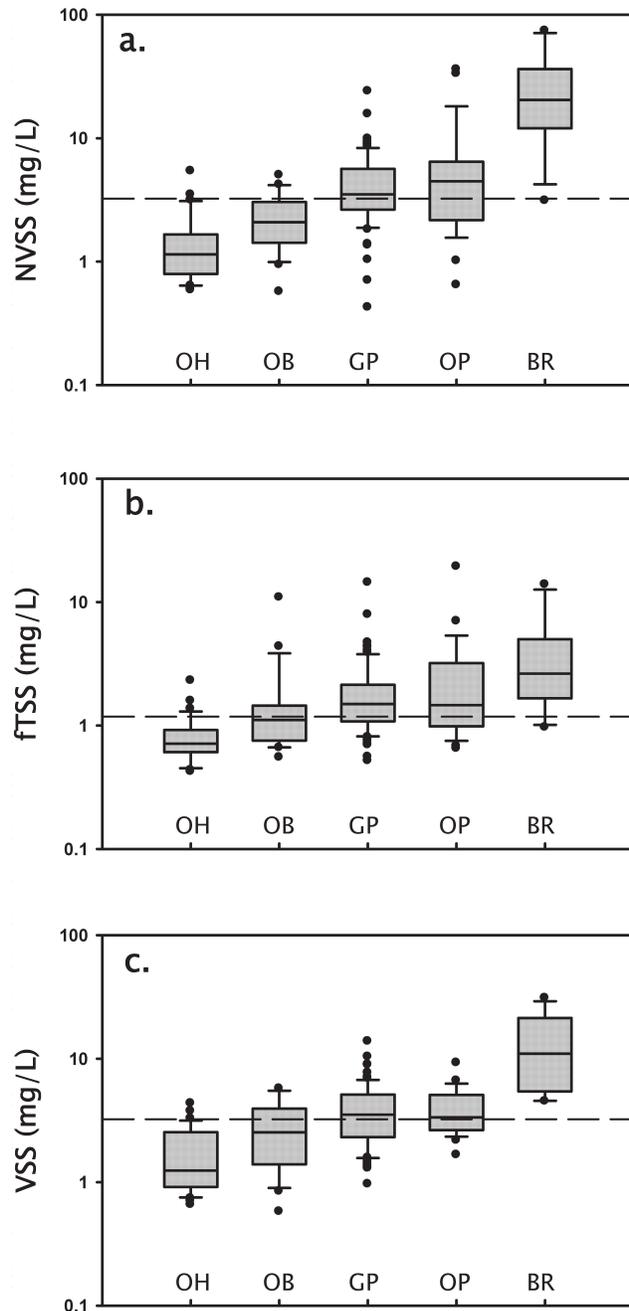


Figure 4.—Distributions, by section, of reservoir mean values of nonvolatile suspended solids (NVSS), filterable suspended solids (fTSS) and volatile suspended solids (VSS).

was 5.2 $\mu\text{g/L}$ and 88% of reservoir mean Chl values were smaller than the statewide median (Fig. 2d). In contrast, in the Big Rivers section the median was 51 $\mu\text{g/L}$ and reservoir mean Chl values uniformly exceeded the statewide median. Within the Ozark Border and Plains sections, median Chl closely matched the statewide value and were two to three times the typical value in the Ozark Highlands (Fig. 2d).

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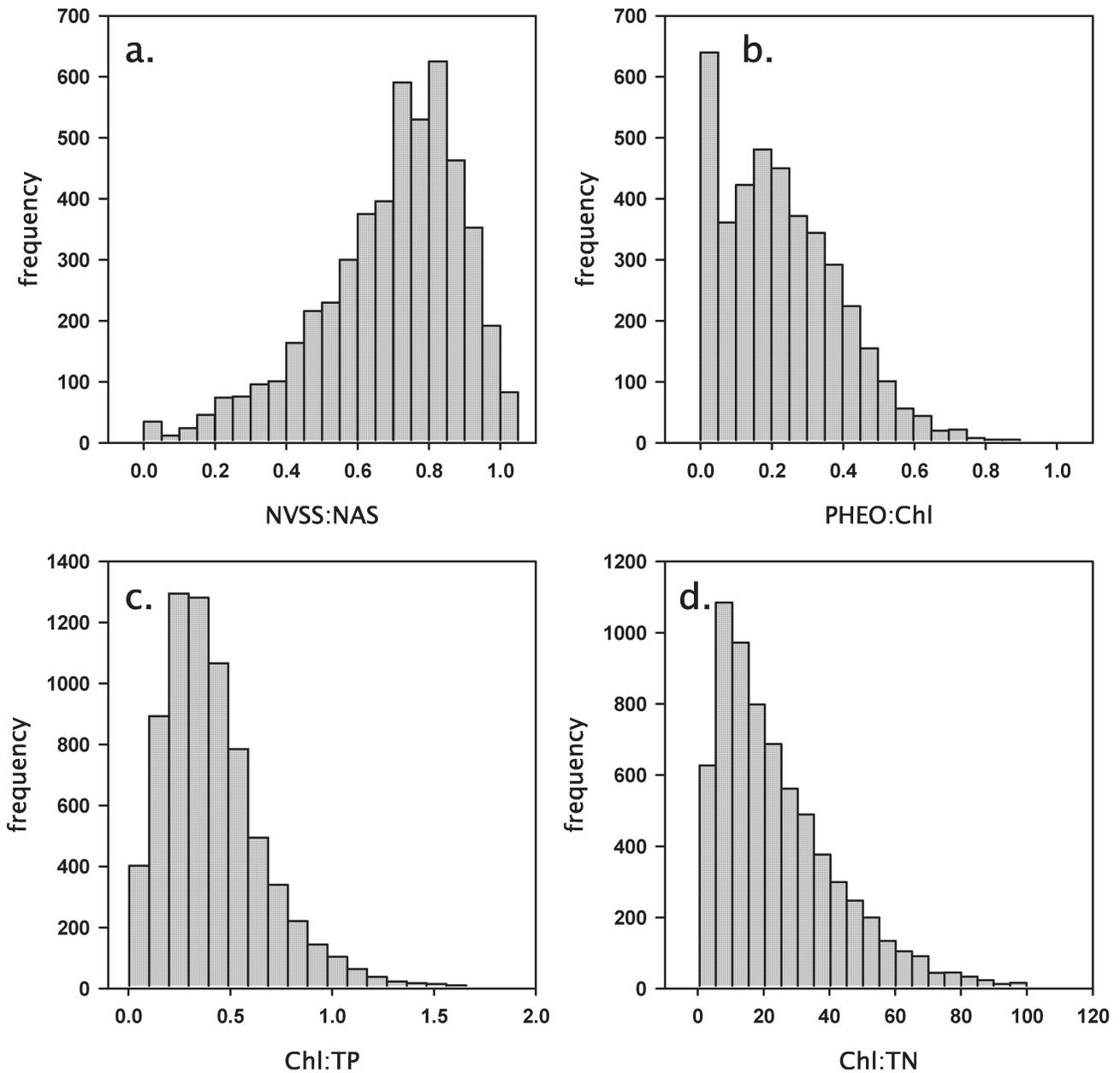


Figure 5.-Frequency distributions of ratios described in the text: NVSS:NAS ($n = 4982$); Pheo:Chl ($n = 4021$); Chl:TP ($n = 7225$); and Chl:TN ($n = 6876$) in individual observations. Off-scale outliers are not shown in b ($n = 14$, $\text{max} = 2.1$), c ($n = 12$, $\text{max} = 3.7$) and d ($n = 9$, $\text{max} = 240$).

Individual Chl measurements in the data set ranged from <1 to $680 \mu\text{g/L}$ ($n = 7265$), and among the 145 reservoirs with ≥ 20 samples (>5 summer seasons) the maximum Chl observed averaged 26 times the minimum (median = 18, range 4–135). In these intensively sampled reservoirs, maximum Chl was strongly related to the reservoir mean ($r^2 = 0.67$, $n = 145$) with a slope of 4.3, and the mean of the top two Chl values in each reservoir was also strongly related to the reservoir mean with a slope of 3.9 ($r^2 = 0.74$). In both cases

the intercepts were nonsignificant, so the maximum algal biomass can reasonably be estimated arithmetically at about four times the reservoir mean.

Pheophytin was measured in over half our Chl samples (Fig. 5b; $n = 4021$), and this degradation pigment averaged 23% of uncorrected Chl (median = 21%, range from 0 to 209%). The inter-quartile range was 10–34% with values $>60\%$ in 3% of samples.

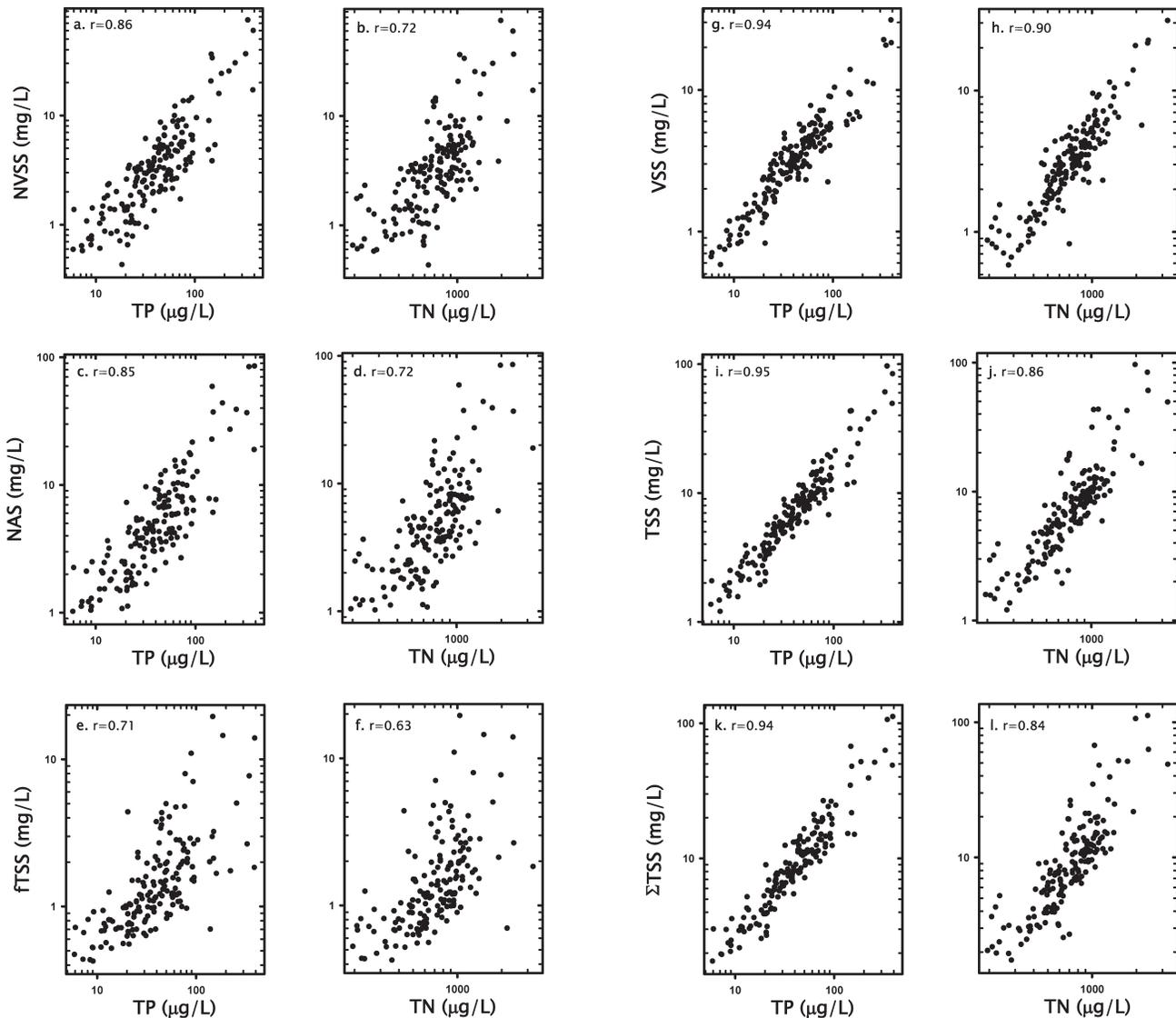


Figure 6.—Relations of the seston components NVSS, NAS, fTSS, VSS, TSS, and Σ TSS (abbreviations described in the text) to plant nutrients (TP and TN) using the reservoir mean data set ($n = 163$). Four reservoirs lack fTSS, NAS and Σ TSS data.

Algal Chl in Missouri reservoirs is primarily contained in small algae, measured as ultraplankton ($<11 \mu\text{m}$) or nanoplankton ($<35 \mu\text{m}$). On average, ultraplankton accounted for 72% of algal Chl (median = 75%, $n = 2182$), but individual values ranged from 6% to unity. In samples where both fractions were measured ($n = 479$), ultraplankton averaged 69% and nanoplankton 83% of algal Chl; this result suggests an average of 17% of Chl was $>35 \mu\text{m}$ and about 14% was in the 11–35 μm fraction. Statewide, percent ultraplankton Chl was not strongly correlated with nutrients but showed a weak negative correlation with latitude ($r = -0.28$) and weak positive correlation with lake area ($r = 0.28$). This result suggests the abundance of algal taxa $>11 \mu\text{m}$ increases slightly

among small and moderate reservoirs located in the northern region of the state.

Biomass of the major algal divisions increased across the range of Chl values during summer 2000, except for Chrysophyta (Table 3). In this data set Chl values were strongly related to total phytoplankton biovolume ($\text{Chl}_{\log} = 0.876 \cdot \text{BioVol}_{\log} - 4.24$, $r^2 = 0.80$, $n = 60$, biovolume as $\mu\text{m}^3/\text{mL}$). The average Chl content, at $\sim 1\%$ of wet weight, is close to the average (0.94%) for 17 taxa presented by Reynolds (1984). As a proportion (%) of total summer biomass, the dominant taxonomic division was the Cyanophyta (median 46%, range <0.1 –95%) with Bacillariophyta ranked second (median 17%, range 0–76%), but each major division ranked

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Table 3.—Proportion of phytoplankton (as % of total biomass) in major algal taxonomic divisions in Missouri reservoirs during summer 2000 (n = 60 reservoirs) and correlation (r) of biomass to seasonal mean Chl (both variables log₁₀-transformed; “n.s.” = p > 0.05). Values of “n” show the number of reservoirs in which at least one member of each division occurred.

Division	n	Median	Mean	25%	75%	Max.	r
Bacillariophyta	59	17	24	6	38	76	0.59
Chlorophyta	60	6	8	3	11	47	0.83
Chrysophyta	50	1	6	<1	4	91	n.s.
Cryptophyta	60	6	8	3	10	43	0.71
Cyanophyta	60	46	44	20	68	95	0.70
Pyrrhophyta	53	2	8	<1	10	59	0.31
Miscellaneous	54	<1	2	<1	2	20	0.38

first in biomass in at least one reservoir (Table 3). A median of 26 algal genera (range 15–37) were observed in individual reservoirs. Twenty algal genera were common enough to be dominants (representing at least 20% of the total biovolume) in one or more reservoirs. Among these taxa, the Cyanobacteria *Anabaena* and *Cylindrospermopsis* were dominants in 13 and 12 reservoirs, respectively, followed by cyanobacterium *Aphanizomenon* (8 reservoirs) and diatoms *Stephanodiscus* (8 reservoirs) and *Cyclotella* (7 reservoirs). In six reservoirs no single genus made up >20% of total biomass. Dominant taxa were typically limited to one (33 reservoirs) or two (22 reservoirs) genera.

In 2003, picoplankton (<2 μm) were numerically dominant in most reservoirs, comprising a median 81% of counts (range 24–99%). Cyanobacteria *Synechococcus* (median 1.2 μm), *Synechocystis* (median 1.5 μm) and unknown unicellular cyanobacteria (family Chroococcaceae, median 0.8 μm) were the only picoplankton taxa observed. These algae typically composed <2% of total biovolume (median 1.4%, range 0.07–24%) but this proportion declined with reservoir fertility (r = -0.38 with log₁₀ Chl). Picoplankton averaged 4% of total biomass in reservoirs with seasonal mean Chl <5 μg/L (n = 15), but only 0.7% in reservoirs with Chl >25 μg/L (n = 14). In addition to picoplankton, 2003 data included numerous small colonial cyanobacteria (especially *Cyanogranis* and *Cyanocatena*) not effectively preserved in 2000.

Most patterns in the taxonomic and algal biomass analysis were similar in the two collection periods. An exception was the occurrence of *Cylindrospermopsis raciborskii*; in 2000 it was found in 29 reservoirs (0.1–74% of biovolume, dominant in 12) but in 2003 occurred in only 16 (0.2–79% of biovolume, dominant in 3). This difference may be inter-annual variation or an artifact of comparing single samples (2003) with seasonal composites (2000). In both years, cyanobacteria biovolume, as a proportion of total biovolume (logit-transformed – Downing *et al.* 2001), was positively correlated with Chl, TP, TN, and total biovolume (all log₁₀

transformed r = 0.15 to 0.55; the 2003 TP correlation was not significant).

At the level of the reservoir mean, TP_{log} explained 83% of cross-system variation in Chl_{log} among Missouri reservoirs (Fig. 7a; n = 167); TN_{log} explained slightly less variation (Fig. 7b). In multiple regression, TN_{log} entered as a second variable and explained about 2% additional variation not accounted for by TP_{log}. Omitting Big Rivers lakes from the analyses resulted in a slight reduction in the r² value between Chl_{log} and nutrients but had virtually no influence on regression coefficients in the respective models. This result suggests the statewide Chl-nutrient relation can be treated as a continuum across the suite of reservoirs and oxbow/scour lakes occurring within the state.

The Chl-nutrient relations in Missouri reservoirs also can be pictured graphically using a Carlson Trophic State Index (TSI) deviation plot (Fig. 8; Carlson and Havens 2005). Based on TSI calculations, Chl was larger than predicted by TP in 35% of the reservoir means (TSI(Chl)–TSI(TP) >1; Fig. 8a), less than predicted in 40% and within 1 TSI unit in the remainder (25%). Across regions, deviations were mostly positive in the Ozark Highlands, and the proportion of negative values increased along the following sequence: Ozark Border > Glacial Plains > Osage Plains and Big Rivers, where all deviations were negative. In a parallel analysis based on TSI(TN), deviations were mostly positive (Fig. 8b), and the lack of agreement with TSI(TP) results from TN:TP ratios in Missouri reservoirs (Fig. 3) being low relative to lake data used to construct the TSI(TN) index (Kratzer and Brezonik 1981). For TSI(TN) to equal TSI based on observed Chl in our data set, TN would have to increase, on average, by 68% (inter-quartile range 30–102%).

Reservoir data collected after 1990, include measurements of nonalgal mineral seston in the particulate and filtrate fractions, and show NAS explains an additional 5% of variation in Chl_{log} over the single variable model with TP_{log} (Table 4). This improvement was consistent in data sets at both levels

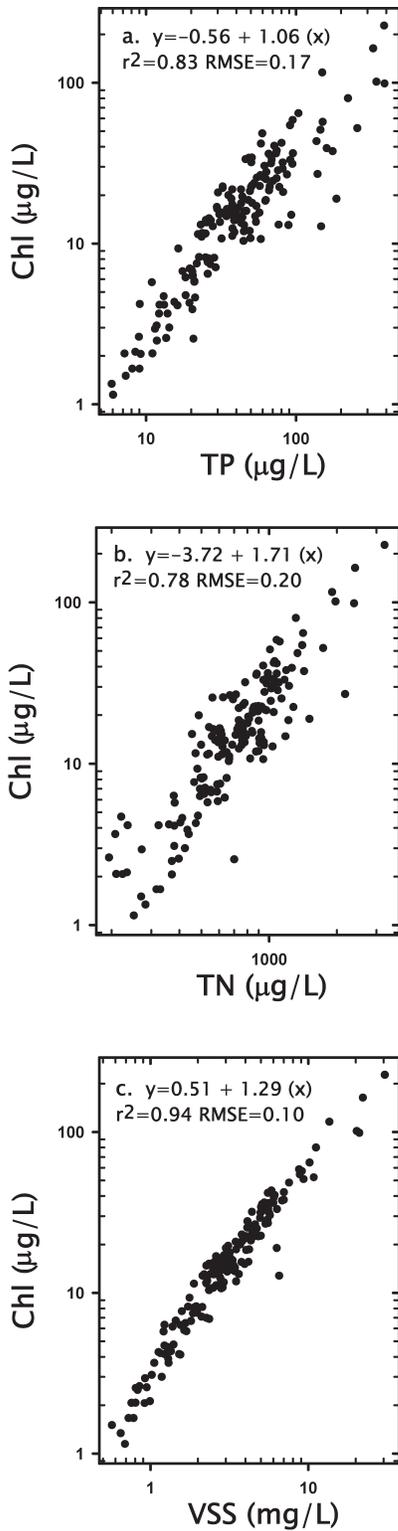


Figure 7.-Relation of Chl to TP, TN, and VSS using the reservoir mean data set (n = 167).

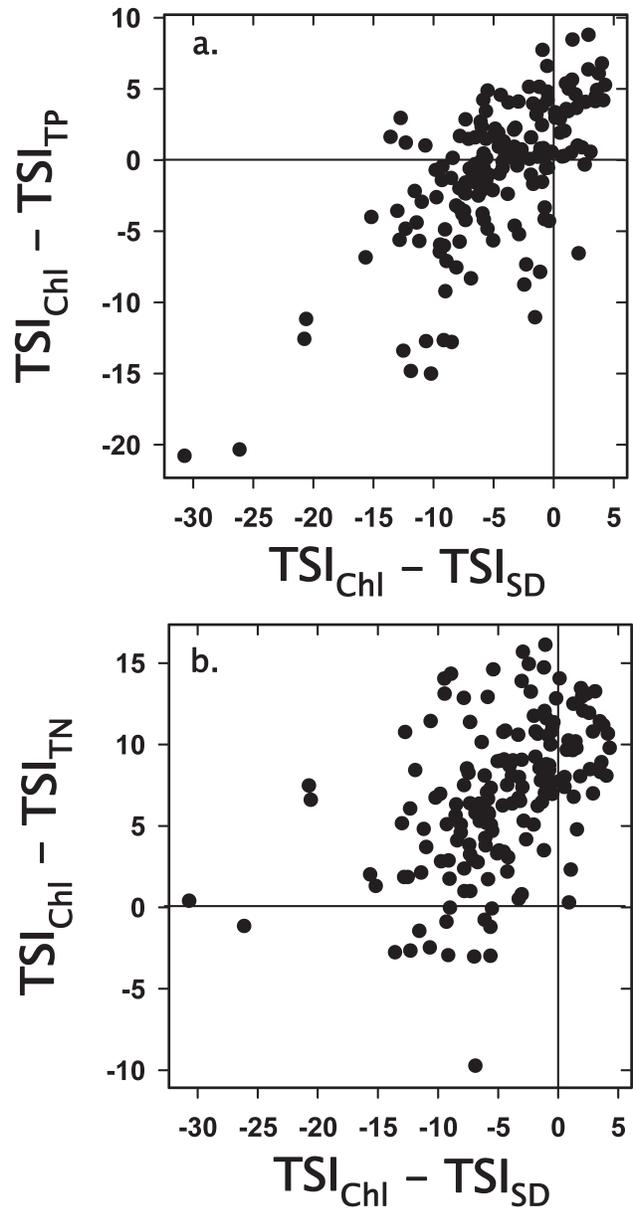


Figure 8.-Carlson Trophic State Index (TSI) deviation plots for 167 Missouri reservoirs. Plotted values are differences between TSI values based on Chl versus Secchi depth (SD), Chl versus TP, or Chl versus TN (using reservoir means). Calculations of TSI values are based equations in Carlson and Havens (2005).

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Table 4.—Regression models of variation in chlorophyll as affected by TP, NAS, and TN:TP for unaveraged individual observations and reservoir means. Analyses were limited to observations including measurements of all four variables.

Individual Observations (n = 4979)		r²	RMSE
1	$\text{Chl}_{\log} = -0.48 + 1.02 (\text{TP}_{\log})$	0.64	0.300
2	$\text{Chl}_{\log} = -0.76 + 1.37(\text{TP}_{\log}) - 0.39 (\text{NAS}_{\log})$	0.69	0.277
3	$\text{Chl}_{\log} = -1.65 + 1.57(\text{TP}_{\log}) - 0.39(\text{NAS}_{\log}) + 0.45(\text{TN:TP}_{\log})$	0.71	0.271
Reservoir Means (n=163)			
7	$\text{Chl}_{\log} = -0.59 + 1.09(\text{TP}_{\log})$	0.84	0.172
8	$\text{Chl}_{\log} = -0.94 + 1.51(\text{TP}_{\log}) - 0.48(\text{NAS}_{\log})$	0.89	0.142
9	$\text{Chl}_{\log} = -1.44 + 1.61(\text{TP}_{\log}) - 0.45(\text{NAS}_{\log}) + 0.26(\text{TN:TP}_{\log})$	0.90	0.140

of aggregation: individual measurements (n = 4979) and reservoir means (n = 163). In both cases NAS had a negative coefficient, and results were similar when analyses were based only on mineral seston in the filtrate fraction (fTSS_{\log}). Including a measure of mineral seston in the model resulted in a steeper slope coefficient for TP_{\log} relative to the single variable model (Table 4). Addition of TN:TP_{\log} resulted in minor improvements in the regression models with a positive coefficient (Table 4).

Deviations of $\text{TSI}(\text{Chl}) - \text{TSI}(\text{TP})$ were negatively correlated with log-transformed measurements of mineral seston (Fig. 9a and 9b; reservoir means). Likewise, a comparison of Chl values from Missouri reservoirs with values predicted using the Chl-TP model of Jones and Bachmann (1976) shows a hyperbolic relation over the range of mineral seston values (Fig. 10a and 10b). Most predicted values fit within the 95% confidence limits of the original model; among those falling below the lower confidence limit the median values of fTSS and NAS values (7.3 and 30.0 mg/L, respectively) were some 4 and 7.5 times larger than in the rest of the data set. Among reservoir means (n = 167), ratios of observed Chl/predicted Chl values (Fig. 10) were perfectly correlated with $\text{TSI}(\text{Chl}) - \text{TSI}(\text{TP})$ deviations because of the similarity of the Jones-Bachmann equation and the Chl-TP equation of Carlson (1977). These two approaches closely agree and nicely illustrate the cross-system decrease in Chl:TP associated with increasing mineral materials in the seston.

Based on TSI analyses and the Jones-Bachmann Chl-TP relation, Chl:TP ratios (as $\mu\text{g/L}:\mu\text{g/L}$) in Missouri reservoirs would be expected to increase by about an order of magnitude across the observed TP range and have a geometric mean of 0.44, with an inter-quartile range of 0.34–0.56. Among individual Missouri samples, however, mean Chl:TP was 0.34 (Fig. 5c; n = 7225) with a median of 0.37 and an inter-quartile range of 0.24–0.55. Some 4% of the Chl:TP ratios were >1.0 (Fig. 11a); these peak ratios were largely from samples with mid-range TP values (median = 46 $\mu\text{g/L}$ TP,

inter-quartile range 34–73 $\mu\text{g/L}$ TP) and were associated with modest levels of mineral seston (median = 1.2 mg/L fTSS and 4.0 mg/L NAS). Empirical Chl:TP patterns in the literature suggest Chl:TP ratios >1 are most common among TP-rich water bodies (>150 $\mu\text{g/L}$), but this was not the case in Missouri (Fig. 11a). Lower than predicted Chl:TP in TP-rich lakes is probably due to mineral seston and associated inflow events, with possible additional influence of low TN ratios in these enriched water bodies (Fig. 3).

The geometric mean for the Chl:TN ratio in the Missouri data was 18.3 (Fig. 5d; n = 6876 as $\mu\text{g/L}:\text{mg/L}$) with a median of 20.0 and an inter-quartile range of 10.5–34.4. Ratios of Chl:TN were variable across the observed TP range but the wedge-shaped distribution showed an upper edge that increased from ~50 at 10 $\mu\text{g/L}$ TP to ~100 at 100 $\mu\text{g/L}$ TP (as TP_{\log} ; Fig. 11b), and average Chl:TN increased by over three-fold over this range of TP (from about 11 to 35). Higher Chl:TN ratios in the more TP-rich reservoirs probably reflect an increased influence of N-limitation in these water bodies.

Chlorophyll was more strongly related to VSS, a measure of organic particulates in the seston, than to either TP or TN (Fig. 7) with a much smaller RMSE than the Chl-nutrient models. The Chl-VSS regression shows an accelerated increase in Chl_{\log} relative to VSS_{\log} (slope = 1.29 in the reservoir mean data, Fig 7c) amounting to about a three-fold change across the distribution range. Algal biomass (as \log_{10} bio-volume) in the 2000 survey data has a nearly identical slope (1.28) relative to seasonal mean VSS_{\log} ($\text{BioVol}_{\log} = 5.59 + 1.28 * \text{VSS}_{\log}$, $r^2 = 0.81$, n = 60, RMSE = 0.21). These patterns indicate algal biomass accounts for an increasing proportion of organic solids as Missouri reservoirs are enriched with nutrients; as such, seston composition tracks regional differences in fertility.

Among individual samples (n = 6971) Chl averaged 0.5% of VSS (median = 0.5%) with some 10% of values <0.2% or >0.9%. This proportion differed significantly among regions

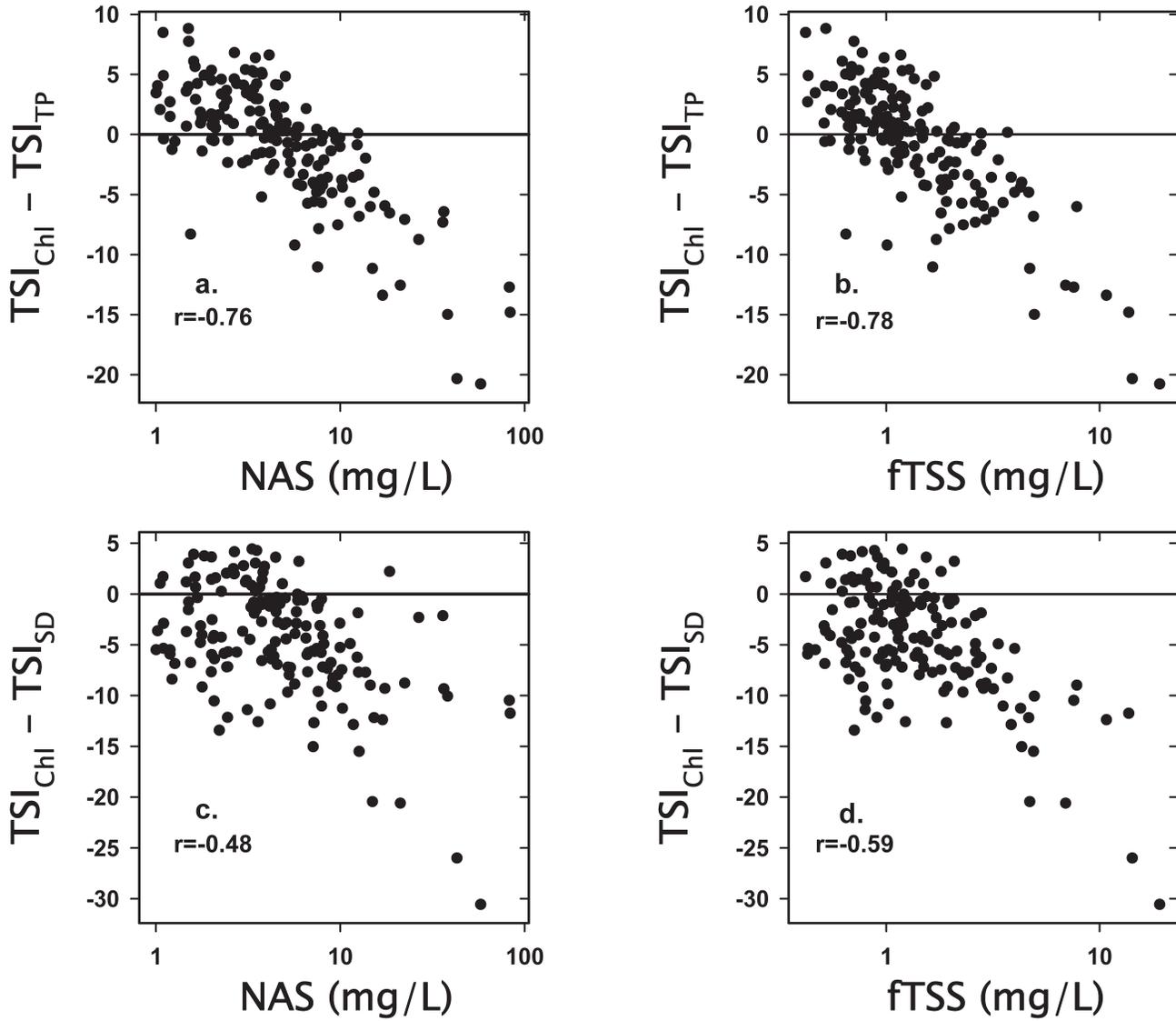


Figure 9.-Carlson Trophic State Index (TSI) deviations versus NAS and ftSS for reservoir means ($n = 163$). TSI deviations were estimated as in Fig. 8.

(one-way ANOVA, $p < 0.001$) with means ranging from 0.44% in the Ozark Highlands to $>0.60\%$ in the Osage Plains and Big Rivers sections. In the 2000 data, Chl averaged 1.1% of algal wet weight (median = 0.9%, range 0.6–5.4%), or $\sim 2\%$ as dry weight (assuming a 50% water content, Reynolds 1984). Phytoplankton biomass (dry) averaged 29% of VSS (median = 27%, range = 8–84%, $n = 60$). Among 93% of the reservoirs sampled in 2000 algal biomass was less than half of VSS. These data indicate, that while algal biomass increases as a proportion of organic solids with reservoir trophic state (Fig. 7c), there is a broad dominance of detritus, bacteria, or other materials in the particulate organic pool in Missouri reservoirs, a characteristic of organic seston in lakes worldwide (Wetzel 2001).

Relations of VSS to other variables suggest an autochthonous origin for organic seston in Missouri reservoirs. In stepwise regression with unaveraged data ($n = 6928$) Chl_{log} accounted for 75% of the variation in VSS_{log} , and adding $NVSS_{log}$, an indicator of terrigenous inputs, only accounted for an additional 3% of unexplained variation. Residuals from the $VSS_{log}-Chl_{log}$ regression were positively related to $NVSS$ among samples with > 10 mg/L; this condition is usually associated with turbid inflow events and is more common in the Plains (mean $\sim 13\%$) than the Ozark sections (mean $\sim 1\%$). Among samples with $NVSS > 10$ mg/L ($n = 772$), VSS in excess of the amount predicted by the $VSS_{log}-Chl_{log}$ regression averaged only 9% of $NVSS$ (median = 7%, range 38–244%). This analysis suggests VSS is a minor component

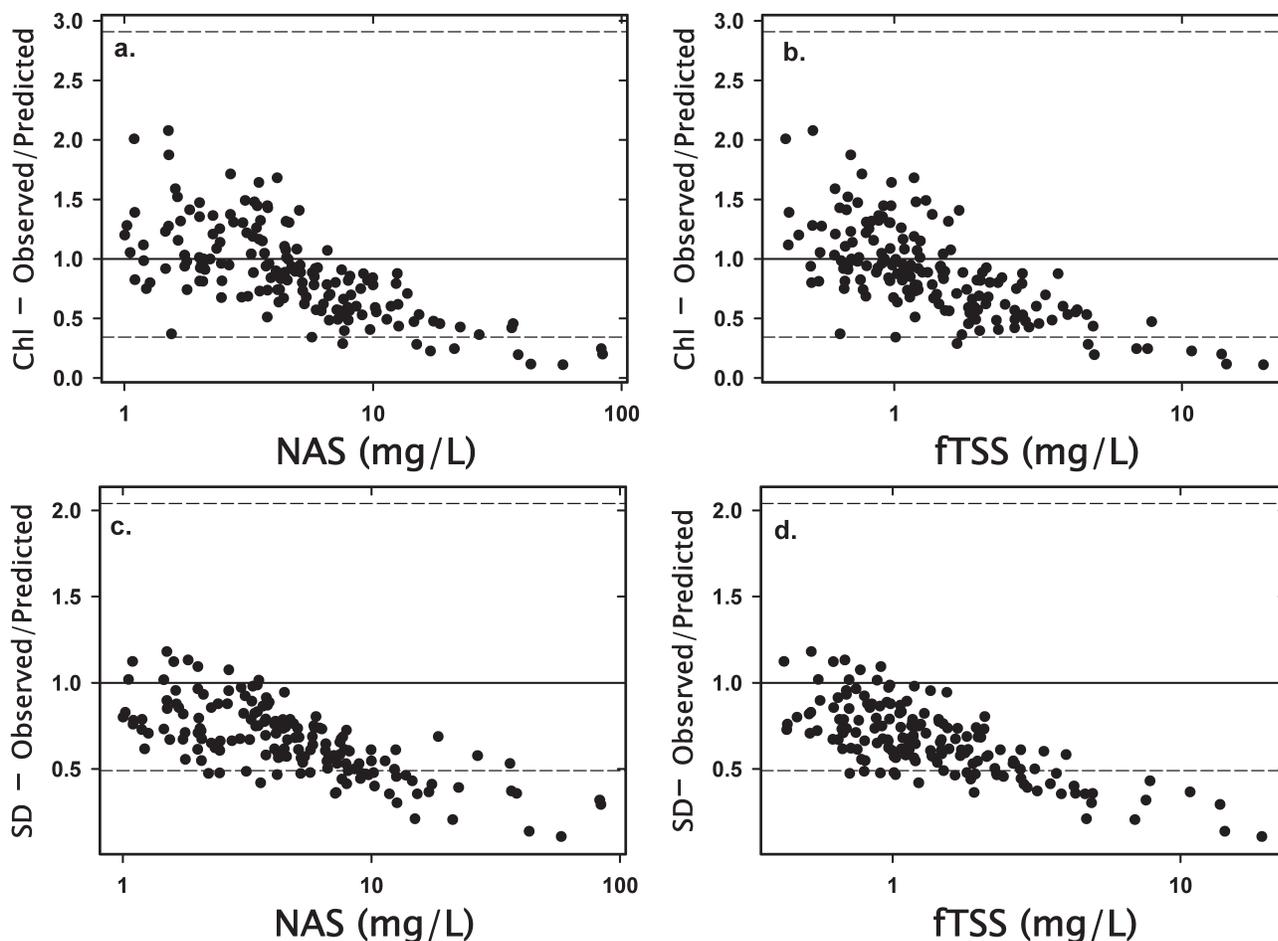


Figure 10.—Ratios of observed/predicted Chl and Secchi depth (SD) to NAS and ftSS in reservoir mean data set ($n = 163$). Predicted Chl and SD are based on regression models of Jones and Bachmann (1976) and Jones and Bachmann (1978), respectively. Dashed lines indicated the upper and lower 95% confidence limits of the Jones and Bachmann regressions.

of turbid inflows, a finding consistent with the dominance of NVSS in Missouri streams (typically >80%; Perkins and Jones 1994, Perkins *et al.* 1998). Overall, VSS from allochthonous sources seem like a minor component of these near dam samples from Missouri reservoirs.

The value of 10 $\mu\text{g/L}$ Chl has been identified at the breakpoint where algal biomass becomes apparent in lake water and nuisance algal blooms occur at increasing frequency (Bachmann and Jones 1974, Walker 1984, Walmsley 1984). Among Missouri reservoirs the occurrence of Chl >10 $\mu\text{g/L}$ increases in a sigmoid pattern with nutrients (Fig. 12a and 12b); the change is most rapid between ~ 15 and 25 $\mu\text{g/L}$ TP with the average frequency of Chl >10 $\mu\text{g/L}$ increasing from ~ 7 to >50% across this range. In reservoirs with mean TP >35 $\mu\text{g/L}$, some 84% of Chl values are >10 $\mu\text{g/L}$, and at TP >65 $\mu\text{g/L}$ frequency increases to 90%. There is also a sharp response within the mid-range of TN values (Fig. 12b); Chl >10 $\mu\text{g/L}$ accounts for only $\sim 4\%$ of samples in reservoirs with 350–450 $\mu\text{g/L}$ TN, but occurrence jumps 10-fold to $\sim 40\%$

among reservoirs with 450–600 $\mu\text{g/L}$ TN. In reservoirs with ~ 740 $\mu\text{g/L}$ TN, the statewide median value, about 70% of samples have Chl >10 $\mu\text{g/L}$ (Fig. 12b).

Secchi transparency

Median Secchi depth was 0.9 m (range 0.15–4.3 m; Table 2) and inter-regional differences in transparency showed the opposite pattern of NVSS (Fig. 2e); in the Ozark Highlands median Secchi (1.9 m) was double the statewide median and six times the Big Rivers value (0.3 m). Secchi values in the Plains sections were typically less than half of measurements in the Ozark Highlands. Among reservoir means, variation in TSS_{\log} explained 95% of cross-system variation in Secchi_{\log} (Fig. 13a). But given the strong inter-correlation among seston materials in the data set, NTU_{\log} explained 92% of Secchi_{\log} variation, NVSS_{\log} 87%, NAS_{\log} 87%, VSS_{\log} 78%, and Chl 70% (Fig. 13c). These measures of seston particles were strongly correlated with TP ($r = 0.85$ to 0.95) and TP

explained 90% of Secchi_{\log} variation (Fig. 13b). Fine particulates (fTSS_{\log}) accounted for 68% of Secchi_{\log} variation, and when combined with TSS_{\log} as ΣTSS (our estimate of all particles in the seston), 96% of variation in Secchi_{\log} was explained (Fig. 13d). Stepwise multiple regressions suggest inorganic materials largely determined transparency; adding either Chl_{\log} or VSS_{\log} increased the coefficient of determination by only about 7% over the single variable NAS_{\log} model (87%).

Dissolved color (absorption at 440 nm) was negatively correlated with Secchi depth ($r = -0.52$, $n = 253$, log-transformed 2002 data). Color, however, was positively correlated with suspended solids, especially fTSS ($r = 0.71$), which had a much stronger influence on transparency. A regression with ΣTSS_{\log} explained 85% of variation in individual measurements of Secchi depth and adding color to the model increased explained variation by only 0.3% (2002 data).

Relations among Chl, TP, and Secchi can also be pictured using a Carlson TSI deviation plot (Fig. 8; Carlson and Havens 2005) to show that TSI based on Secchi typically over-predicts TSI based on Chl (data points fall to the left of zero on the X-axis in both panels). This pattern results from light being scattered or absorbed by small particles and is characteristic of 90% of reservoir means in our data set. On average $\text{TSI}(\text{SD})$ exceeded $\text{TSI}(\text{Chl})$ by 5 units, and in 25% of the reservoirs this difference was >8 (maximum 31). Among reservoir means, these TSI differences showed a negative correlation with our measurements of mineral particulates in the seston (Fig. 9c and 9d; NAS and fTSS). When the data set was limited to reservoir means with <8 mg/L NAS ($n = 126$) the TSI difference values were mostly negative but not correlated with mineral seston, suggesting that some factor other than our measures of mineral turbidity contributes to low transparency in these water bodies (Fig. 9c).

Despite the pattern of negative $\text{TSI}(\text{Chl}) - \text{TSI}(\text{SD})$ values, nearly three-quarters of reservoir mean Secchi values fit within the 95% confidence limits of the Chl-Secchi model by Jones and Bachmann (1978). Consistent with the TSI analysis, most predictions were below the average (95% for reservoir means) and only 5% of reservoir means were larger than the model prediction (Fig. 10c and 10d). Secchi depths positioned below the lower confidence limit of the Jones-Bachmann model averaged about one-third the predicted value and were associated with more than three times the NAS , and fTSS measured in reservoirs wherein Jones-Bachmann model provided reasonable estimates of Secchi (Fig. 10c and 10d). Among reservoir means, both NAS_{\log} and fTSS_{\log} accounted for $>48\%$ of variation in the ratio of observed Secchi/predicted Secchi (analysis restricted to observations with NAS measurement; $n = 163$). Color explained only 9% of the variation in observed/predicted Secchi compared to $>37\%$ for NAS and fTSS (unaveraged

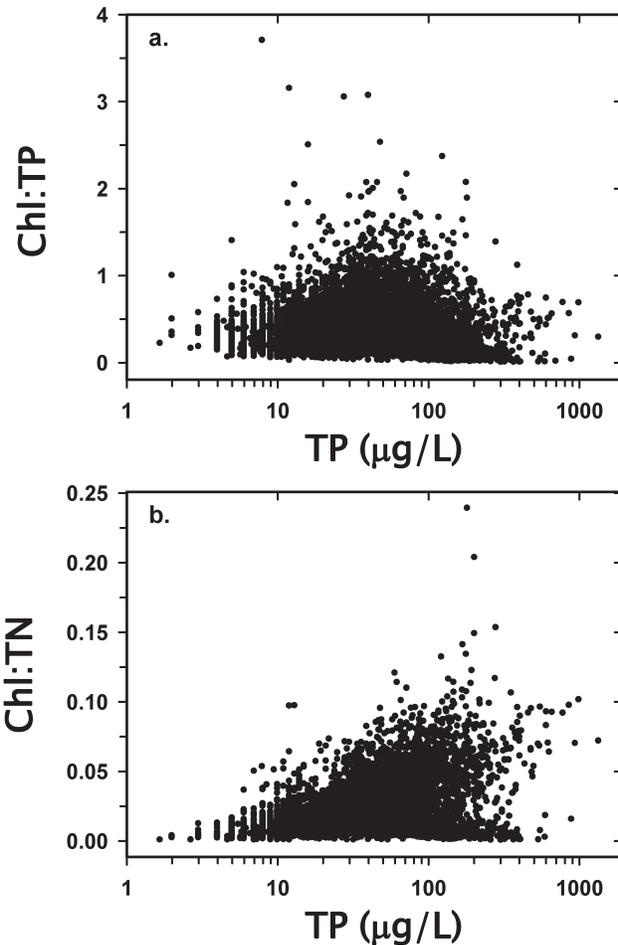


Figure 11.—Relation of Chl-nutrient ratios (Chl:TP, $n = 7225$, and Chl:TN, $n = 6876$) to TP in unaveraged observations (units as $\mu\text{g/L}:\text{mg/L}$ for TN).

observations from 2002, data not shown). Also, although observed/predicted Secchi declined with increasing color, 82% of these ratios were <1 , even among observations with low color. These findings suggest relatively low transparency in Missouri reservoirs is not from dissolved colored materials.

Secchi transparency of <1 m has been associated with impaired water quality (Bachmann and Jones 1974, Canfield and Bachmann 1981). As with $\text{Chl} > 10 \mu\text{g/L}$, the frequency of Secchi <1 m shows a sigmoidal increase with reservoir nutrients (Fig. 12c and 12d). In reservoirs with $15 \mu\text{g/L}$ TP the occurrence rate of Secchi <1 m averages only $\sim 5\%$, but between 25 and $40 \mu\text{g/L}$ TP the frequency increases from 20% to 50%. At $>65 \mu\text{g/L}$ TP, more than 80% of Secchi readings are <1 m. Based on TN values (Fig. 12d), the frequency of Secchi values <1 m increase from an average of $\sim 4\%$ among reservoirs with $400\text{--}450 \mu\text{g/L}$ TN to $\sim 40\%$ among reservoirs with $500\text{--}550 \mu\text{g/L}$ TN; at $740 \mu\text{g/L}$, the statewide median, frequency increases to $>50\%$.

Nutrients, seston and transparency of Missouri reservoirs and oxbow lakes: an analysis of regional limnology

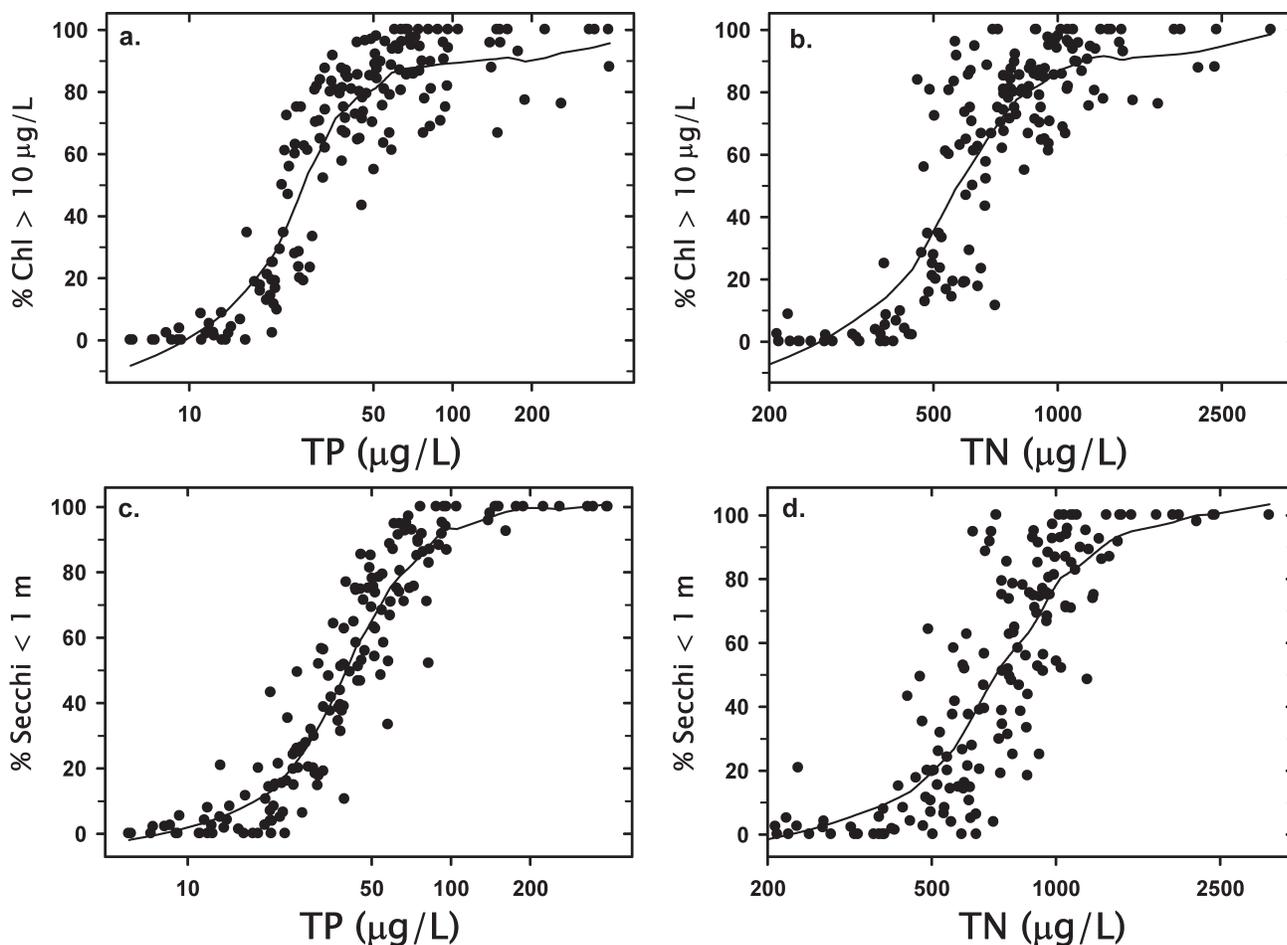


Figure 12.-Relation of the proportion of all observations from a given reservoir with Chl >10 µg/L or Secchi depth <1 m (n = 167) to mean TP and TN. Solid lines were fitted by locally weighted regression (LOWESS).

Trophic State

Trophic state criteria proposed by Jones and Knowlton (1993) were modified using the summary by Nürnberg (1996) to classify Missouri reservoirs (Table 5). About 80% of the reservoirs were mesotrophic or eutrophic based on nutrients and Chl, while oligotrophic and hypereutrophic water bodies were present in near-equal proportions (at 6–11% of the total; Table 5). There were clear regional patterns in reservoir trophic state. On the basis of TP, oligotrophic reservoirs were located within the Ozark Highlands (with one exception), along with about half of the mesotrophic impoundments (Table 6). Most remaining mesotrophic reservoirs were in the Ozark Border and Glacial Plains sections. Eutrophic reservoirs occur in each section, but some 76% were located in the Glacial and Osage Plains. Hypereutrophic water bodies were split between the Big Rivers and Plains sections. This general characterization of regional patterns using TP was similar when based on other trophic state variables.

Trophic state criteria based on TN are modified upward somewhat from the provisional categories of Jones and Knowlton (1993) in response to patterns in this larger data set, but remain slightly lower than criteria for temperate lakes worldwide (Nürnberg 1996). This adjustment is needed because in many Missouri reservoirs TN was not abundant relative to TP (Fig. 3). Included in this analysis are trophic state criteria based on Secchi depth (Table 5). Threshold values were calculated using the strong regression relation between Secchi and TP (Fig. 13b) and TP criteria from Table 5. For example, the threshold value of 10 µg/L TP between oligo- and mesotrophic water bodies equates to a Secchi of 2.6 m based on the regression relation (Fig. 13b). This cutpoint and the one between meso- and eutrophic systems, 1.3 m, is only 65% of the worldwide thresholds of 4 and 2 m proposed by Nürnberg (1996). Furthermore, our threshold of 0.45 between eutrophic and hypereutrophic systems is less than half the 1-m value proposed by Nürnberg (1996). These differences reflect that light regimes in Missouri reservoirs

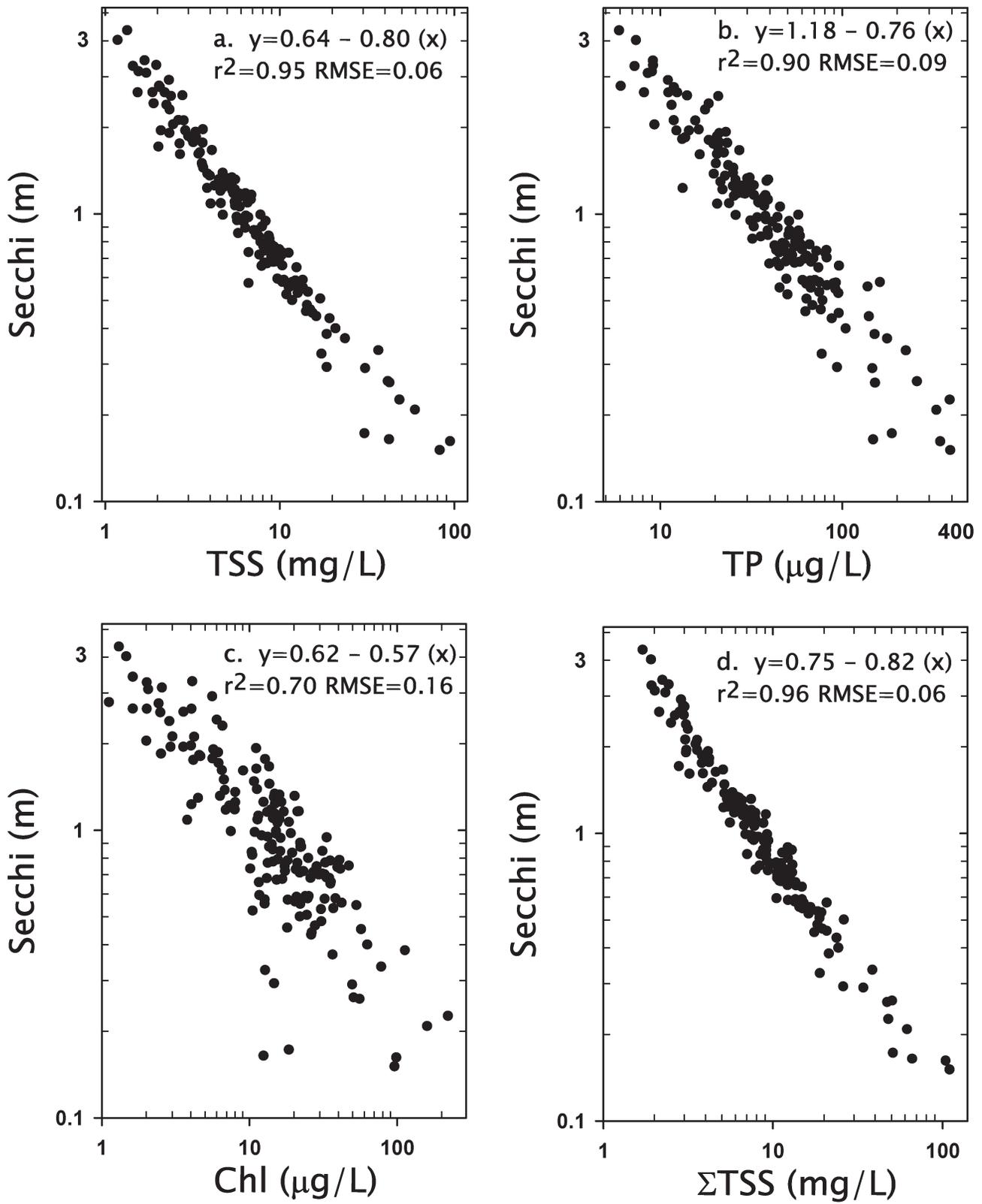


Figure 13.-Relation of Secchi depth to TSS, TP, Chl (n = 167), and the sum of TSS and fTSS = ΣTSS (n = 163) in the reservoir mean data set.

Nutrients, seston and transparency of Missouri reservoirs
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Table 5.—Trophic state criteria based on total phosphorus, total nitrogen, chlorophyll and Secch depth modified from criteria proposed by Jones and Knowlton (1993) and the percentage of reservoirs from this data set that fall within each designation.

Trophic State	Total P µg/L		Total N µg/L		Chlorophyll µg/L		Secchi m	
	Criterion	% of Reservoirs	Criterion	% of Reservoirs	Criterion	% of Reservoirs	Criterion	% of Reservoirs
Oligotrophic	<10	6	<350	8	<3	9	≥2.6	8
Mesotrophic	≥10–25	22	≥350–550	19	≥3–9	19	≥1.3–<2.6	22
Eutrophic	≥25–100	63	≥550–1200	62	≥9–40	62	≥0.45–<1.3	60
Hypereutrophic	≥100	10	≥1200	11	≥40	10	<0.45	11

Table 6.—Percent occurrence of trophic state categories (based on total phosphorus) by physiographic section.

Trophic State	n	Physiographic Section				
		Ozark Highlands	Ozark Border	Glacial Plains	Osage Plains	Big Rivers
Oligotrophic	10	90%	10%	—	—	—
Mesotrophic	36	47%	22%	28%	3%	—
Eutrophic	105	8%	12%	54%	22%	4%
Hypereutrophic	16	—	—	38%	19%	44%

are frequently below the norm established by the empirical Secchi-Chl relation (Fig. 8–10). Chlorophyll is considered the key variable controlling transparency in most temperate lakes. In Missouri reservoirs, transparency is not universally a reliable estimate of algal biomass, but given the tight link between Secchi and TP (Fig. 13b) it serves as a simple metric of nutrient status.

Discussion

This analysis of Missouri limnology, based on summer collections from 167 water bodies sampled in 1978–2007, characterizes 73 lake systems not previously considered (Jones and Knowlton 1993). The current data set includes about nine times (TSS, Chl, and TP) to 16 times (TN) more samples than the early study. Despite these differences, both analyses show about 80% of lentic systems in Missouri are mesotrophic or eutrophic (Table 5), which is similar to lakes elsewhere in the Midwest (Jones and Bachmann 1978, Lillie and Mason 1983, Heiskary *et al.* 1987, Spacie and Loeb 1990, Fulmer and Cooke 1990).

Differences in reservoir limnology among the major sections of Missouri are tied to regional variation in geomorphology, soils and land cover (Tables 1, 2 and 6; Fig. 1, 2, and 4). The major contrast is between near equal numbers of hypereutrophic and oligotrophic water bodies. Hypereutrophic lakes of the Big River Section are located in rich bottomland soils, and their shallow morphometry is conducive to internal cycling of nutrients and mineral seston (Table 2; Knowlton and Jones 1997, Jeppesen *et al.* 1999, Jones and Knowlton

2005b). Hypereutrophic reservoirs in the Plains have agricultural watersheds and rapid hydraulic flushing rates (Jones *et al.* 2008). In the Ozark Highlands and Border sections oligotrophic reservoirs benefit from forested watersheds, low hydrologic flushing rates and up-stream impoundments; features associated with low nutrients (Jones *et al.* 2004, Jones *et al.* 2008). Table Rock Lake, a large reservoir on the White River, is also oligotrophic based on its TP content near the dam but has high nutrient concentrations in several tributary arms (Knowlton and Jones 1989a, Obrecht *et al.* 2005). This regional analysis compares near-dam conditions and does not consider the longitudinal gradients that characterize large reservoirs throughout Missouri (Jones and Novak 1981, Knowlton and Jones 1989a, 1995, Perkins and Jones 2000).

Reservoirs in the Missouri Plains typically have about three times the TP, NVSS, VSS, and Chl; twice the TN; and half of the transparency of a reservoir in the Ozark Highlands (Table 2; Fig. 2). Most Ozark Border reservoirs have intermediate trophic state characteristics and reflect the ecotonal nature of this section. The broad trophic state continuum in Missouri is largely determined by nonpoint source nutrient inputs. A statewide analysis showed cropland, a surrogate for external nutrient loss from agricultural watersheds, accounts for some 60–70% of the cross-system variation in long-term average nutrient levels in Missouri reservoirs (Jones *et al.* 2004). Anthropogenic disturbances such as tilling, harvest, and application of fertilizers (Turner and Rabalais 1991, Howarth *et al.* 1996) result in cropland being a greater relative source of nutrients than other dominant cover types in Missouri.

The addition of dam height (representing morphometry) and an index of hydrologic flushing rate to the model increased the amount of explained variation to ~77% for both nutrients (Jones *et al.* 2004). These findings are consistent with empirical theory on the role of morphology and hydrology in modifying external nutrient loads to lakes (Edmondson 1961, Vollenweider 1975). Reservoir nutrients show a strong negative relation to forest because of modest nutrient loading from this cover type. The relative distribution of cropland and forest (Table 1) in Missouri largely accounts for regional patterns in reservoir trophic state (Table 6). This quantitative link between land cover and nonpoint nutrient input is why reservoir nutrients increase along a gradient to the north and west in parallel to increases in cropland and a general decline in forest cover. Because of this pattern, latitude and longitude account for about a quarter of cross-system variation in reservoir TP_{log} and a third of TN_{log} variation. Anthropogenic activities obscure natural geology-water chemistry relations and explain why nutrients are not correlated with conductivity in this data set (Vighi and Chaudani 1985).

In Missouri reservoirs TN:TP ratios decline with trophic state (Fig. 3), which is the case for fresh waters worldwide (Downing and McCauley 1992). Reservoir nitrogen levels are lower than found in many lakes worldwide (Nürnberg 1996); this shortfall has been a consistent feature of the monitoring program (Jones and Knowlton 1993). Reasons for low nitrogen are likely tied to ambient soil fertility, regional farming practices, and the mix of grass, forest, and cropland throughout the state (Table 1; Jones *et al.* 2004). Proportionately low TN relative to TP is the basis for setting the upper limit of mesotrophic reservoirs at 550 µg/L TN (Table 5) rather than 650 µg/L as proposed by Nürnberg (1996). Current TN criteria for oligo- and hypereutrophic reservoirs match those for worldwide lakes (Nürnberg 1996) and are reasonable cutpoints for the Missouri data. The TN trophic state criteria (Table 5) supplant the provisional classification system proposed by Jones and Knowlton (1993).

About half the TN:TP ratios were <20 and some 10% were <10, suggesting potential N-limitation (Forsberg and Ryding 1980) and *in situ* experiments have demonstrated nitrogen stimulation of plankton in some reservoirs (Perkins and Jones 2000), but the response is not universal (Knowlton and Jones 1996). Nitrogen stimulation may be a condition that occurs periodically (Prepas and Trimbee 1988) or contemporaneously with P (Dodds *et al.* 1989). Nitrogen limitation and co-limitation with P was found experimentally in central plains reservoirs (Dzialowski *et al.* 2005) and is known to occur in a broad range of lake types (Elser *et al.* 1990, Maberly *et al.* 2002). Low TN:TP ratios in Missouri reservoirs tend to co-occur with high measures of mineral seston and low transparency, conditions favoring light rather than nutrient limitation of algal biomass. Overall, the contribution of TN to our Chl regression models was small once variation was

accounted for by TP_{log} (model not shown). It seems N-limitation occasionally occurs in Missouri reservoirs, but small variation in long-term average Chl-TP suggests N does not routinely depress biomass below expectations based on TP. The strength of the Chl-TN relation (Fig. 7b) is attributable to the strong correlation between TN and TP (Fig. 3a and 3b).

The empirical link between Chl and TP in Missouri reservoirs has been evaluated previously (Hoyer and Jones 1983, Jones and Knowlton 1993, 2005b, Kaiser *et al.* 1994, Jones *et al.* 1998, Knowlton and Jones 2000). The Chl-TP fit among reservoir means in this analysis (Fig. 7) is based on an expanded data set (50% larger, n = 167 versus 111) relative to the detailed assessment by Jones and Knowlton (2005b). Regression coefficients and fit (Fig. 7) are similar to previous Chl-TP models, and the slope coefficient of near unity matches the relation reported for other temperate lakes (Jones and Knowlton 2005b). The expanded data set does not show the curvilinearity seen in early assessments (Jones and Knowlton 1993) or the sigmoid shape seen in temperate lakes with broader nutrient ranges than occur in Missouri (Forsberg and Ryding 1980, McCauley *et al.* 1989, Prairie *et al.* 1989).

Mineral turbidity is typically an episodic influence in Missouri and results in an ephemeral decrease in Chl:TP ratios as a result of reduced light and sediment-bound TP (Jones and Knowlton 2005b). Its influence on the Chl-TP relation is seasonal, being most prevalent in early summer (Jones and Knowlton 2005b). Accounting for mineral turbidity, as measured by NAS_{log} levels, improves Chl-TP regressions in Missouri reservoirs (Table 4). The model shows Chl declines by half (from 21 to 10 µg/L Chl) in a Missouri reservoir with median TP (39 µg/L) when NAS increases from 2 to 10 mg/L. In these systems the geometric mean Chl:TP ratio was 0.34 rather than 0.44, which would be expected by the Jones-Bachmann regression (Fig. 5c), and maximum Chl:TP values were generally found in reservoirs of mid-level fertility with low mineral seston (Fig. 11a). TSI-deviations (Fig. 9) and ratios of observed/predicted Chl based on the Chl-TP regression of Jones and Bachmann (1976) illustrate the cross-system decline in Chl:TP associated with increasing mineral seston (Fig. 10). These findings are consistent with light-limitation of phytoplankton by mineral seston which has been quantified in a broad range of turbid systems (Grobelaar 1985, Doukoulil 1994, Knowlton and Jones 2000). Across regions, the fractions of NAS (NVSS and fTSS; Fig. 4) were larger among Plains and Big Rivers sections than the Ozark Highlands and Ozark Border. Strong biotic control of Chl is unlikely in these reservoirs because summer zooplankton communities have been dominated by small-bodied taxa (Canfield and Jones 1996).

An interesting outcome of adding a continuous measure of mineral seston to the Chl-TP analysis is that NAS_{log} accounts

for some 31% of variation not accounted for by TP_{log} (Table 4), resulting in a sharp increase in the slope associated with reservoir mean TP_{log} (from 1.09 to 1.51). This slope value closely matches that of the Chl-TP cross-system analysis of Dillon and Rigler (1974), Jones and Bachmann (1976), and Carlson (1977). The intercept decreases when NAS_{log} is included (Table 4). The interpretation is that once the negative influence of NAS_{log} is accounted for in the model, Chl:TP accelerates across the range of reservoir fertility in Missouri in the global, cross-system pattern of Jones-Bachmann and the TSI assessment. Addition of TN:TP added little to the overall relation (Table 4).

Chlorophyll values vary within and among Missouri reservoirs (Jones and Novak 1981, Knowlton *et al.* 1984, Jones and Kaiser 1988, Knowlton and Jones 1990, Jones and Knowlton 2005b, Knowlton and Jones 2006a, 2006b, Perkins and Jones 2000). Among individual samples, Chl values varied across three orders of magnitude (<1–680 $\mu\text{g/L}$, $n = 7265$) and within the most intensively sampled reservoirs maximum observed Chl averaged 26 times the minimum. Maximum Chl in Missouri reservoirs can be estimated at about four times the long-term reservoir mean Chl. Past studies suggest that maximum Chl is typically between 1.7 and 2.6 times the mean (Smith 2003), and the larger maximum in Missouri likely stems from the long collection record increasing the likelihood of sampling ephemeral bloom conditions (Jones and Knowlton 2005b).

Limnologists have long recognized the inter-correlation between Secchi transparency and other measures of lake trophic state (Edmondson 1972, Bachmann and Jones 1974, Vollenweider 1975, Carlson 1977) with the view that nutrients ultimately determine transparency by controlling algal biomass that dominates seston in lakes worldwide. In Missouri reservoirs our measure of total seston, ΣTSS , explains a remarkable 96% of the variation in mean Secchi depth (Fig. 13d), however, this fit largely results from nonalgal particles controlling light penetration. The inorganic fraction NAS (including the larger NVSS and small fTSS) explains 87% of total variation in mean Secchi depth, and adding Chl to the model only explains an additional 7%. Nonalgal suspended solids and Chl are both highly correlated to TP ($r = 0.85$ and 0.91 respectively). This analysis suggests the link between transparency and algal biomass (Fig. 13c) is probably indirect, mediated by the mutual association of Secchi and Chl with nutrients and the nonalgal particles associated with them.

The departure of Missouri reservoirs from the conventional paradigm of algal biomass controlling transparency suggests Secchi depth is not a trophic state metric in the same capacity as lakes in other regions. In Missouri, Secchi depth is a strong correlate of nutrient status (especially TP) rather than an indication of algal biomass. Consequently, proposed

threshold values to identify trophic state categories based on Secchi (Table 5) are shallower than conventional cutpoints for most lakes (Nürnberg 1996), and TSI values based on Secchi (Fig. 8 and 9) generally overestimate algal biomass of Missouri systems.

Relative to algal biomass, transparency in Missouri reservoirs is less than predicted by published Secchi-Chl regression models (Carlson 1977, Jones and Bachmann 1978, Nürnberg 1996, Jones *et al.* 2003). Nonalgal seston, chiefly clay minerals and other inorganic particles, accounts for much of this difference (Fig. 9 and 10). Even in Missouri reservoirs with low NAS, Secchi falls short of model predictions. Available data suggest color does not account for this difference; nor are deep Chl maxima a major influence on Secchi depth (Knowlton and Jones 1989b). The median ratio of Secchi depth to surface Chl from concurrent samples (unpublished data, $n = 4880$) was 1.04, indicating subsurface Chl peaks are uncommon within this zone of the water column and infrequently influence Secchi depth.

Pheophytin is a degradation pigment representing dying algae (Kalff *et al.* 1972, Erikson 1999). There are no conventional criteria to interpret a typical proportion of pheo-pigments in a healthy phytoplankton community, but contributions of 16-60% of measured Chl in sea- and freshwater have been reported (Marker *et al.* 1980). Jones (1977) found pheophytin was usually <5% and rarely in excess of 10% of total pigment in eutrophic lake samples while Erikson (1999) found values of >30% in a deeply mixed water column with poor light. As a framework for interpretation, these findings suggest low quality algal pigment is common in Missouri samples where the median pheophytin value was about 21% and a quarter of all samples contained >34% (Fig. 5b). This conclusion is consistent with the high proportion of detritus in the organic seston. Algal biomass and VSS data from 2000 and 2003 suggest living phytoplankton typically compose less than one-third of the organic particulate matter in Missouri reservoirs, and the strong correlation between Chl and VSS (Fig. 7c) points toward algal origin of the detritus. The strength of the Chl-VSS relation and the similarity between the slope of the relation (1.29; Fig. 7c) and the slope of the regression of algal biomass on VSS (1.28) indicates phytoplankton accounts for an increasing proportion of organic solids with nutrient enrichment. Available data suggest other sources are a small fraction of this organic material. Total zooplankton biomass in Midwestern water bodies seldom exceeds 0.5 mg/L (Canfield and Jones 1996) and is typically <0.25 mg/L, and median bacterial biomass in Missouri reservoirs was only 0.072 mg/L as carbon (or about 0.14 mg/L as organic matter, Thorpe and Jones 2005). Based on a median VSS of 3 mg/L (Table 2), only ~ 15% of the organic particulates would be zooplankton and bacteria. Allochthonous organic matter is likely most important during ephemeral inflow events that are dominated by inorganic tripton ($NVSS \geq 10$ mg/L). The

data are consistent with VSS at near-dam sites in Missouri reservoirs being composed mostly of algal detritus and the phytoplankton producing this material.

The strong link between VSS and plant nutrients in these samples results from phytoplankton control of organic seston. As a consequence, VSS is closely associated with land cover, and a regression including cropland, dam height, and flushing rate explains 67% of cross-system variation in VSS (Jones and Knowlton 2005a). These same landscape and reservoir features explain less variation in NVSS (about 57%) suggesting that indirect effects of catchments, operating through nutrients, generally have greater influence on organic seston in Missouri reservoirs than more direct effects of erosion (Jones and Knowlton 2005a).

Limited data on algal taxa from 2000 and 2003 (Table 3) suggest Cyanophyta and, less so, Bacillariophyta compose the largest proportion of summer phytoplankton biomass in these reservoirs. This composition is expected in meso- to eutrophic temperate lakes (Reynolds 1984, Watson *et al.* 1997). Algal size distribution indicates small forms (<11 μm) dominate most communities, with larger forms more common among Glacial Plains reservoirs. The dramatic increase in the proportion of microplankton (>35 μm) across the trophic continuum described by Watson *et al.* (1992) was not evident, and the apparent dominance of communities by small Cyanophyta warrants additional study. Algal biomass in cyanobacteria increases with trophic status in these reservoirs, a pattern typical of north-temperate lakes (Downing *et al.* 2001). The trend, however, is weak across the measured range (few oligotrophic reservoirs and no floodplain lakes were represented in the phytoplankton data set).

Other metrics of water quality impairment, such as nuisance-level algal blooms and reduced transparency, show abrupt, nonlinear increases with reservoir fertility. The frequency of Chl values >10 $\mu\text{g/L}$, a breakpoint where nuisance conditions occur (Bachmann and Jones 1974, Walker 1984, Walmsley 1984), increases sharply across nutrient levels spanning the mesotrophic range (Fig. 12; Table 5). Most reservoirs with nutrients near the meso-eutrophic boundary support Chl values >10 $\mu\text{g/L}$ more than 50% of the time and have Secchi transparency <1 m (Fig. 12). The sigmoid patterns between nutrients and metrics of impaired water quality (Fig. 12) provide a practical basis for lake management efforts in Missouri. If the goal is to prevent algal biomass from becoming apparent and preserve water clarity, then oligo- and mesotrophic reservoirs should be the focus of nutrient control. Large changes would be required to reduce bloom frequency and increase transparency in eutrophic reservoirs (Fig. 12).

Overall, this comparative analysis is consistent with conclusions drawn by Duarte and Kalff (1989) that the geographical setting influences lake chemistry and biology. Trophic state and seston characteristics of Missouri reservoirs are closely

tied to nonpoint source nutrient inputs, largely determined by cropland agriculture (Jones *et al.* 2004, Jones and Knowlton 2005a, Jones *et al.* 2008) which increases across a north-west axis within the state. This gradient in land cover largely accounts for differences among individual impoundments and the regional patterns among sections within the state (Table 6). The trophic state gradient in Missouri reflects forest-prairie intersection in this midcontinent ecotonal zone (Bailey *et al.* 1994). The unique lakes in the Big Rivers section are consistent with shallow water bodies in rich alluvium (Knowlton and Jones 1997) and are among the most nutrient-rich and turbid lentic systems in our sample. Suspended solids data show all fractions of this material are strongly correlated with plant nutrients with the proportion of mineral seston increasing over this trophic state range. Mineral seston is a characteristic of many meso- and eutrophic reservoirs located outside of the Ozark Highlands and has a measurable influence on algal biomass and light. As a continuous variable in empirical models, mineral seston reduces the cross-system yield of algal chlorophyll per unit of phosphorus and controls reservoir transparency much more than algal biomass. Secchi depth is a better predictor of nutrients in these systems (especially TP) than algal biomass. These relations were demonstrated empirically with regression and shown graphically with TSI-deviation diagrams with close agreement between the two approaches. Conventional approaches to lake management (Edmondson 1961, Vollenweider 1975) must be adjusted to account for mineral seston in Missouri reservoirs.

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References

- Bachmann, R.W. and J.R. Jones. 1974. Phosphorus inputs and algal blooms in lakes. *Iowa State J. Res.* 49:155-160.
- Bailey, R.G., P.E. Avers, T. King, W.H. McNab (eds.). 1994. Ecoregions and subregions of the United States (map). Washington, D.C.: USDA Forest Service. 1:750,000.
- Canfield, D.E., Jr. and R.W. Bachmann. 1981. Prediction of total phosphorus concentrations, chlorophyll *a* and Secchi depths in natural and artificial lakes. *Can. J. Fish. Aquat. Sci.* 38:414-423.

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- Canfield, T.J. and J.R. Jones. 1996. Zooplankton abundance, biomass and size-distribution in selected Midwestern waterbodies and relation with trophic state. *J. Freshw. Ecol.* 11:171-181.
- Carlson, R.E. 1977. A trophic state index for lakes. *Limnol. Oceanogr.* 22:361-369.
- Carlson, R.E. and K.E. Havens. 2005. Simple graphical methods for the interpretation of relationships between trophic state variables. *Lake Reserv. Manage.* 21:107-118.
- Dillon, P.J. and F.H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. *Limnol. Oceanogr.* 19:767-773.
- Dodds, W.K., K.R. Johnson and J.C. Prisco. 1989. Simultaneous nitrogen and phosphorus deficiency in natural phytoplankton assemblages: theory, empirical evidence and implications for lake management. *Lake Reserv. Manage.* 5:21-26.
- Dokulil, M.T. 1994. Environmental control of phytoplankton productivity in turbulent turbid systems. *Hydrobiologia* 289:65-72.
- Downing, J.A. and E. McCauley. 1992. The nitrogen:phosphorus relationship in lakes. *Limnol. Oceanogr.* 19:767-773.
- Downing, J.A., S.B. Watson and E. McCauley. 2001. Predicting Cyanobacterial dominance in lakes. *Can. J. Fish. Aquat. Sci.* 58:1905-1908.
- Duarte, C.M. and J. Kalff. 1989. The influence of catchment geology and lake depth on phytoplankton biomass. *Arch. Hydrobiol.* 115:27-40.
- Dzialowski, A.R., S.-H. Wang, N.-C. Lim, W.W. Spotts and D.G. Huggins. 2005. Nutrient limitation of phytoplankton growth in central plains reservoirs, USA. *J. Plank. Res.* 27:587-595.
- Edmondson, W.T. 1961. Changes in Lake Washington following an increase in the nutrient income. *Verh. Internat. Verein. Limnol.* 14:167-175.
- Edmondson, W.T. 1972. Nutrients and phytoplankton in Lake Washington. *In* G.E. Likens (ed.). *Nutrients and Eutrophication: The limiting-nutrient controversy*. Special Symposium, Amer. Soc. Limnol. *Oceanogr.* 1:172-193.
- Elser, J.J., E.R. Marzolf and C.R. Goldman. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichment. *Can. J. Fish. Aquat. Sci.* 47:1468-1477.
- Erickson, R. 1999. Algal respiration and the regulation of phytoplankton biomass in a polymictic tropical lake (Lake Xolotlán, Nicaragua). *Hydrobiologia* 382:17-25.
- Forsberg, C. and S.-O. Ryding. 1980. Eutrophication parameters and trophic state indices in 30 Swedish waste-receiving lakes. *Arch. Hydrobiol.* 89:189-207.
- Fulmer, D.G. and G.D. Cooke. 1990. Evaluating the restoration potential of 19 Ohio reservoirs. *Lake Reserv. Manage.* 6:197-206.
- Gibson, G., R. Carlson, J. Simpson, E. Smeltzer, J. Gerritson, S. Chapra, S. Heiskary, J. Jones and R. Kennedy. 2000. *Nutrient Criteria Technical Guidance Manual Lakes and Reservoirs*. U.S. Environmental Protection Agency. EPA-822-B00-001.
- Grobbelaar, J.U. 1985. Phytoplankton productivity in turbid waters. *J. Plankton Res.* 7:653-663.
- Hatch, L.K. 2003. Factors affecting Iowa lake and reservoir water quality. *Lake Reserv. Manage.* 19:150-159.
- Heiskary, S.A., C.B. Wilson and D.P. Larsen. 1987. Analysis of regional patterns in lake water quality: using ecoregions for lake management in Minnesota. *Lake Reserv. Manage.* 3:337-344.
- Howarth, R.W., G. Gillen, D. Swaney, A. Townsend, N. Jaworski, *et al.* 1996. Regional nitrogen budgets and riverine N & P fluxes for drainages to the North Atlantic Ocean; natural and human influences. *Biogeochemistry* 35:75-139.
- Hoyer, M.V. and J.R. Jones. 1983. Factors affecting the relation between phosphorus and chlorophyll *a* in midwestern reservoirs. *Can. J. Fish. Aquat. Sci.* 40:192-541.
- Jeppesen, E., M. Sondergaard, B. Kronvang, J.P. Jensen, L.M. Svendsen and T.L. Lauridsen. 1999. Lake and catchment management in Denmark. *Hydrobiologia* 395/396:419-432.
- Jones, J.R. and R.W. Bachmann. 1976. Prediction of phosphorus and chlorophyll levels in lakes. *J. Water Poll. Cont. Fed.* 48:2176-2182.
- Jones, J.R. and R.W. Bachmann. 1978. Trophic status of Iowa lakes in relation to origin and glacial geology. *Hydrobiologia* 57:267-273.
- Jones, J.R. and J.R. Novak. 1981. Limnological characteristics of Lake of the Ozarks, Missouri. *Verh. Internat. Verein. Limnol.* 21:919-925.
- Jones, J.R. and M.S. Kaiser. 1988. Limnological characteristics of Lake of the Ozarks, Missouri II: measurements following formation of a large reservoir upstream. *Verh. Internat. Verein. Limnol.* 23:976-984.
- Jones, J.R., M.F. Knowlton and M.S. Kaiser. 1998. Effects of aggregation on chlorophyll-phosphorus relations in Missouri reservoirs. *Lake Reserv. Manage.* 14:1-9.
- Jones, J.R. and M.F. Knowlton. 1993. Limnology of Missouri reservoirs: an analysis of regional patterns. *Lake Reserv. Manage.* 8:17-30.
- Jones, J.R., M.F. Knowlton and K.-G. An. 2003. Trophic state, seasonal patterns and empirical models in South Korean reservoirs. *Lake Reserv. Manage.* 19:64-78.
- Jones, J.R., M.F. Knowlton, D.V. Obrecht and E.A. Cook. 2004. Importance of landscape variables and morphology on nutrients in Missouri reservoirs. *Can. J. Fish. Aquat. Sci.* 61:1503-1512.
- Jones, J.R. and M.F. Knowlton. 2005a. Suspended solids in Missouri reservoirs in relation to catchment features and internal processes. *Water Research* 39:3629-3635.
- Jones, J.R. and M.F. Knowlton. 2005b. Chlorophyll response to nutrients and non-algal seston in Missouri reservoirs and oxbow lakes. *Lake Reserv. Manage.* 21:361-371.
- Jones, J.R., M.F. Knowlton and D.V. Obrecht. 2008. Role of land cover and hydrology in determining nutrients in mid-continent reservoirs: implications for nutrient criteria and management. *Lake Reserv. Manage.* 24:1-10.
- Jones, R.I. 1977. Factors controlling phytoplankton production and succession in a highly eutrophic lake (Kinnego Bay, Lough Neagh). *J. Ecol.* 65:547-559.
- Kaiser, M.S., P.L. Speckman and J.R. Jones. 1994. Statistical models for limiting nutrient relations in inland waters. *J. Am. Statistical Assoc. Applications and Case Studies.* 89:410-423.
- Kalff, J., H.E. Welch and S.H. Holmgren. 1972. Pigment cycles in two high-arctic Canadian lakes. *Verh. Internat. Verein. Limnol.* 18:250-256.
- Knowlton, M.F., M.V. Hoyer and J.R. Jones. 1984. Sources of variability in phosphorus and chlorophyll and their effects on use of lake survey data. *Water Res. Bull.* 20:397-407.

- Knowlton, M.F. and J.R. Jones. 1989a. Summer distribution of nutrients, phytoplankton and dissolved oxygen in relation to hydrology in Table Rock Lake, a large midwestern reservoir. *Arch. Hydrobiol. Suppl.* 83:197-225.
- Knowlton, M.F. and J.R. Jones. 1989b. Comparison of surfaces and depth integrated composite samples for estimating algal biomass and phosphorus values, and notes on the vertical distribution of autotrophs in midwestern lakes. *Arch. Hydrobiol. Suppl.* 83:175-196.
- Knowlton, M.F. and J.R. Jones. 1990. Occurrence and prediction of algal blooms in Lake Taneycomo. *Lake Reserv. Manage.* 6:143-152.
- Knowlton, M.F. and J.R. Jones. 1995. Temporal and spatial dynamics of suspended sediment, nutrients, and algal biomass in Mark Twain Lake, Missouri. *Arch. Hydrobiol.* 135:145-178.
- Knowlton, M.F. and J.R. Jones. 1996. Experimental evidence of light and nutrient limitation of algal growth in a turbid midwest reservoir. *Arch. Hydrobiol.* 135:321-335.
- Knowlton, M.F. and J.R. Jones. 1997. Trophic status of Missouri River floodplain lakes in relation to basin type and connectivity. *Wetlands* 17:468-475.
- Knowlton, M.F. and J.R. Jones. 2000. Non-algal seston, light, nutrients and chlorophyll in Missouri reservoirs. *Lake Reserv. Manage.* 16:322-332.
- Knowlton, M.F. and J.R. Jones. 2006a. Temporal variation and assessment of trophic state indicators in Missouri reservoirs: implication for lake monitoring and management. *Lake Reserv. Manage.* 22:261-271.
- Knowlton, M.F. and J.R. Jones. 2006b. Natural variability in lakes and reservoirs should be recognized in setting nutrient criteria. *Lake Reserv. Manage.* 22:161-166.
- Kratzer, C.R. and P.L. Brezonik. 1981. A Carlson-type trophic state index for nitrogen in Florida lakes. *Water Res. Bull.* 17: 713-715.
- Lillie, R.A. and J.W. Mason. 1983. *Limnological characteristics of Wisconsin lakes.* Tech. bull. No. 138., Dept. Nat. Resour., Madison, WI.
- Maberly, S.C., L. King, M.M. Dent, R.I. Jones and C.E. Gibson. 2002. Nutrient limitation of phytoplankton and periphyton growth in upland lakes. *Freshw. Biol.* 47:2136-2152.
- Marker, A., E. Nusch, H. Rai and B. Riemann. 1980. The measurement of photosynthetic pigments in freshwaters and standardization of methods: conclusions and recommendations. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 14:91-106.
- McCauley, E., J.A. Downing and S. Watson. 1989. Sigmoid relationships between nutrients and chlorophyll among lakes. *Can. J. Fish. Aquat. Sci.* 46:1171-1175.
- Moyle, J.B. 1956. Relationship between the chemistry of Minnesota surface water and wildlife management. *J. Wild. Manage.* 20:303-320.
- Nigh, T.A. and W.A. Schroeder. 2002. *Atlas of Missouri ecoregions.* Missouri Department of Conservation. 212p.
- Nürnberg, G. 1996. Trophic state of clear and colored, soft- and hardwater lakes with special consideration of nutrients, anoxia, phytoplankton and fish. *Lake Reserv. Manage.* 12:432-447.
- Obrecht, D., A.P. Thorpe and J.R. Jones. 2005. Responses in the James River Arm of Table Rock Lake, Missouri (USA) to point-source phosphorus reduction. *Verh. Internat. Verein. Limnol.* 29:1043-1048.
- Perkins, B.D. and J.R. Jones. 1994. Temporal variability in a midwestern stream during spring. *Verh. Internat. Verein. Limnol.* 25:1471-1476.
- Perkins, B.D., K. Lohman, E.E. Van Nieuwenhuysse and J.R. Jones. 1998. An examination of land cover and stream water quality among physiographic provinces of Missouri, U.S.A. *Verh. Internat. Verein. Limnol.* 26:940-947.
- Perkins, B.D. and J.R. Jones. 2000. Limnological characteristics of Lake of the Ozarks, Missouri III: seasonal patterns in nutrients, chlorophyll and algal bioassays. *Verh. Internat. Verein. Limnol.* 27:2218-2224.
- Prepas, E.E. and A.M. Trimbee. 1988. Evaluation of indicators of nitrogen limitation in deep prairie lakes with laboratory bioassays and limnocorrals. *Hydrobiologia* 158:269-276.
- Prairie, Y.T., C.M. Duarte and J. Kalf. 1989. Unifying nutrient-chlorophyll relationships in lakes. *Can. J. Fish. Aquat. Sci.* 46:1176-1182.
- Reynolds, C.S. 1984. *The ecology of freshwater phytoplankton.* Cambridge University Press, Cambridge. 384pp.
- Spacie, A. and S.L. Loeb. 1990. Long-term trends in trophic state of Indiana lakes (USA) following phosphorus reduction. *Verh. Internat. Verein. Limnol.* 24:464-469.
- Smith, V. 2003. Eutrophication of freshwater and coastal marine ecosystems: A global problem. *Environ. Sci. Pollut. Res.* 10:1101-1112.
- Thom, R.H. and J.H. Wilson. 1980. The natural divisions of Missouri. *Trans. Mo. Acad. Sci.* 4:9-23.
- Thorpe, A.P. and J.R. Jones. 2005. Bacterial abundance in Missouri (USA) reservoirs in relation to trophic state and global patterns. *Verh. Internat. Verein. Limnol.* 29:239-245.
- Turner, R.E. and N.N. Rabalais. 1991. Changes in Mississippi River water quality this century. *BioScience* 41:140-147.
- Thornton, K.W., B.L. Kimmel and F.E. Payne. 1990. *Reservoir limnology: ecological perspectives.* Wiley Interscience, New York. 246p.
- Vighi, M. and G. Chiaudani. 1985. A simple method to estimate lake phosphorus concentrations resulting from natural background, loadings. *Water Res.* 19:987-991.
- Vollenweider, R.A. 1975. Input-output models: with special reference to the phosphorus loading concept in limnology. *Schweiz. Z. Hydrol.* 37:53-84.
- Walker, W.W. 1984. Statistical bases for mean chlorophyll *a* criteria. *Lake Reserv. Manage.* 2:57-62.
- Walmsley, R.D. 1984. A chlorophyll *a* trophic status classification system for South African impoundments. *J. Environ. Qual.* 13:97-104.
- Watanabe, S. 2004. Subsurface light conditions and light attenuation mechanisms in Missouri reservoirs. MS Thesis. University of Missouri, Columbia. 94pp.
- Watson, S.B., E. McCauley and J.A. Downing. 1992. Sigmoid relationships between phosphorus, algal biomass, and algal community structure. *Can. J. Fish. Aquat. Sci.* 49:2605-2610.
- Watson, S.B., E. McCauley and J.A. Downing. 1997. Patterns in phytoplankton taxonomic composition across temperate lakes of different nutrient status. *Limnol. Oceanogr.* 42:487-495.
- Wetzel, R.G. 2001. *Limnology: Lake and River Ecosystems.* Third Edition. Academic Press. 1006pp.