

# Non-Algal Seston, Light, Nutrients and Chlorophyll in Missouri Reservoirs

Matthew F. Knowlton and John R. Jones

School of Natural Resources  
302 Anheuser-Busch Natural Resources Building  
University of Missouri, Columbia MO 65211-7240

## ABSTRACT

Knowlton, M. F. and J. R. Jones. 2000. Non-algal seston, light, nutrients and chlorophyll in Missouri reservoirs. *Lake and Reserv. Manage.* 16(4):322-332.

Limnological measurements were performed at five or six Missouri reservoirs in June-September 1992-1995 to examine the relation of light conditions and non-algal seston (NAS) to chlorophyll (CHL) and dissolved nutrient concentrations. NAS was estimated as the sum of non-volatile suspended solids and filterable (Whatman 934AH filter) suspended solids. Mean mixed layer irradiance ( $I_{mix}$ ) varied  $\approx 20$  fold among observations, largely due to variation in light attenuation by NAS. In 42% of the observations,  $I_{mix}$  was less than  $7 E \cdot m^{-2} \cdot d^{-1}$ , a range where light limitation is likely. NAS comprised 15-96% (mean= 58%) of total seston and accounted for 89% of the temporal and inter-site variation in  $I_{mix}$ . NAS was strongly correlated to total phosphorus (TP) and soluble reactive phosphorus (SRP) concentrations ( $r=0.91$  and  $r=0.84$ , respectively,  $p<0.0001$ ). When  $NAS > 5 mg \cdot L^{-1}$  or  $I_{mix}$  was  $< 5 E \cdot m^{-2} \cdot d^{-1}$ , SRP and dissolved inorganic N (DIN) were usually at concentrations capable of saturating algal nutrient uptake ( $SRP > 3 \mu g \cdot L^{-1}$ ,  $DIN > 50 \mu g \cdot L^{-1}$ ), suggesting light limitation replaced nutrient limitation under those conditions. Light limitation resulting from NAS in turbid lakes may alter the relationship of phytoplankton to phosphorus, yielding a CHL-TP relationship that is dome-shaped rather than asymptotic. Variation in the relation of NAS to TP will affect how CHL responds to nutrients in individual waterbodies.

Key Words: reservoirs, phosphorus, nitrogen, chlorophyll, light limitation, non-algal seston, nutrient limitation.

Non-algal seston (NAS), consisting principally of suspended minerals from inflowing streams or lake bottoms, is a common feature of many natural and artificial lakes (Kirk 1985, Carlson 1991, Havens 1995). NAS inputs are often accompanied by increased nutrient concentrations and light limitation of algal growth (Kimmel et al. 1990, Lind et al. 1992), both of which can increase ratios of nutrient availability to algal demand. Consequently, increased NAS is often associated with indications of reduced nutrient limitation such as lower biomass:nutrient ratios (Jones and Novak 1981, Walker 1982, Carlson 1991, Jones and Knowlton 1993, Havens 1994). Understanding the influence of NAS on algal growth and nutrient dependence is important because empirical algal-nutrient relations are a basic tool in lake management and are fundamentally linked to the phenomenon of nutrient limitation. Algal-nutrient models may be of little use for lakes in which nutrients are not limiting to algal growth, or where nutrient limitation is frequently relieved by light limitation, nutrient inputs or other factors such as high loss rates from grazing.

NAS is most likely to affect phytoplankton nutrient status by reducing light availability and, consequently, algal growth and nutrient demand. Light limitation should supplant nutrient limitation when average mixed layer irradiance drops below the "column compensation point" (Talling 1971) at which growth just balances losses. The irradiance at which this balance occurs could vary widely depending on algal community composition and the nature and intensity of loss factors, but field studies from geographically diverse locations suggest that light limitation is likely at irradiances less than about 5 to  $7 E \cdot m^{-2} \cdot d^{-1}$  (Oliver and Ganf 1988, Carignan and Planas 1994, Millard et al. 1996, Knowlton and Jones 1996). Light limitation, or the absence of nutrient limitation, can also be inferred from the presence of dissolved nutrients because nutrient limitation is unlikely when substantial concentrations of inorganic phosphorus (P) and nitrogen (N) are present (Schelske et al. 1978, Reynolds 1997). In most waterbodies soluble reactive phosphorus (SRP) is entirely bioavailable (Bradford and Peters 1987, Lampert and

Sommer 1997) and when present in concentrations greater than  $3 \mu\text{g} \cdot \text{L}^{-1}$  is sufficient saturate the growth requirements of nearly all commonly occurring phytoplankton (Reynolds 1992). Similarly, concentrations of inorganic N greater than  $50\text{-}100 \mu\text{g} \cdot \text{L}^{-1}$  will usually preclude physiological limitation of algal growth by N (Reynolds 1998). Thus joint occurrence of SRP above  $3 \mu\text{g} \cdot \text{L}^{-1}$  and DIN above about  $50 \mu\text{g} \cdot \text{L}^{-1}$  is evidence of N and P sufficiency. In fact, phytoplankton may often be nutrient-sufficient at even lower concentrations (Harris 1986, Hecky and Kilham 1988). If NAS produces light limitation we would expect NAS and dissolved nutrients to be related.

Among reservoirs in Missouri, NAS varies regionally (Jones and Knowlton 1993), it exerts a controlling influence on light conditions in some waterbodies (Jones and Novak 1981, Jones and Knowlton 1993), and is associated with reduced yields of algal biomass relative to total phosphorus (Hoyer and Jones 1983, Jones and Knowlton 1993). In one turbid Missouri reservoir, Knowlton and Jones (1995) found a strong correlation between non-algal light attenuation and nutrients (total nitrogen and total phosphorus), a finding that suggests light limitation increases systematically with nutrient availability. They also found a

weaker, but positive, correlation between non-algal attenuation and total phosphorus among other Missouri reservoirs, but not among waterbodies in Iowa. They recommended a regional approach to assessing the effects of NAS.

To further explore the nature of non-algal materials and their impact on light conditions and algal-nutrient relations we collected survey data from six Missouri reservoirs chosen to represent a gradient in NAS and light conditions (Fig. 1). Our general goal was to explore relationships among NAS, light conditions, nutrients, phytoplankton, and nutrient limitation in these waterbodies to increase our understanding of inter-lake, and inter-regional differences in empirical algal-nutrient relations (Hoyer and Jones 1983, Jones and Knowlton 1993). In this paper we present an analysis of our NAS estimates in relation to our survey data on light attenuation, mixed layer irradiance, nutrient concentrations and algal biomass.

## Materials and Methods

Collections were conducted in Missouri in June-

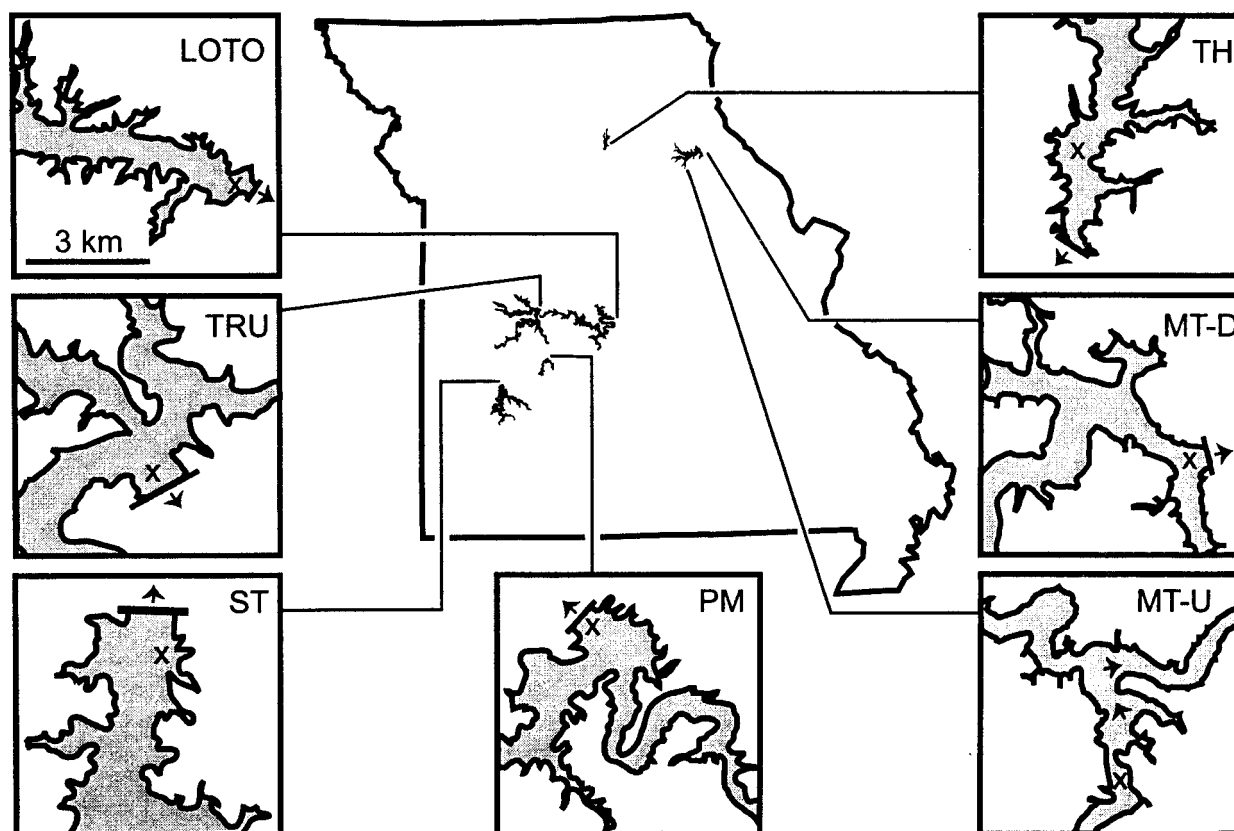


Figure 1.—Study sites and area map. Sampling sites are marked by X's. Reservoir maps share a common scale. Arrows denote direction of outflow or, in MT-D, downlake water movement. Site name abbreviations are defined in the text.

September of 1992-95 at two sites in Mark Twain Lake (an uplake site, MT-U, and downlake site, MT-D) and at single, downlake sites in Thomas Hill Lake (TH), Lake of the Ozarks (LOTO), Pomme de Terre Lake (PM), and Stockton Lake (ST) (Fig. 1). Work in 1992-94 also included one site on Truman Lake (TRU). Reservoir characteristics have been described elsewhere (Knowlton and Jones 1989, Jones and Knowlton 1993, Knowlton and Jones 1995). Major morphological and hydrologic features are listed in Table 1.

Sites were sampled 2-3 times per year. Surface water ( $\approx 100$  L) was composited in a pre-rinsed plastic tub and 4 L collected in a polyethylene bottle for analysis. Samples were stored in the dark 1-2 hours at ambient temperature. Water was then filtered to prepare samples for chlorophyll (CHL) and suspended solids and filtrates for nutrient analysis. Replicate aliquots of filtered and unfiltered water were then dispensed into borosilicate glass tubes for storage. Prepared samples were kept on ice or under refrigeration 1-2 days until analysis.

Water samples were analyzed for total phosphorus (TP - Prepas and Rigler 1982) and total nitrogen (TN - Crumpton et al. 1992), CHL (Gelman A-E glass fiber filters - Sartory and Grobbelaar 1984, Knowlton 1984), total, volatile and non-volatile suspended solids (Whatman 934AH glass fiber filters - American Public Health Association 1985), nephelometric turbidity (American Public Health Association 1985), soluble reactive phosphorus (SRP- Gelman GN-6 filters - American Public Health Association 1985), ammonium-N (Stainton et al. 1977), nitrate-nitrite-N (American Public Health Association 1985). Total phosphorus, TN, and turbidity were measured for both filtered (Whatman 934AH glass fiber filters) and unfiltered lake water. All analyses were performed in triplicate except SRP and turbidity which were measured in duplicate. Dissolved inorganic nitrogen (DIN) was

estimated as the sum of ammonium-N and nitrate-nitrite-N.

In 1992, filterable seston (seston remaining in water passed through Whatman 934-AH filters) was collected on tared  $0.45 \mu\text{m}$  membrane filters (Gelman GN-6), dried to a constant weight and weighed. Turbidity of membrane filtered water was also measured in order to determine the relation between turbidity and dry weight concentration of the filterable seston. Absorbance of the filtrates was also recorded at 440 nm as an measurement of dissolved color (Kirk 1983).

Physical and optical conditions were assessed at the time of sample collection by measuring Secchi depth, temperature and oxygen depth profiles (YSI Model 51 oxygen meter), and vertical diffuse attenuation ( $k_{par}$ ) of photosynthetically active radiation (PAR - Li-Cor LI-1000 data logger with spherical submersible quantum sensor and deck mounted reference cell). Estimates of recent mixed depth ( $Z_{mix}$ ) for each site visit were made from temperature and oxygen profiles. Mixed depth was generally determined as recommended by Talling (1971) except in cases where large oxygen gradients indicated shallower depths of recent mixing. For five observations mixed depth was not estimated because of instrument failure or because sharp multiple thermoclines near the surface and missing oxygen data made meaningful assessment of recent mixing untenable.

Mean incident solar irradiance as PAR ( $\text{E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) was estimated for the five day period prior to each site visit by use of pyrhelimeter data (Li-Cor model LI-200SZ meter) recorded by the University of Missouri Atmospheric Sciences Department at several sites in Missouri (P. Guinan, personal communication). Irradiance at Mark Twain and Thomas Hill lakes was estimated from measurements made near the towns of Clifton Hill, Auxvasse, or Novelty, Missouri, or from an average of these depending on which sites

Table 1.-Study site features. Sites are: Stockton Lake (ST), Pomme de Terre Lake (PM), Lake of the Ozarks (LOTO), Truman Lake (TRU), Thomas Hill Lake (TH) and Mark Twain Lake (MT).

	Surface Area (ha)	Mean Depth (m)	Catchment Area (km <sup>2</sup> )	Shoreline Development	Retention Time (years)
ST	10031	10.9	3006	11.3	1.2
PM	3194	9.3	1583	8.7	0.6
LOTO	24170	10.4	36300	38	0.3
TRU	22510	6.6	29800	29	0.2
TH	1781	4.9	381	6.5	1.0
MT	7550	8.9	6000	14.9	0.5

were in operation at the time. Irradiance for the other lakes was estimated from Clifton Hill data in 1992 when this was the only site in operation and from data collected near Lamar, Missouri in 1993-95. Pyrheliometer measurements were converted to PAR assuming that 1 megajoule total shortwave irradiance = 2.05 Einsteins PAR (Stefan et al. 1983).

Mean mixed layer irradiance ( $I_{mix}$ ) was calculated according to Riley (1957):

$$I_{mix} = PAR \cdot (1 - e^{-(k_{par} \cdot Z_{mix})}) \cdot (k_{par} \cdot Z_{mix})^{-1} \quad (1)$$

Data analysis including simple, multiple and stepwise regressions was conducted using procedures in the SAS System (SAS, 1982).

## Results

### *Ambient conditions*

Light conditions, nutrients, and algal biomass all varied by >8-fold (Table 2) with most variation occurring over time at individual sites. Among reservoirs, average light attenuation, CHL, and total N and P were lowest in Stockton Lake. The two study sites on

Mark Twain Lake were usually the most turbid and nutrient-rich and also exhibited a wider range of TP, SRP, DIN, CHL, and  $k_{par}$  than the others. Light attenuation was typically 2-4 times higher in Mark Twain, Thomas Hill and Truman lakes than in Stockton, Pomme de Terre, and Lake of the Ozarks.

The uplake site on Mark Twain Lake, which is in a relatively narrow and protected portion of the reservoir (Fig. 1), had a mean mixed depth ( $Z_{mix}$ ) of 3.6 m compared to mean mixed depths of 4.9-6.4 m for the other sites (Table 2). Mixing depth was variable at all sites, however, exhibiting ranges of 5-18 m. Deeper strata were undersaturated with dissolved oxygen and anoxia was observed at least occasionally at all sites. Stratification and hypolimnetic anoxia were most stable at Stockton, Pomme de Terre, and Mark Twain lakes. Truman and Lake of the Ozarks, with their short water residence times (Table 1) had weaker stratification. Thomas Hill, the shallowest of the reservoirs (Table 1) was the only site where the mixing zone frequently extended to the lake bottom.

Average mixed layer irradiance differed by  $\approx 3$ -fold among sites, from 4.7  $E \cdot m^{-2} \cdot d^{-1}$  at Thomas Hill to 15.5  $E \cdot m^{-2} \cdot d^{-1}$  in Stockton, but varied from 4-18 fold over time at individual sites.

Thomas Hill Lake was the only site where SRP was always detectable ( $>1 \mu g \cdot L^{-1}$ ) although concentrations

Table 2.—Means and standard deviations of selected variables. For sites ST, PM, and LOTO n=11; for sites TH, MT-D and MT-U n=12; and for site TRU n=7 for all variables except  $Z_{mix}$  and  $I_{mix}$  for which n=10 for ST and PM, n=11 for MT-U and n=5 for TRU.

	$k_{par}$ ( $m^{-1}$ )	SD (m)	$Z_{mix}$ (m)	$I_{mix}$ ( $E \cdot m^{-2} \cdot d^{-1}$ )	TP ( $\mu g \cdot L^{-1}$ )	SRP ( $\mu g \cdot L^{-1}$ )	TN ( $\mu g \cdot L^{-1}$ )	DIN ( $\mu g \cdot L^{-1}$ )	CHL ( $\mu g \cdot L^{-1}$ )
ST	0.6	3.0	5.8	16	12	<1	340	30	7
	$\pm 0.1$	$\pm 1.0$	$\pm 3.2$	$\pm 7$	$\pm 4$	$\pm 0.9$	$\pm 70$	$\pm 50$	$\pm 2$
PM	0.8	2.0	4.9	13	23	<1	530	10	13
	$\pm 0.2$	$\pm 0.5$	$\pm 2.2$	$\pm 5$	$\pm 6$	$\pm 0.9$	$\pm 70$	$\pm 8$	$\pm 5$
LOTO	0.8	2.4	6.4	12	26	2	580	70	13
	$\pm 0.2$	$\pm 0.9$	$\pm 4.9$	$\pm 5$	$\pm 11$	$\pm 1.3$	$\pm 140$	$\pm 90$	$\pm 7$
TRU	1.5	1.3	5.5	7	45	3	740	160	21
	$\pm 0.7$	$\pm 0.6$	$\pm 2.3$	$\pm 4$	$\pm 23$	$\pm 3.5$	$\pm 210$	$\pm 180$	$\pm 12$
TH	2.1	0.8	5.1	5	45	7	720	130	14
	$\pm 0.6$	$\pm 0.4$	$\pm 1.7$	$\pm 4$	$\pm 13$	$\pm 4.6$	$\pm 80$	$\pm 50$	$\pm 4$
MT-D	1.6	1.5	5.0	7	58	17	1280	520	18
	$\pm 1.0$	$\pm 0.7$	$\pm 2.0$	$\pm 4$	$\pm 46$	$\pm 30$	$\pm 480$	$\pm 370$	$\pm 10$
MT-U	2.3	0.9	3.6	7	83	23	1340	440	25
	$\pm 1.0$	$\pm 0.5$	$\pm 1.8$	$\pm 5$	$\pm 43$	$\pm 36$	$\pm 300$	$\pm 250$	$\pm 16$

were usually (10/12 observations) less than  $10 \mu\text{g} \cdot \text{L}^{-1}$ . In contrast, SRP in Pomme de Terre Lake exceeded  $1 \mu\text{g} \cdot \text{L}^{-1}$  only once and in Stockton Lake SRP was never greater than  $2 \mu\text{g} \cdot \text{L}^{-1}$ , a concentration exceeded in Lake of the Ozarks only twice. SRP in Mark Twain Lake was highly variable, ranging from less than  $1 \mu\text{g} \cdot \text{L}^{-1}$  to over  $70 \mu\text{g} \cdot \text{L}^{-1}$  at both sites. DIN fell below  $50 \mu\text{g} \cdot \text{L}^{-1}$  only once at the Mark Twain-Uplake site and at Thomas Hill Lake, twice at Mark Twain-Downlake and three times in Truman Lake. In contrast, DIN never exceeded  $20 \mu\text{g} \cdot \text{L}^{-1}$  at Pomme de Terre Lake and exceeded  $50 \mu\text{g} \cdot \text{L}^{-1}$  only twice at Stockton Lake. At Lake of the Ozarks DIN exceeded  $50 \mu\text{g} \cdot \text{L}^{-1}$  three times.

### Nonalgal Seston

Inorganic particles, especially clay minerals, sometimes dominate the seston in Mark Twain Lake and other turbid reservoirs in Missouri (Jones and Knowlton, 1993, Knowlton and Jones, 1995). This tripton often includes particles small enough to pass through the glass fiber filters (Whatman 934-AH) used to measure non-volatile suspended solids (NVSS). Among samples collected in this study, filtration removed as little as 7% of the total nephelometric turbidity (mean=61% removed by filtration). For samples

with filtrate turbidity  $>1$  NTU, passing filtrates through  $0.45 \mu\text{m}$  membrane filters removed  $>90\%$  of the residual turbidity. We measured the dry weight of filtrate seston ( $\text{TSS}_{\text{filt}}$ ) collected on membrane filters of 29 samples and found that turbidity removed by membrane filtration (in NTUs) bore an approximate 1:1 relationship with  $\text{TSS}_{\text{filt}}$  ( $\text{TSS}_{\text{filt}} = 1.00 \cdot \text{NTU} + 0.24$ ,  $r^2 = 0.99$ ,  $p < 0.0001$ ,  $\text{MSE} = 1.71$ , intercept not significant). We used this relation to estimate  $\text{TSS}_{\text{filt}}$  from filtrate turbidity and then estimated total non-algal seston (NAS) as:

$$\text{NAS} (\text{mg} \cdot \text{L}^{-1}) = \text{NVSS} + \text{TSS}_{\text{filt}} \quad (2)$$

Average NAS differed by  $>13$  fold among sites, from  $1.2 \text{ mg} \cdot \text{L}^{-1}$  for Pomme de Terre Lake to  $16.3 \text{ mg} \cdot \text{L}^{-1}$  for Mark Twain-Uplake (Table 3) with a range of  $0.5\text{--}43 \text{ mg} \cdot \text{L}^{-1}$  in individual observations. An average of 43% of NAS was in the filtrate fraction. As a proportion of total seston ( $\sum \text{TSS} = \text{NAS} + \text{VSS}$ ), NAS ranged from 15–96% with site averages ranging from 32% at Pomme de Terre Lake to 83% for Thomas Hill Lake (Table 3).

### Fractional Light Attenuation

Absorbance of membrane filtrates at 440 nm ( $g_{440}$ , Kirk 1983) measured in 1992 ( $n=20$ ) ranged between

Table 3.—Means and standard deviations of non-algal seston concentration, the proportion of NAS in total seston and the proportions of vertical light attenuation due to phytoplankton pigments ( $k_{\text{chl}}$ ), non-algal seston ( $k_{\text{nas}}$ ) and water plus dissolved materials ( $k_w$ ). Methods of estimation are described in the text.

	n	NAS $\text{mg} \cdot \text{L}^{-1}$	NAS (% $\sum \text{TSS}$ )	$k_{\text{chl}}/k$ (%)	$k_{\text{nas}}/k$ (%)	$k_w/k$ (%)
ST	10	1.3 $\pm 0.8$	44 $\pm 12$	18 $\pm 4$	17 $\pm 9$	64 $\pm 11$
PM	10	1.2 $\pm 0.7$	32 $\pm 13$	25 $\pm 9$	12 $\pm 6$	63 $\pm 12$
LOTO	10	2.2 $\pm 1.5$	50 $\pm 13$	23 $\pm 9$	19 $\pm 8$	58 $\pm 14$
TRU	5	5.3 $\pm 5.3$	53 $\pm 17$	20 $\pm 9$	25 $\pm 13$	55 $\pm 17$
TH	12	12.6 $\pm 7.4$	83 $\pm 6$	11 $\pm 4$	44 $\pm 14$	45 $\pm 13$
MT-D	12	11.1 $\pm 13.8$	65 $\pm 23$	20 $\pm 10$	38 $\pm 29$	42 $\pm 26$
MT-U	12	16.3 $\pm 14.7$	71 $\pm 20$	20 $\pm 13$	45 $\pm 27$	35 $\pm 20$

0.88 and 1.84  $\text{m}^{-1}$  for lakes Truman, Thomas Hill and Mark Twain and between 0.09 and 0.78  $\text{m}^{-1}$  for the other sites. These values correspond roughly to a range of color of only 1-20  $\text{mg} \cdot \text{L}^{-1}$  as platinum-cobalt (University of Missouri, unpublished data), thus water in these reservoirs was not strongly colored (Carlson 1991).

To estimate the relative contribution of NAS to light attenuation we used an indirect, regression-based approach (Oliver 1990). Using CHL (in  $\mu\text{g} \cdot \text{L}^{-1}$ ) as an index of algal biomass, and NAS in  $\text{mg} \cdot \text{L}^{-1}$ , we derived a multiple regression ( $n=71$ ,  $r^2=0.92$ ,  $\text{MSE}=0.066$ ,  $p<0.0001$ ):

$$k_{par} = 0.0154 \cdot \text{CHL} + 0.077 \cdot \text{NAS} + 0.577 \quad (3)$$

The coefficient for CHL (0.0154  $\text{m}^{-1}$ ) is similar to an average value (0.0149  $\text{m}^{-1}$ ) recently derived from the literature by Krause-Jensen and Sand-Jensen (1998). We used the regression coefficients for CHL and NAS to estimate fractional light attenuation for phytoplankton and non-algal seston, calculating the combined contribution of water and soluble substances by difference (Table 3).

Light attenuation by NAS ( $k_{nas}$ ) ranged from 0.4 to 3.3  $\text{m}^{-1}$  with about 20% of the observations exceeding 1.0  $\text{m}^{-1}$ . In contrast, attenuation by phytoplankton pigments ( $k_{chl}$ ) ranged only from 0.06 to 0.8  $\text{m}^{-1}$  (mean=0.24  $\text{m}^{-1}$ ) and attenuation by water and dissolved color ( $k_w$ ) never exceeded 1.3  $\text{m}^{-1}$  (mean=0.58  $\text{m}^{-1}$ ). The uptake site on Mark Twain Lake had the highest average attenuation for both algal and non-algal seston.

Despite the weak coloration of water in these lakes,  $k_w$  was the largest of the three components of  $k_{par}$  at every site except Mark Twain-Uplake (Table 3). In Pomme de Terre and Stockton lakes,  $k_w$  averaged over 60% of  $k_{par}$ . Attenuation by NAS averaged about 40% of  $k_{par}$  in Thomas Hill and Mark Twain Lakes but ranged up to 90% of  $k_{par}$  in individual observations. Attenuation by NAS was usually less than 20% of  $k_{par}$  in Stockton, Pomme de Terre and Lake of the Ozarks. Attenuation due to phytoplankton CHL averaged only 11% of  $k_{par}$  in Thomas Hill compared to means of 18-25% for the other sites.

Of the three components of  $k_{par}$ ,  $k_{nas}$  was the most variable with an overall coefficient of variation ( $\text{CV} = 100 \cdot \text{SD} \cdot \text{mean}^{-1}$ ) of 134%. CV's for  $k_{chl}$  and  $k_w$  were 67% and 44%, respectively. Because of its greater variability, variation in  $k_{nas}$  had a larger influence on overall variability in light attenuation than  $k_w$  and  $k_{chl}$  despite one or both of these coefficients exceeding  $k_{nas}$  in over 80% of our observations. In partitioning the variation in light attenuation with stepwise multiple regression (SAS, 1982),  $k_{nas}$ ,  $k_w$  and  $k_{chl}$  accounted for 89%, 8% and 3%, respectively, of the total variation in  $k_{par}$  in the

data set as a whole. Among the three least turbid sites (Stockton, Pomme de Terre and Lake of the Ozarks) this trend was reversed with  $k_{nas}$ ,  $k_w$ , and  $k_{chl}$  accounting for 11%, 27%, and 62%, respectively, of the variation in  $k_{par}$ .

### $I_{mix}$

Of the three measurements determining  $I_{mix}$  (equation 1) incident PAR with a CV of 21% was the least variable and consequently contributed least to variation in underwater irradiance. Light attenuation (CV=63%) and mixed depth (CV=55%) were similarly variable and jointly accounted for most variation in  $I_{mix}$ . Light attenuation and NAS were highly correlated ( $r=0.94$ ,  $p<0.0001$ ), thus NAS was a major factor in determining the upper limit of mixed layer irradiance for a given range of incident light and mixed depth (Fig. 2). When NAS exceeded about 15  $\text{mg} \cdot \text{L}^{-1}$ ,  $I_{mix}$  was always less than 5  $\text{E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . But low irradiance was not restricted to situations of high turbidity,  $I_{mix}$  as low as 2  $\text{E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  was observed under relatively transparent conditions ( $\text{NAS} < 2$ ,  $k_{par} < 1$ ) because of deep mixing or cloud cover.

### Nutrients, NAS and $I_{mix}$

Concentrations of NAS (Fig. 3) were strongly and positively related to TP ( $r=0.91$ ,  $p<0.0001$ ) and SRP ( $r=0.84$ ,  $p<0.0001$ ) and, to a lesser extent, DIN ( $r=0.62$ ,  $p<0.0001$ ). SRP and DIN at or below their detection limits (1  $\mu\text{g} \cdot \text{L}^{-1}$  and 5  $\mu\text{g} \cdot \text{L}^{-1}$ , respectively) were only observed at NAS concentrations below 5  $\text{mg} \cdot \text{L}^{-1}$ . In that range of NAS ( $n=43$ ), SRP exceeded 3  $\mu\text{g} \cdot \text{L}^{-1}$  in only 6 observations, but high DIN was common, exceeding 50  $\mu\text{g} \cdot \text{L}^{-1}$  in 13 observations and ranging up to 880  $\mu\text{g} \cdot \text{L}^{-1}$ .

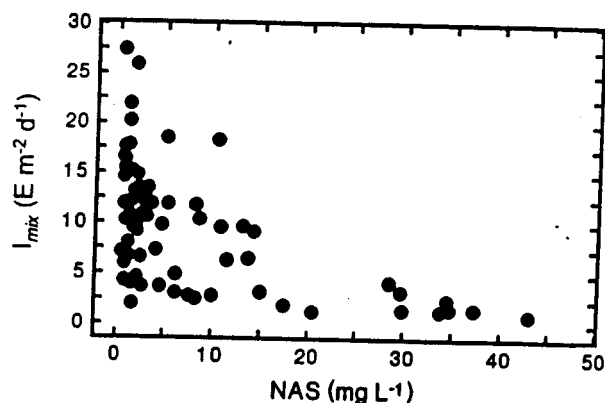


Figure 2.—Relation of mean mixed layer irradiance ( $I_{mix}$ ) to non-algal seston (NAS).

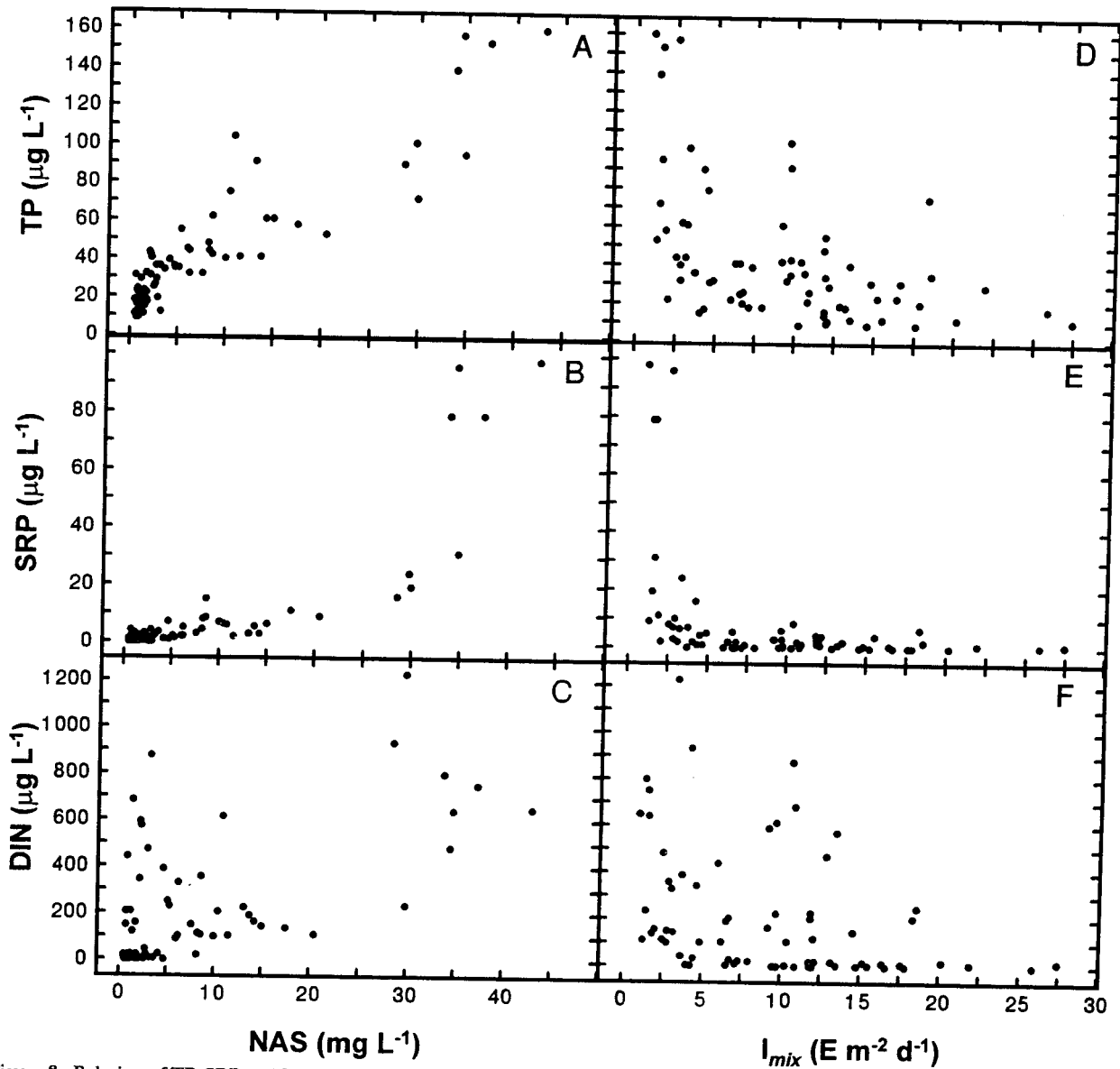


Figure 3.—Relation of TP, SRP and DIN to non-algal seston (NAS) and mean mixed layer irradiance ( $I_{mix}$ ).

Nutrients declined, more or less hyperbolically with increasing  $I_{mix}$ , especially SRP. After linearizing the data by double  $\log_{10}$  transformation the correlation of  $I_{mix}$  to SRP was  $-0.68$  ( $p < 0.001$ ), compared to correlations of  $-0.60$  ( $p < 0.0001$ ) and  $-0.49$  ( $p < 0.0001$ ) for TP and DIN.

### Biomass and P

A plot of our CHL and TP measurements (Fig. 4) has the wedge shape typical of plots for unaveraged, untransformed data (Knowlton and Jones 1995). Minimum CHL was more or less constant across the range

of TP, but maximum CHL increased with TP. SRP also increased with TP ( $r = 0.85$ ,  $p < 0.0001$ ). Detectable SRP ( $\geq 1 \mu\text{g L}^{-1}$ ) was always present at TP greater than  $36 \mu\text{g L}^{-1}$  and usually exceeded  $3 \mu\text{g L}^{-1}$  (Fig. 4).

Ratios of CHL:TP declined with increasing SRP and NAS and were typically lower at values of  $I_{mix}$  less than  $5 \text{ E m}^{-2} \text{d}^{-1}$  than at higher irradiances (Fig. 5). But variation in CHL:TP was large, and only observations from the most turbid conditions ( $\text{NAS} > 30 \text{ mg L}^{-1}$ ,  $I_{mix} < 2 \text{ E m}^{-2} \text{d}^{-1}$ ) usually had CHL:TP below the range exhibited under conditions of higher irradiances, low SRP and low NAS where phosphorus limitation seems most likely. CHL:TP showed only a weak negative correlation ( $r = -0.32$ ,  $p = 0.0048$ ) to DIN (Fig. 5d).

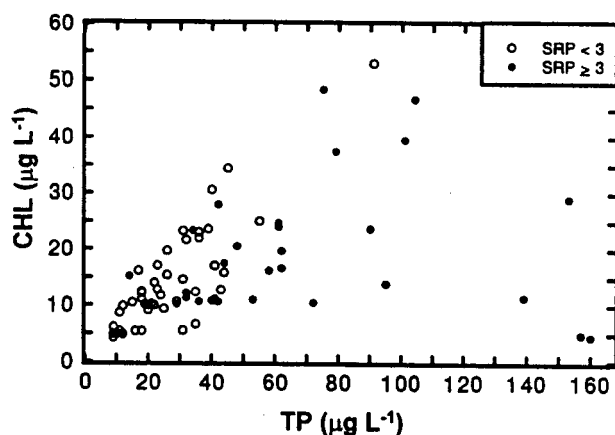


Figure 4.—Relation of chlorophyll (CHL) to total phosphorus (TP) for observations with SRP  $\geq 3 \mu\text{g} \cdot \text{L}^{-1}$  (solid circles) or  $< 3 \mu\text{g} \cdot \text{L}^{-1}$  (open circles).

## Discussion

### *NAS and Light Limitation*

Non-algal seston is a limnological feature of Missouri reservoirs that varies widely among regions in the state (Jones and Knowlton 1993). It has drawn our attention for that reason and because of the possible influence of these materials on phytoplankton dynamics and related lake management issues. As a step in the quantification of non-algal seston, we have defined NAS as the mineral (non-volatile) fraction of seston retained by Whatman 934-AH glass fiber filters, plus all seston not retained by these filters, under the assumption that these fractions are dominated by allochthonous or resuspended minerals. This assumption seems reasonable, if approximate. In all likelihood, some portion of NVSS and TSS<sub>fit</sub> are of algal origin and some portion of VSS is not. Given the large fraction of the seston sometimes missed by conventional TSS determinations (up to 84% in this data set), NAS as we have measured it (NVSS + TSS<sub>fit</sub>) at least provides a better index of non-algal seston than NVSS alone (Jones and Knowlton 1993) or TSS corrected for algal biomass (e.g., Philips et al. 1995).

Our interest in NAS is focused on its effect on light attenuation and underwater irradiance. In the reservoirs examined, NAS was largely responsible for inter-lake variation in transparency although NAS seldom accounted for even half of  $k_{par}$ . The greatest attenuation was usually attributable to water and dissolved color even though water in these reservoirs is not strongly colored (Table 3). This result was not unexpected because clays and other suspended minerals affect light more through non-absorptive scatter-

ing than absorption, while the opposite is true of water and dissolved substances (Kirk 1983). Vertical light attenuation varies in direct proportion to absorption but only in proportion to the square root of scattering (Kirk 1985). Thus light attenuation by NAS is relatively weak on a specific weight basis.

Similarly, specific attenuation by NAS is also weak compared to that of algal pigments. Expressed on an equal weight basis our estimated attenuation coefficient for CHL is 200 times that of NAS (equation 3). Together  $k_{chl}$  and  $k_w$  nearly always contributed more to total attenuation than  $k_{nas}$ , but unlike NAS and phytoplankton, dissolved color seems to have been relatively constant within and among lakes and NAS was much more variable among lakes than CHL. Thus on an inter-lake basis, NAS dominated variation in transparency and underwater irradiance. On an intra-lake basis, however, NAS was of consequence only in the three most turbid reservoirs. Phytoplankton controlled light attenuation in Stockton, Pomme de Terre and Lake of the Ozarks.

Low light can reduce algal growth to the point where nutrient supply exceeds demand. Work in lakes and marine habitats around the world discussed by Oliver and Ganf (1988) and Carignan and Planas (1994) suggests that mean mixed layer irradiance less than about  $7 \text{ E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  may preclude nutrient limitation. Work in Lake Ontario (Millard et al. 1996) and Mark Twain Lake (Knowlton and Jones 1996) indicates that critical irradiance may be somewhat lower ( $4.6 \text{ E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) in those systems. In this study,  $I_{mix}$  was below  $7 \text{ E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  in 42% of our observations, including about 60% of measurements from Truman and Mark Twain lakes, and 83% of measurements from Thomas Hill Lake. In the other lakes  $I_{mix}$  was less than  $7 \text{ E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  in fewer than 20% of observations and occurred only during periods of unusually deep mixing (8-20 m).

We have no completely unequivocal information on the nutrient status of phytoplankton in this study, but concentrations of dissolved nutrients permit some useful inferences. Typical phytoplankton have such a high affinity for inorganic nutrients that uptake, especially for P, can greatly exceed growth requirements and rapid recycling of nutrients can supply algal needs at very low ambient concentrations (Reynolds 1992, Reynolds 1997). Thus it has long been recognized that the absence of inorganic N and P provides no guarantee that nutrients are limiting to growth. Conversely, the presence of measurable inorganic N and P suggests the absence of N and P limitation. For our purposes, we have accepted concentrations of  $3 \mu\text{g} \cdot \text{L}^{-1}$  SRP and  $50 \mu\text{g} \cdot \text{L}^{-1}$  DIN as indicators of non-nutrient limitation of algal growth following the analysis and arguments put forth by Reynolds (Reynolds 1992,



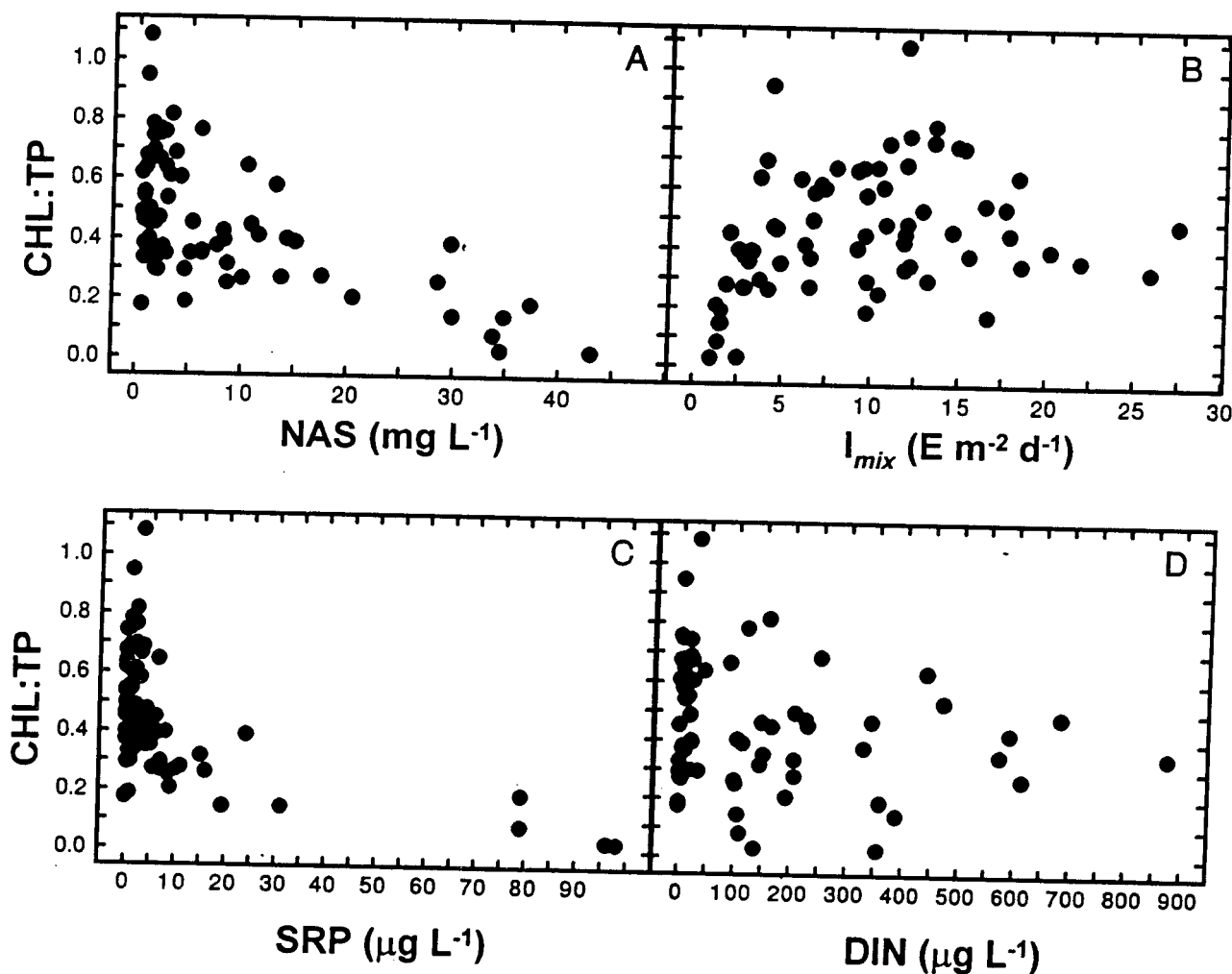


Figure 5.—Relation of chlorophyll:total P (CHL:TP) ratio to NAS,  $I_{mix}$ , SRP, and DIN.

Reynolds 1998). Considering the capability of most algae to take up and store nutrients, especially P, in excess of their immediate needs (Reynolds 1984), these criteria probably under-represent the frequency of N and P sufficiency. As for other algal nutrients, growth limitation seems unlikely apart from possible silica limitation of diatoms. We did not measure silica in this study, but in previous work on these reservoirs (Jones and Knowlton 1993) we sometimes found silica concentration less than  $0.2 \text{ mg} \cdot \text{L}^{-1}$  in Pomme de Terre, Stockton and Truman lakes. Other nutrients were probably available in excess of algal demand. We conducted algal growth bioassays concurrent to this study (University of Missouri, unpublished data) and found addition of N and P in combination always produced greater growth as CHL and particulate N than in controls. Thus sufficiency of N and P can be taken to indicate overall nutrient sufficiency for at least some populations in the phytoplankton community.

Among our observations, 61% had SRP above  $1 \text{ } \mu\text{g} \cdot \text{L}^{-1}$ , 34% had SRP above  $3 \text{ } \mu\text{g} \cdot \text{L}^{-1}$ . DIN exceeded  $50 \text{ } \mu\text{g} \cdot \text{L}^{-1}$  in 54% of our observations and exceeded  $100 \text{ } \mu\text{g} \cdot \text{L}^{-1}$  in 51%. About a fourth of our observations had both SRP above  $3 \text{ } \mu\text{g} \cdot \text{L}^{-1}$  and DIN above  $50 \text{ } \mu\text{g} \cdot \text{L}^{-1}$ . These data suggest that non-nutrient limitation of phytoplankton was a relatively frequent phenomenon in these reservoirs, a finding consistent with the high frequency of low light conditions.

The presence of nutrients sufficient to saturate algal demands might owe to the intervention of other limiting factors independent of light conditions. Of these, heavy grazing by zooplankton or dilution by inflows seem the most likely candidates (Reynolds 1997). In general, Missouri reservoirs tend to lack large ( $>1 \text{ mm}$ ) *Daphnia* (Canfield and Jones 1996), the zooplankton most commonly associated with grazing control of algal biomass (Mazumder 1994), but we can not rule out some herbivore influence on CHL. Because of the downlake locations of most of our sam-

pling sites (Fig. 1), however, dilution by inflow events was probably not an influential factor except, perhaps, at the uplake site on Mark Twain Lake. In Mark Twain Lake, inflows are usually very turbid (Knowlton and Jones 1995), thus the effects of rapid flushing and light limitation would be difficult to distinguish in any case. Nutrient inputs from upwelling, deepened mixing or regeneration of materials following a population decline are other examples of phenomena that might increase dissolved nutrients in the absence of light limitation and may have influenced our results. Also, replacing nutrient limitation with light limitation would not necessarily produce increases in dissolved nutrients, especially in the short term. Thus it is understandable that our data show no exact correspondence between  $I_{mix}$  and dissolved N and P (Fig. 3). We observed undetectable SRP ( $<1 \mu\text{g} \cdot \text{L}^{-1}$ ) and DIN ( $<5 \mu\text{g} \cdot \text{L}^{-1}$ ) at irradiances less than  $4 \text{E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  and found presumably saturating concentrations of P and N in the upper range of  $I_{mix}$  (Fig. 3). Nonetheless, there was a preponderance of high SRP and DIN values when irradiance was low. Of 25 observations with  $I_{mix}$  less than  $5 \text{E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  only four had DIN less than  $50 \mu\text{g} \cdot \text{L}^{-1}$  and only six had SRP less than  $3 \mu\text{g} \cdot \text{L}^{-1}$ . Higher irradiance did not preclude high DIN, but of 47 observations with  $I_{mix}$  above  $5 \text{E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ , only eight had SRP greater than  $3 \mu\text{g} \cdot \text{L}^{-1}$ . Thus most occurrences of potentially growth-saturating concentrations of SRP may be the result of light limitation. The fact that NAS and SRP are highly correlated (Fig. 3b) suggests that NAS may provide a reasonable index of potential light limitation.

### Light Limitation and Algal-Nutrient Relations

The expected relationship between phytoplankton biomass and phosphorus is non-linear (McCauley et al. 1989, Reynolds 1992) as seems to be the case among reservoirs in Missouri (Jones and Knowlton 1993). This is partly because P becomes decreasingly likely to limit algal growth as its supply increases (Reynolds 1992) and thus biomass comes under the control of other growth limiting factors such as light or nitrogen. Our data support this explanation insofar as dissolved nutrient concentrations indicate that P may often be growth-saturating in the upper range of TP in these waterbodies. Of 28 observations with TP exceeding  $40 \mu\text{g} \cdot \text{L}^{-1}$ , 79% had SRP greater than  $3 \mu\text{g} \cdot \text{L}^{-1}$  (Fig. 4) and half had SRP greater than  $6 \mu\text{g} \cdot \text{L}^{-1}$ . Surprisingly, nitrogen limitation may be even less frequent than phosphorus limitation in this upper range of TP. Only three observations with TP greater than  $40 \mu\text{g} \cdot \text{L}^{-1}$  had DIN less than  $50 \mu\text{g} \cdot \text{L}^{-1}$  and a great

majority (86%) had DIN over  $100 \mu\text{g} \cdot \text{L}^{-1}$ . Irradiance, NAS and TP were highly intercorrelated in these data (e.g., Fig. 2, 3). Of the observations with TP over  $40 \mu\text{g} \cdot \text{L}^{-1}$  all but two had NAS exceeding  $5 \text{mg} \cdot \text{L}^{-1}$ ,  $I_{mix}$  less than  $5 \text{E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ , or both. Thus light limitation is a plausible explanation for the frequent lack of nutrient deficiency in evidence for this upper range of TP.

Among the reservoirs in this study NAS and non-algal light attenuation are strongly correlated to TP (Fig. 3). Non-algal attenuation and TP are also positively correlated in a larger group of Missouri reservoirs we have previously compared (Knowlton and Jones 1995). We did not, however, find any correlation between non-algal attenuation and TP among lakes and reservoirs in Iowa (Knowlton and Jones 1995) and we have identified several reservoirs in Missouri where the NAS-TP relation seems not to hold (University of Missouri unpublished data).

These findings are important because they suggest that fundamental differences exist between expected nutrient-algal models for different lakes. Under the standard scenario of asymptotic algal-nutrient relations (Reynolds 1992), biomass in the asymptotic range is light limited with ambient light reduced to the critical irradiance (column compensation point) at which growth and losses balance (Wofsy 1983). The asymptotic biomass and nutrient levels at which it occurs are partly a function of non-algal light attenuation and thus may vary overtime and among lakes with changing light conditions. But if non-algal light attenuation increases systematically with nutrients the expected relationship becomes domed, rather than asymptotic, with biomass declining over the upper range of nutrients as light available for algal growth diminishes. This is a pattern we have previously observed in Mark Twain Lake (Knowlton and Jones 1995) and which may apply to other water bodies in which nutrients and non-algal attenuation are related (James and Havens 1997).

**ACKNOWLEDGMENTS:** This work was funded by the Missouri Department of Natural Resources. Thanks to the numerous students and staff of the University of Missouri who helped in the field. We also thank two anonymous reviewer for their valuable suggestions.

### References

- American Public Health Association. 1985. Standard methods for the examination of water and wastewater. 16th. American Public Health Association, New York, NY.
- Bradford, M. E. and R. H. Peters. 1987. The relationship between chemically analyzed phosphorus fractions and bioavailable phosphorus. *Limnol. Oceanogr.* 32:1124-1137.

- Canfield, T. J. and J. R. Jones. 1996. Zooplankton abundance, biomass, and size-distribution in selected Midwestern waterbodies and relation with trophic state. *J. Freshwater Ecol.* 11:171-181.
- Carignan, R. and D. Planas. 1994. Recognition of nutrient and light limitation in turbid mixed layers: three approaches compared in the Paraná floodplain (Argentina). *Limnol. Oceanogr.* 39:580-596.
- Carlson, R. E. 1991. Expanding the trophic state concept to identify non-nutrient limited lakes and reservoirs. P. 59-71. *In: Proceedings of a National Conference on Enhancing the States' Lake Management Programs: Monitoring and Lake Impact Assessment - U.S. Environmental Protection Agency.*
- Crumpton, W. G., T. M. Isenhardt and P. D. Mitchell. 1992. Nitrate and organic N analyses with second-derivative spectroscopy. *Limnol. Oceanogr.* 37:907-913.
- Harris, G. P. 1986. *Phytoplankton Ecology*. Chapman and Hall. London. 384 p.
- Havens, K. E. 1994. Seasonal and spatial variation in nutrient limitation in a shallow sub-tropical lake (Lake Okeechobee, Florida) as evidenced by trophic state index deviations. *Arch. Hydrobiol.* 131:39-53.
- Havens, K. E. 1995. Particulate light attenuation in a large subtropical lake. *Can. J. Fish. Aquat. Sci.* 52:1803-1811.
- Hecky, R. E. and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.* 33:796-822.
- 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.* 40:192-199.
- James, R. T. and K. E. Havens. 1997. Algal bloom probability in a large subtropical lake. *Water Resour. Bull.* 32:995-1006.
- Jones, J. R. and M. F. Knowlton. 1993. Limnology of Missouri reservoirs: An analysis of regional patterns. *Lake and Reserv. Manage.* 8:17-30.
- Jones, J. R. and J. T. Novak. 1981. Limnological characteristics of Lake of the Ozarks, Missouri. *Verh. Int. Ver. Theoret. Angew. Limnol.* 21:919-925.
- Kimmel, B. L., O. T. Lind, and L. J. Paulson. 1990. Reservoir primary production. Chapter 6 in *Reservoir Limnology: Ecological perspectives*. K. W. Thornton, B. L. Kimmel and F. E. Payne (eds.). John Wiley and Sons, NY.
- Kirk, J. T. O. 1983. *Light and photosynthesis in aquatic ecosystems*. Cambridge University Press. Cambridge. 401 p.
- Kirk, J. T. O. 1985. Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. *Hydrobiol.* 125:195-208.
- Knowlton, M. F. 1984. Flow-through microcuvette for fluorometric determination of chlorophyll. *Water Res. Bull.* 20:795-799.
- Knowlton, M. F. and J. R. Jones. 1989. Comparison of surface and depth-integrated composite samples for estimating algal biomass and phosphorus values and notes on the vertical distribution of algae and photosynthetic bacteria in midwestern lakes. *Arch. Hydrobiol./Suppl.* 83:175-196.
- 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.
- Krause-Jensen, D. and S. Sand-Jensen. 1998. Light attenuation and photosynthesis of aquatic plant communities. *Limnol. Oceanogr.* 43:396-407.
- Lampert, W. and U. Sommer. 1997. *Limnology*. Oxford University Press, New York. 382 p.
- Lind, O. T., R. Doyle, D. S. Vodopich, B. G. Trotter, J. Gualberto Limón and L. Dávalos-Lind. 1992. Clay turbidity: Regulation of phytoplankton production in a large, nutrient-rich tropical lake. *Limnol. Oceanogr.* 37:549-565.
- Mazumder, A. 1994. Phosphorus-chlorophyll relationships under contrasting herbivory and thermal stratification: predictions and patterns. *Can. J. Fish. Aquat. Sci.* 51:390-400.
- 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.
- Millard, E. S., D. D. Myles, O. E. Johannsson and K. M. Ralph. 1996. Seasonal phosphorus deficiency of Lake Ontario phytoplankton at two index stations: light versus phosphorus limitation of growth. *Can. J. Fish. Aquat. Sci.* 53:1112-1124.
- Oliver, R. L. 1990. Optical properties of waters in the Murray-Darling Basin, South-eastern Australia. *Aust. J. Mar. Freshwater Res.* 41:581-601.
- Oliver, R. L. and G. G. Ganf. 1988. The optical properties of a turbid reservoir and its phytoplankton in relation to photosynthesis and growth (Mount Bold Reservoir, South Australia). *J. Plank. Res.* 10:1155-1177.
- Phlips, E. J., T. C. Lynch and S. Badyal. 1995. Chlorophyll a, tripton, color, and light availability in a shallow tropical inner-shelf lagoon, Florida Bay, USA. *Marine Ecol. Progr. Series.* 127:223-234.
- Prepas, E. E. and F. A. Rigler. 1982. Improvements in quantifying the phosphorus concentration in lake water. *Can. J. Fish. Aquat. Sci.* 39:822-829.
- Reynolds, C. S. 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge.
- Reynolds, C. S. 1992. Eutrophication and the management of planktonic algae. What Vollenweider couldn't tell us. P. 4-29. *In: Eutrophication: Research and Application to Water Supply*. Sutcliffe, D.W. and J.G. Jones eds. *Freshwater Biological Association, Ambleside.*
- Reynolds, C. S. 1997. *Vegetation processes in the pelagic: A model for ecosystem theory*. Ecological Institute. Oldendorf/Luhe, Germany.
- Reynolds, C. S. 1998. What factors influence the species composition of phytoplankton in lakes of different trophic status? *Hydrobiol.* 369/370:11-26.
- Riley, G. A. 1957. Phytoplankton of the north central Sargasso Sea. *Limnol. Oceanogr.* 2:252-270.
- Sartory, D. P. and J. U. Grobbelaar. 1984. Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiol.* 114:177-187.
- SAS. 1982. *SAS User's Guide: Statistics*. 1982 Edition. SAS Institute Inc. Cary, NC.
- Schelske, C. L., E. D. Rothman and M. S. Simmonds. 1978. Comparison of bioassay procedures for growth-limiting nutrients in the Laurentian Great Lakes. *Mitt. Internat. Verein. Limnol.* 21:65-80.
- Stainton, M. P., M. S. Capel and F. A. J. Armstrong. 1977. *Chemical Analysis of Fresh Water*. 2nd. Can. Fish. Mar. Serv. Misc. Spec. Pub. No. 25. Winnipeg, Manitoba.
- Stefan, H. G., J. J. Cardoni, F. R. Schiebe and C. M. Cooper. 1983. Model of light penetration in a turbid lake. *Water Resources Res.* 19:109-120.
- Talling, J. F. 1971. The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. *Mitt. Internat. Verein. Limnol.* 19:214-243.
- Walker, W. W., Jr. 1982. An empirical analysis of phosphorus, nitrogen, and turbidity effects on reservoir chlorophyll a levels. *Can. Water Resour. J.* 7:88-107.
- Wofsy, S. C. 1983. A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters. *Limnol. Oceanogr.* 28:1141-1155.