

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 $\Phi\text{g/L}$, 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 $\Phi\text{g/L}$ 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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