

Temporal and spatial dynamics of suspended sediment, nutrients, and algal biomass in Mark Twain Lake, Missouri¹

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With 19 figures in the text

Abstract: Suspended sediment, nutrients and algal chlorophyll (CHL) were monitored over a 29 month period at 19 sites in Mark Twain Lake, a 7550 ha reservoir in northeastern Missouri. Sampling began during a record drought and continued through subsequent periods of average rainfall. Turbid inflows (≈ 1000 mg/L TSS) during flood events produced consistently high concentrations of suspended sediment (> 200 mg/L) and nutrients (TP > 300 μ g/L, TN > 2 mg/L) in headwater areas, but effects in the reservoir mainstem varied with thermal regime. Inflows during winter mixing affected the entire waterbody while inflows during stratified periods had little effect on surface strata in the mainstem. Loading of nutrients and sediment to the trophogenic zone thus depended less on quantity of inputs than their timing. The size range of suspended materials initially declined with increasing hydraulic residence time but subsequently increased as organic, presumably, autochthonous seston replaced allochthonous minerals as the dominant particle type. Algal blooms seemed to increase sedimentary loss of mineral seston from the epilimnion. Dynamics of phosphorus and suspended sediment were closely parallel and dominated by fluvial inputs. Dynamics of TN, organic N, nitrate and ammonia, however, seemed equally affected by external inputs and internal cycling and TN exhibited far less year to year variation than TSS or TP. CHL time series revealed numerous brief blooms with little temporal or spatial consistency. Phytoplankton may have become nutrient limited during blooms but were probably light limited except during clear water periods near the start and end of the study. On the basis of growth experiments and maximum areal CHL, algal biomass was probably light limited at irradiances $< 2-5$ $E\ m^{-2}\ d^{-1}$, a range comprising 79 % of our observations. The strong relation between phosphorus and suspended material in Mark Twain Lake holds for other Missouri reservoirs and

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results in a dome-shaped CHL-TP relation in which phytoplankton are P-limited at low TP (low turbidity) and light limited at high TP (high turbidity). This trend is less evident among Iowa lakes and is probably region-specific.

Introduction

Nonalgal turbidity is an important environmental factor in many lakes and especially in those with catchments with highly erodible soils (HERGENRADER & HAMMER 1971, HOWARD-WILLIAMS 1985, LIND 1986). This group includes artificial lakes whose location on large rivers makes them repositories for freshly eroded soils containing high concentrations of plant nutrients and finely divided mineral particles (SØBALLE & KIMMEL 1990). Loading of these materials to reservoirs can have antagonistic effects on algal productivity by increasing nutrient supplies while reducing availability of light (JONES & NOVAK 1981, HOYER & JONES 1983). Inputs of sediment and nutrients to reservoirs are often dominated by major storms (KENNEDY et al. 1981, JAMES et al. 1987) that result in highly variable conditions for algal growth over time. And the complex morphology of large reservoir basins can produce extreme spatial variation. Understanding the interplay of nutrients, suspended sediments, hydrology, and morphology is essential to understanding algal dynamics in these systems (KENNEDY & WALKER 1990, KIMMEL et al. 1990).

Factors controlling nonalgal turbidity in lakes vary regionally and undoubtedly represent a continuum of effects (SØBALLE & KIMMEL 1990). We were interested in the upper extreme of the continuum for midwestern reservoirs. Mark Twain Lake, Missouri, drains an agricultural basin ($\approx 6000 \text{ km}^2$) with high rates of soil erosion (SCS 1988) which annually contribute about 15 kg of sediment for each square meter of lake surface (FINNEY 1986). Previous work on reservoirs in the region (JONES & KNOWLTON 1993) has ranked Mark Twain Lake among the most turbid large reservoirs in the state. A record drought in northern Missouri in 1987–1989 ended with near average rainfall in 1990, a sequence of hydrologic conditions that produced unusually large variation in sediment inputs to Mark Twain Lake.

On the basis of comparative studies of lakes in the region (HOYER & JONES 1983, JONES & KNOWLTON 1993, KNOWLTON & JONES 1993) we hypothesized that nutrients would constrain algal dynamics during drought periods when sediment and nutrient inputs were low, but that phytoplankton would tend toward light limitation under more typical hydrologic conditions. In order to test this hypothesis and gain insight into temporal and spatial dynamics of this large waterbody we monitored suspended sediment, nutrients, algal biomass and related variables at 19 sites on the lake for 29 months during the drought and post-drought period in 1989–1991. Among our specific objecti-

ves were: to determine the relation of lake-wide variation in suspended sediment and nutrient concentrations to inflow and thermal regime; to quantify and compare factors (suspended sediment, algal biomass, incident light, mixed depth) controlling underwater irradiance; to estimate the relative importance of nutrient deficiency versus light limitation in controlling algal biomass. We were also interested in the seasonality and spatial distribution of algal blooms and whether regional models of algal-nutrient relations would provide reasonable predictions of average algal biomass for a waterbody with such variable nutrient and light conditions.

Data base

Routine collection of water samples and field data began in July 1989. Nineteen sampling sites (Fig. 1) were established in fall 1989 and sampled during ice-free periods at 3 to 5 week intervals through November 1991. Routine sampling included measure-

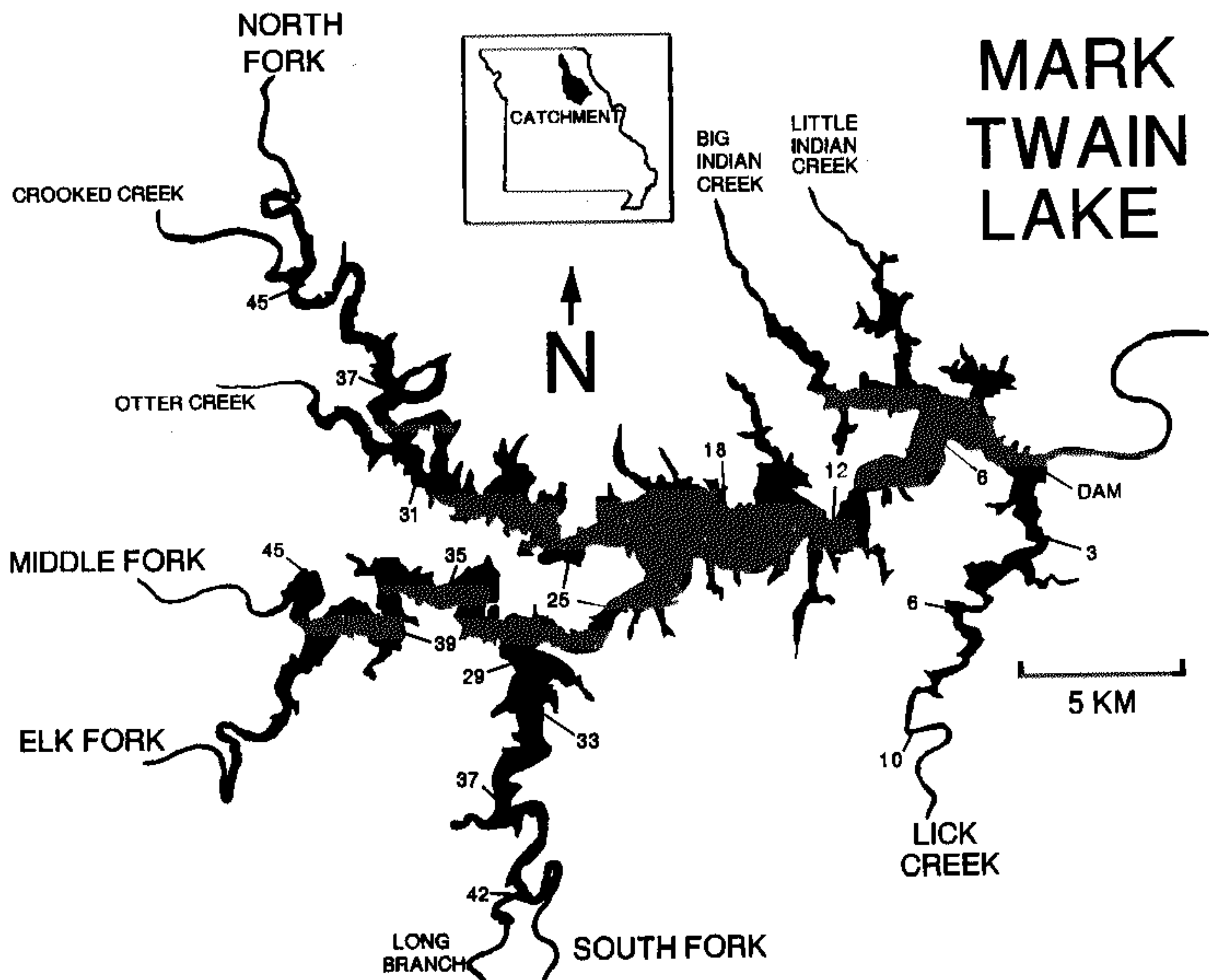


Fig. 1. Mark Twain Lake (surface elevation = 187 m MSL) and the catchment and major tributaries of the Salt River. Routine sample sites are designated by their distance (km) from the dam along the river channel.

ment of Secchi disk transparency, temperature and dissolved oxygen profiles (YSI Model 51B meter) and collection of water samples from the surface (4 L) and several subsurface depths (0.06 L). Vertical extinction of PAR (k_{par}) was determined in about a third of the observations ($n=230$) using a Li-Cor LI-1000 data logger with spherical submersible quantum sensor and deck mounted reference cell.

Subsurface samples were analyzed for specific conductance (25 °C) and nephelometric turbidity. Unfiltered surface samples were analyzed for chlorophyll (CHL), total phosphorus (TP), total nitrogen (TN), nephelometric turbidity, absorbance (440 nm), specific conductance (25 °C), and suspended solids. Suspended solids were measured gravimetrically from the residue retained by glass fiber filters (Whatman 934-AH). Total, volatile (550 °C), and non-volatile fractions of suspended solids were determined. Additional analyses of TP, TN, turbidity and absorbance, plus determinations of ammonium-N ($\text{NH}_4\text{-N}$) and nitrate-nitrite-N ($\text{NO}_3\text{-N}$), were conducted on the filtrate of surface water samples passed through glass fiber filters used in CHL determinations (Gelman A-E). The filtrate fraction represents both truly dissolved materials and those associated with finely divided particles not retained by the glass fiber filters (nominal retention of 1–1.5 μm). Analyses were performed according to A.P.H.A. (1976) except CHL (SARATORY & GROBBELAAR 1984, KNOWLTON 1984), TP (PREPAS & RIGLER 1983), TN (CRUMPTON et al. 1992), and ammonium-N (STAINTON et al. 1977). Analyses of nutrients, suspended solids and chlorophyll were performed in duplicate.

The suspended sediments recovered in our routine surface samples included a large and variable proportion of particles not retained by the glass fiber filters (gff) with which we measured suspended solids (Whatman AH-934) and prepared filtrates for nutrient analysis (Gelman A-E). In extreme cases, filtration reduced turbidity by <5%. Results did not differ substantially between the Gelman and Whatman filters. To quantify the mass of suspended material in this smaller fraction we used tared membrane filters (0.45 μm – Gelman Metrical GN-6) to collect solids from gff filtrates. Membrane filtration removed $\approx 95\%$ ($x=96.6\%$, range 84.5 to 99.6%) of turbidity not removed by gff filtration. The reduction in turbidity due to membrane filtration was highly correlated with the dry weight of materials retained by the membrane filters. The standard curve passed through the origin and did not greatly differ between two series of samples collected and processed 10 months apart. So we used turbidity of gff filtrates to estimate “filtrate” TSS (TSS_{filt}) from a quadratic regression fitted to the data ($n=31$; $r^2=0.994$; $p<0.0001$):

$$\text{TSS}_{\text{filt}} = 0.932 \cdot \text{NTU} + 0.0038 \cdot \text{NTU}^2 \quad (1)$$

We estimated the overall total suspended solids (ΣTSS) as the sum of TSS_{filt} and suspended solids retained by filters (TSS_{gff}).

Incident irradiance was not continuously recorded during the study but we estimated potential daily mean PAR (I_{pdm} , $\text{E m}^{-2} \text{d}^{-1}$) using solar altitude models described by KIRK (1983) assuming a maximum instantaneous incident irradiance of $2000 \mu\text{E m}^{-2} \text{s}^{-1}$ at a solar altitude of 90° . Potential PAR was converted to estimates of actual PAR with a regression formula ($n=464$, $r^2=0.80$):

$$\text{PAR} = 0.303 \cdot I_{\text{pdm}} + 0.0768 \cdot \% \text{MOS} + 0.0045 \cdot I_{\text{pdm}} \cdot \% \text{MOS} - 1.514 \quad (2)$$

where %MOS = daily "percent minutes of sunshine" recorded at the National Weather Service Office near Columbia, Missouri approximately 90 km to the southwest (N.O.A.A. 1991). The regression was derived from a 16 month series of continuous pyronometer measurements taken in 1992–1993 near Clifton Hill, Missouri, about 50 km west of Mark Twain Lake and 80 km north of the N.O.A.A. recording site (University of Missouri unpublished data). We assumed 1 megajoule total shortwave irradiance = 2.05 Einsteins PAR (STEFAN et al. 1983). Because irradiance was not measured on site, estimates of daily irradiance by this method are not precise and the regression model producing the estimates "smoothed" the results so that variation in predicted daily irradiance might be less extreme than variation in actual irradiance. Because of these problems we restricted our use to weekly mean values (PAR_7). In our calibration data set, estimated weekly means were usually within 10% of measured values.

Daily records of lake surface elevation and discharge at gauging stations above and below Mark Twain Lake were obtained from the U.S. Army Corps of Engineers, the U.S. Geological Survey and the U.S. Soil Conservation Service. Daily total inflow was estimated from gauged outflow and change in lake volume and inflow from specific tributaries was estimated from gauge records, total inflow, and catchment area. Estimates of recent mixed depth (Z_{mix}) for each sampling site and date were made from temperature and oxygen profiles with reference to turbidity and conductivity profiles. We generally determined mixed depth as recommended by TALLING (1971) except in cases where large oxygen, turbidity, or conductivity gradients indicated shallower depths of recent mixing. Estimated mixed depths were corrected for basin morphology using polynomial regressions fitted to tables of surface elevation-lake volume data. These tables were prepared from planimetric measurements of pre-impoundment topographic maps. One regression was developed for each of the 19 routine sampling sites based on local basin dimensions. Seven day running means of average irradiance in the mixed layer (\bar{I}_{mix}) was calculated according to RILEY (1957):

$$\bar{I}_{mix} = PAR_7 \cdot (1 - e^{-k_{par} \cdot Z_{mix}}) / (k_{par} \cdot Z_{mix}) \quad (3)$$

When used with reference to individual samples \bar{I}_{mix} and PAR_7 values are means for the week ending at the time of sample collection. We estimated light attenuation by phytoplankton pigments (k_{chl}) as $k_{chl} = 0.02 \cdot CHL$ (KIRK 1983, REYNOLDS 1984) and attenuation by non-algal materials (k_{na}) as $k_{na} = k_{par} - k_{chl}$. We estimated irradiance available for photosynthesis (\bar{I}_{avail}) from incident irradiance and mixed depth by substituting k_{na} for k_{par} in equation 3.

Between September 1989 and November 1991 we completed 28 in situ algal growth experiments in which unfiltered lake water collected near the surface was incubated 3–8 days in polyethylene cubitainers (1, 4, or 10L) with or without added nutrients at 2–7 depths. Treatment groups usually consisted of controls (no additions), P (+8–150 $\mu\text{g-P/L}$), N (+150–1500 $\mu\text{g-N/L}$). In some early experiments an N+P treatment was also employed. Phosphorus was added as potassium phosphate and nitrogen as ammonium nitrate.

Containers were incubated in situ attached to weighted lines suspended from anchored floats. After incubation, containers were transported in the dark to the laboratory, where they were mixed and subsampled (0.25 L) for duplicate chlorophyll deter-

minations from each container. Additional details of procedures are given by KNOWLTON & JONES (in press).

Site description

Physical features

The basin of Mark Twain Lake is in northeastern Missouri (39° 30' N, 91° 50' W) in the former flood plains of the North, Middle, and South forks of the Salt River and their tributaries (Fig. 1). Two thirds of the total catchment area of $\approx 6000 \text{ km}^2$ drains into the four largest streams, the North Fork (26 % of total catchment), South Fork (14 %), Middle Fork (14 %) and Elk Fork (12 %). The remaining catchment is divided among Long Branch (8 %), Lick Creek (6 %), Crooked Creek (5 %), Otter Creek (5 %) and several smaller streams. At conservation pool (surface elevation 184.8 m MSL) the lake has a surface area of 7550 ha and a volume of 0.67 km^3 with mean and maximum depths of 8.9 m and 26 m, respectively.

Some 35 % of the lake's mean volume lies "uplake" from the confluence of Middle Fork and North Fork arms [throughout this paper we use the terms "uplake" and "downlake" in place of their lotic counterparts, "upstream" and "downstream"]. The Lick Creek and Indian Creek arms each comprise about 7.5 % of the total volume and the remaining 50 % lies in the mainstem and small embayments between the confluence and the dam (Fig. 1). Clarence Cannon Dam is a hydropower facility with two turbines capable of combined discharge totaling $\approx 340 \text{ m}^3/\text{s}$. Turbine inlets are located at the base of the dam near the elevation of the former river bed, but flow along the old river channel is blocked by an earthen weir spanning the channel along the face of the dam. The weir crests at 176.8 m MSL and was installed to improve water quality in outflows by reducing the discharge of hypolimnetic water during stratification.

Inflow and lake volume

Flow in the Salt River has been gauged at or near the site of Clarence Cannon Dam since 1940 with annual discharge averaging about twice the present mean volume of the lake. Flows have typically peaked in March or April with minimum flows in November. During the period of record (1983–1992) lake volume varied by a factor of about 3 in response to variation in runoff and discharge (Fig. 2). This study began near the end of a prolonged drought which extended from early 1987 through the end of 1989 and during which total discharge in the Salt River was the lowest for any three year period during 1940–1991. The drought broke with floods in February and March 1990. Other floods occurred in May and June 1990 and in May and July 1991 (Fig. 2). To-

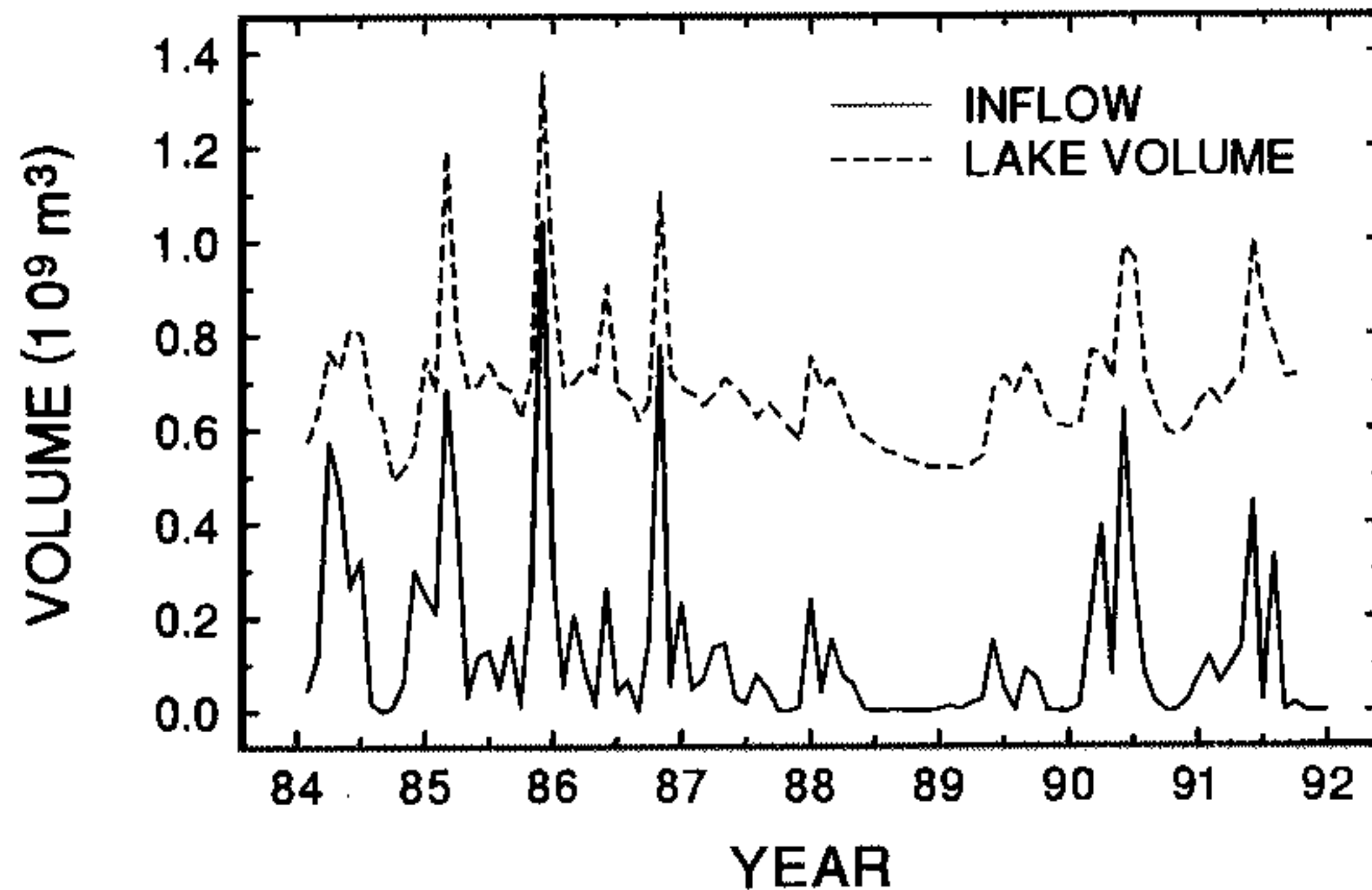


Fig. 2. Monthly total inflow and month-end lake volume of Mark Twain Lake for 1984–1991.

tal inflow and the magnitude of individual flood events in 1990 and 1991 were near average for the period of record (Fig. 2).

Results and discussion

Suspended solids dynamics

Temporal and spatial variation

Non-algal suspended sediment controls the underwater light environment in most lakes in this region (JONES & KNOWLTON 1993) so one objective of this study was to quantify temporal and spatial variability of suspended solids and light conditions with respect to inflow hydrology and thermal conditions.

The unusually large variation in inflow during the study produced equally dramatic variation in suspended sediment and light penetration as recorded by our surface samples and turbidity profiles. Near the end of the 1987–1989 drought, we measured Secchi depths >3.5 m in the reservoir mainstem and turbidity in surface water was <5 NTU over most of the lake (Fig. 3 a) with values <2 NTU in the mainstem. There were several runoff events during the second half of 1989 that increased turbidity in headwater areas and produced interflows that affected the metalimnion downlake (Fig. 2, Fig. 3 a, b). But these minor inputs did not measurably decrease surface water clarity even during fall overturn.

The drought broke with floods in late February and March 1990 which produced turbid conditions (NTU >100) in all arms of the reservoir. A turbidity plume representing inflows of February reached the dam in late March (Fig. 3 c–d). These inputs affected the entire lake and increased surface water tur-

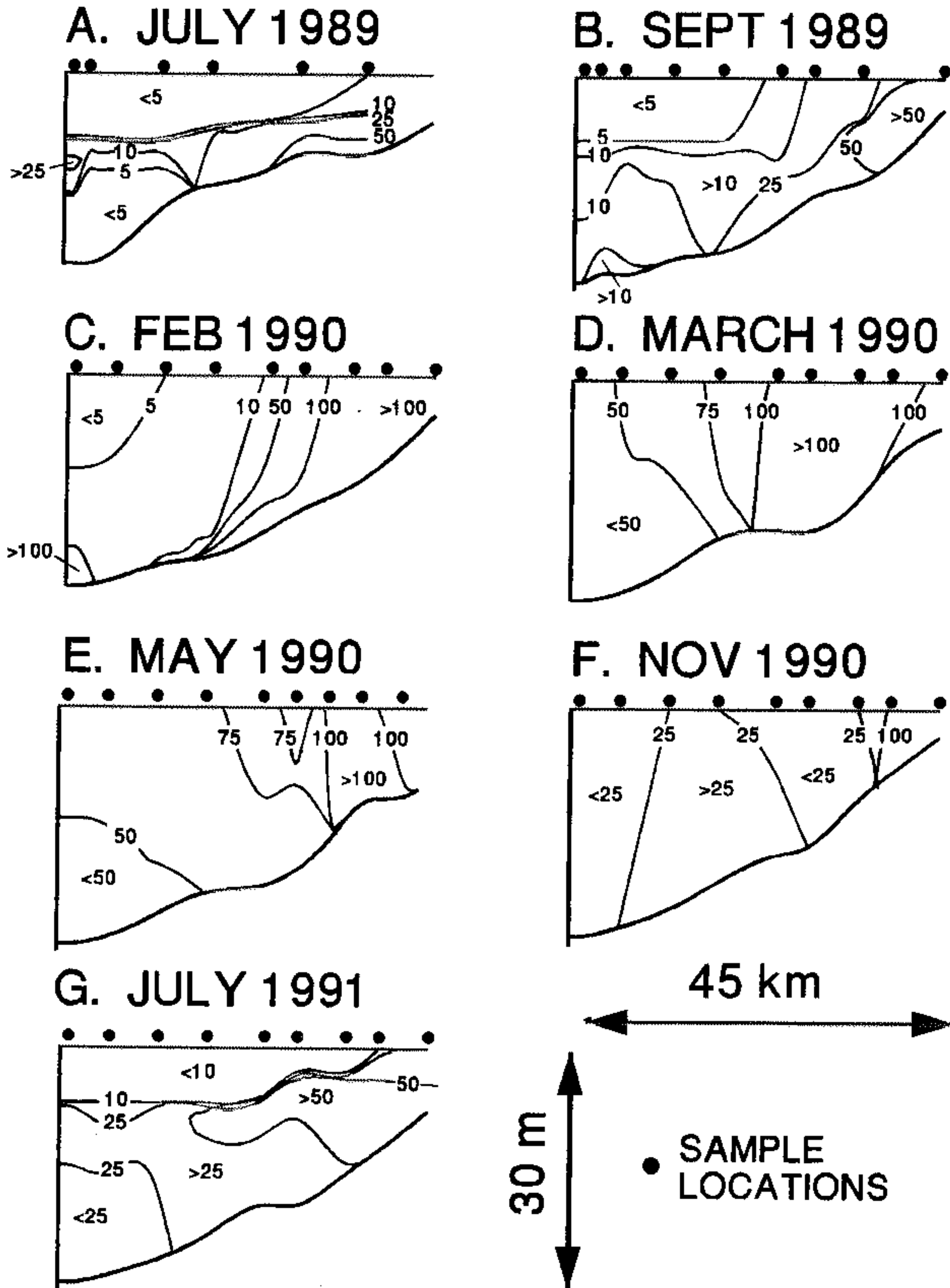


Fig. 3. Spatial distribution of nephelometric turbidity (NTU) in Mark Twain Lake. Data shown are from the dam to the headwaters of the South Fork arm (A,E) or the Middle Fork arm (B,C,D,F & G).

bidity near the dam about ten fold. During this period new inflows were drawn rapidly downlake because of increased discharge through the dam. The total volume released from the lake during March through May 1990 (0.89 km^3) was more than the entire lake volume at the end of February (0.76 km^3). Turbidity in surface water near the dam continued to rise until late May 1990 peaking at 54 NTU ($\Sigma\text{TSS} = 60 \text{ mg/L}$).

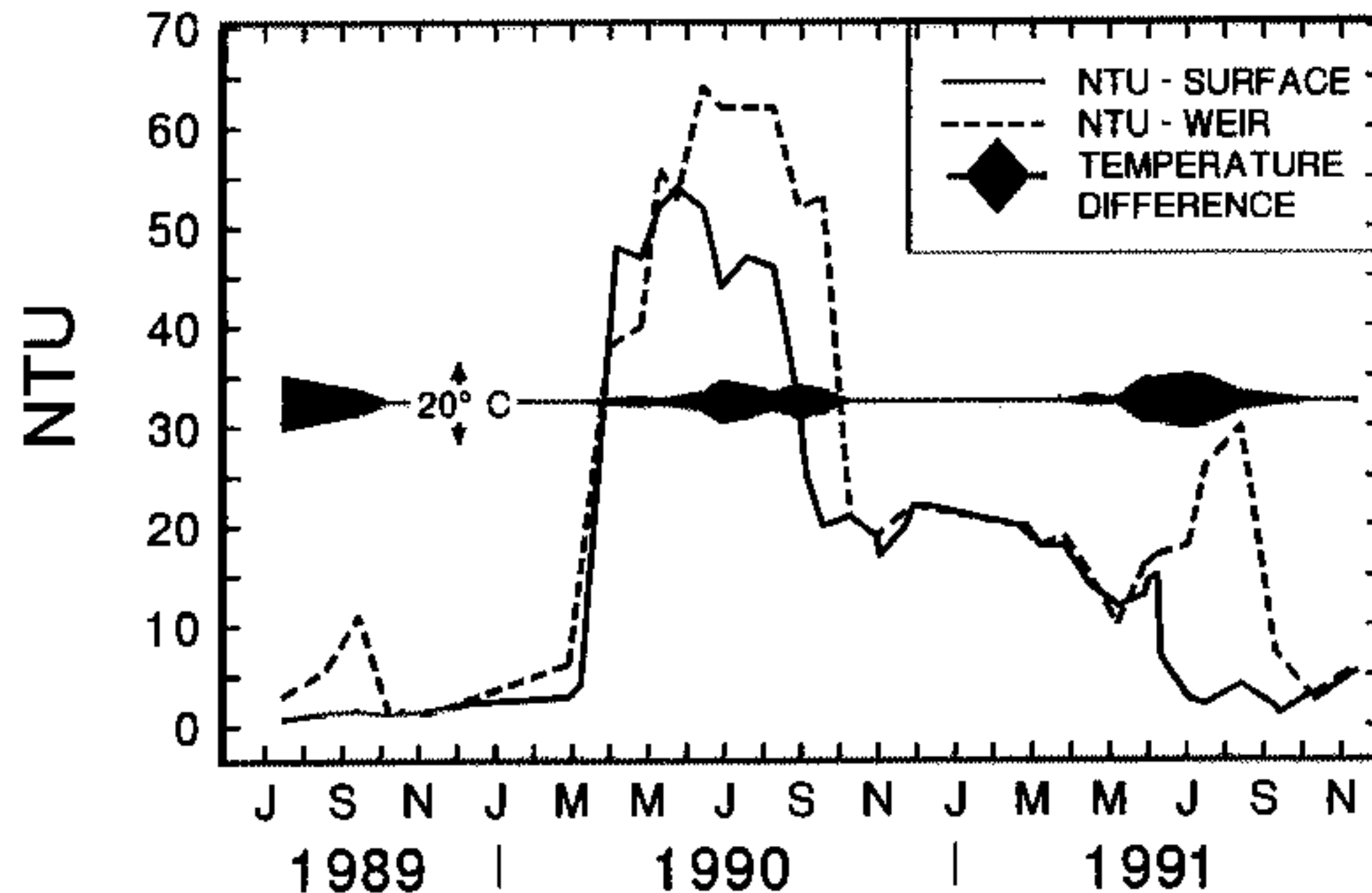


Fig. 4. Nephelometric turbidity (NTU) at the surface and depth of the outflow diversion weir (176.8 m MSL) and the temperature difference between the two depths for a site ≈ 0.3 km uplake from Clarence Cannon Dam (August 1989–November 1991).

In late May 1990 the lake stratified thus confining inflow and outflow to subsurface strata and cutting off sediment input to the surface waters. Turbidity in the epilimnion near the dam declined from >50 to <20 NTU by early September. Uplake areas exhibited even greater declines during this period despite additional floods in June (inflow = 0.28 km^3) which produced turbid inflows to the metalimnion and upper hypolimnion. Turbidity in these layers increased through late June and remained >50 NTU until early autumn when the lake destratified. In late November 1990 turbidity was <30 NTU lakewide except for extreme headwater sites affected by small spates (Fig. 3 f).

Despite normal inflow during 1991, turbidity in the surface water downlake never exceeded the minimum values reached during winter 1990–1991 (Fig. 3 f). Near the dam and in other downlake areas turbidity declined by $>90\%$ during spring and summer 1991 (Fig. 4). The reason for this pattern is that turbid inflows from runoff in June and July formed interflow currents in the metalimnion (Fig. 3 g) which were drawn downlake by the outflow. Fig. 4 shows the time series of turbidity near the dam at both the surface and the depth of the weir crest and illustrates the influence of thermal stratification. Turbidities were nearly identical when the two depths were not isolated by thermal stratification but diverged substantially during summer, especially during 1991 when the sharp decline in surface water turbidity was opposed by a similarly large increase in turbidity in the deeper stratum. Largest declines in surface turbidity in both years occurred during periods of calm, sunny weather which produced large temperature gradients through the surface layer.

During this study, and in most years, brief periods of flooding contribute the bulk of annual water income and sediment loading to the lake. About 75 % of

total inflow in 1989–1991 occurred when discharge in inflowing streams was over 20 times the median gaged discharge (base flow). Before the lake was impounded, an average of 78 % of annual total discharge in the Salt River occurred when flows were >20 times base flow. During such floods, concentrations of suspended solids were typically >1000 mg/L (FINNEY 1986), but samples from our headwater sites typically contained only \approx 300 mg/L Σ TSS during flood events. We measured Σ TSS >1000 mg/L only once, at a headwater site with strong inflow current (>1 m/s). Previous research on suspended sediment in the Salt River showed that relatively large particles of sand and silt make up \approx 57 % of suspended sediment in flood water (FINNEY 1986). Samples of flood water collected from our uplake sites also contained mostly large particles. TSS_{gff} made up an average 73 % of Σ TSS in samples with Σ TSS >300 mg/L ($n=7$, median = 70 %, range 62–90 %) compared to 54 % in less concentrated samples ($n=562$, median = 55 %, range 9–98 %). Inflow currents were usually obvious at headwater sites during floods, but with the exception noted above were always far less than in inflowing rivers. Presumably, most sediment entering Mark Twain Lake is deposited in headwater areas uplake from our sampling sites.

Seston composition and loss factors

Seston dynamics in Mark Twain Lake are dominated by input of suspended sediment during flood events and its subsequent loss through precipitation. But the rate of loss of mineral seston is effected by several factors including the particle size spectrum and, perhaps, algal growth. These factors contribute substantially to temporal and spatial variation in surface layer light conditions.

Purely physical sedimentation of suspended mineral particles probably dominates sediment losses, a fact illustrated by systematic variation we observed in seston size distribution. Lakewide, the relative proportions of the two TSS size fractions (TSS_{gff} and TSS_{flt}) were highly variable but showed consistent patterns when traced over time in relatively discrete masses of water. For example, we traced the progress of a June 1991 flood as it moved downlake in the North Fork Arm. When first sampled near the headwaters, Σ TSS was >400 mg/L in this flood front (Fig. 5 a) and contained a relatively high proportion large particles ($TSS_{gff} : \Sigma$ TSS >60 %). Both Σ TSS and $TSS_{gff} : \Sigma$ TSS declined rapidly with time. When this turbidity front reached the mouth of the North Fork Arm about eight weeks later, TSS_{gff} was only 20 % of Σ TSS. Following simultaneous floods in the North Fork, Middle Fork and South Fork arms in March 1990, recent inflows contained an average \approx 200 mg/L Σ TSS of which about 40 % was TSS_{gff} (Fig. 5 b). Two months later this turbidity front was located near the dam and Σ TSS had dropped to about 60 mg/L of which 15 % was TSS_{gff} .

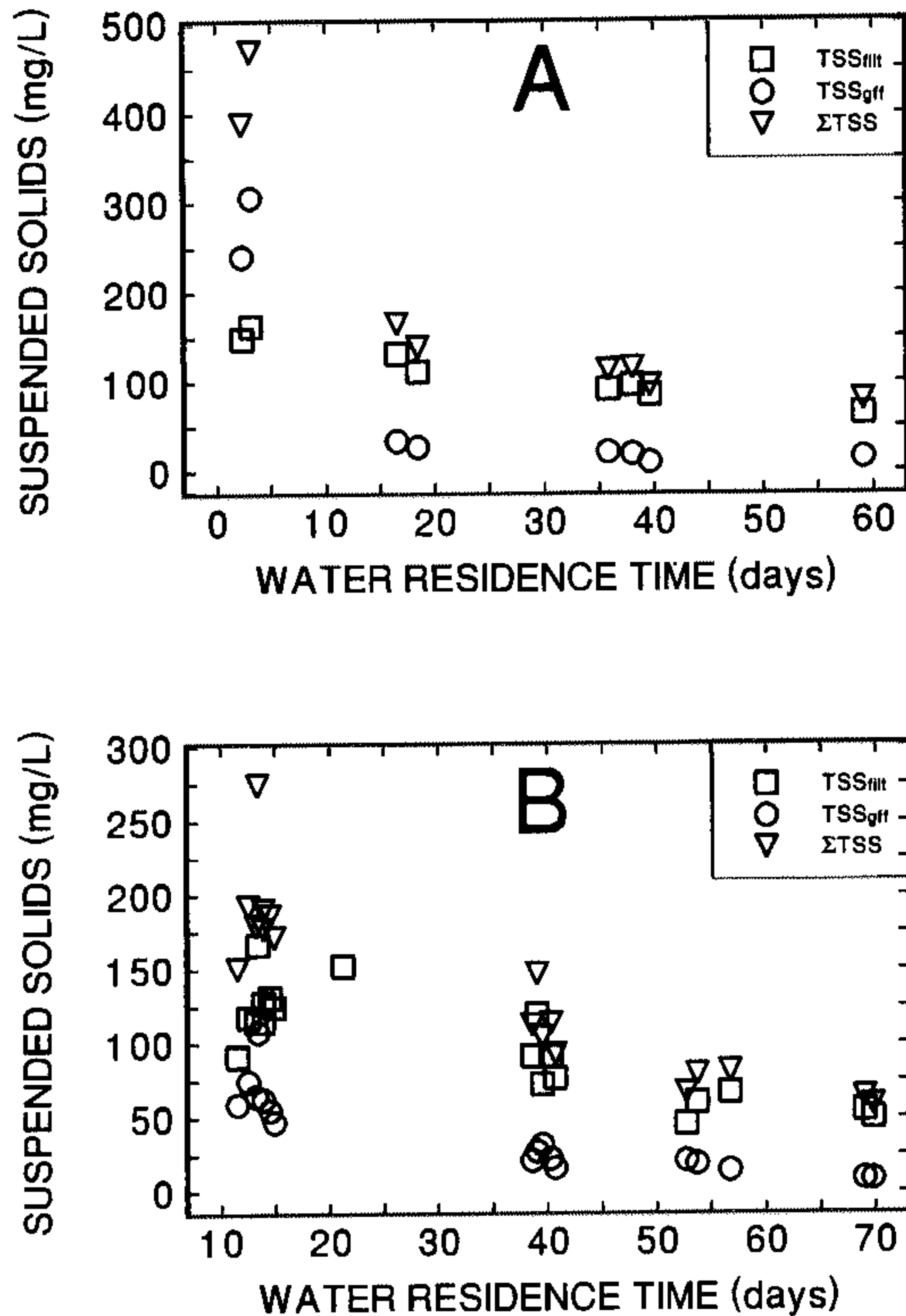


Fig. 5. Effect of water residence time on concentrations of suspended solids following (A) a June 1990 flood in the North Fork arm and (B) a March 1990 flood in the North Fork, Middle Fork, and South Fork arms. Water residence time was estimated from measurements of inflow volume, surface elevation, and lake dimensions assuming plug-flow conditions.

The preceding examples seem to show more rapid sedimentary losses of larger particles in keeping with general expectations of particle settling rates. But time series trends from downlake sites show an opposing pattern and evidence of another mechanism controlling particle size distribution. Near the dam $TSS_{gff} : \Sigma TSS$ dropped precipitously in 1990 with the influx of recent flood waters but generally increased through the remainder of the study period (Fig. 6 a). This trend was accompanied by an increase in the organic content of materials in this size fraction as indicated by the proportion of volatile material (VSS) in TSS_{gff} (Fig. 6 b). These data probably record a transition in the

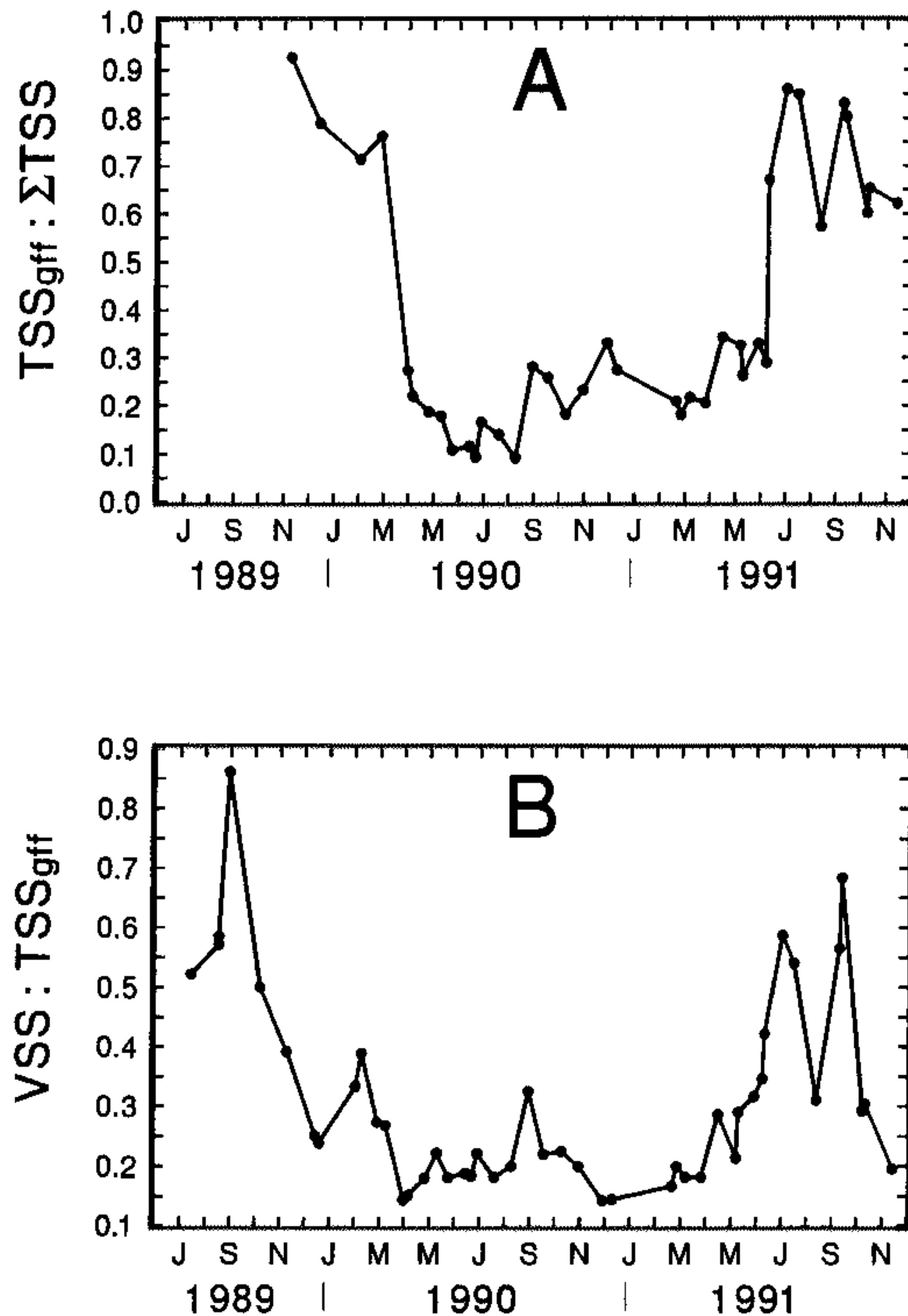


Fig. 6. Temporal variation in suspended solids composition in the surface layer of Mark Twain Lake (Dam sampling site). A – Proportion of “large” particles (TSS_{gff}) in total suspended solids (ΣTSS). B – Proportion of volatile solids (VSS) in particles retained by glass fiber filters (TSS_{gff}).

seston from dominance by allochthonous, mostly mineral, materials to dominance by autochthonous, mostly biogenic particles.

Mineral seston reaching downlake areas was dominated by TSS_{filt} because of the slow settling rates of submicron particles. If governed by purely physical sedimentation we would expect losses of such materials from the surface layer to proceed slowly, but our data record abrupt drops in TSS_{filt} that suggest a possible biotic influence. For example, during an algal bloom in June 1991 TSS_{filt} declined $\approx 70\%$ (from 12.8 to 4.1 mg/L) over a three day period during which CHL increased from 15.4 to 39.7 $\mu\text{g/L}$. This occurred during a period of calm, sunny weather when lake surface temperature increased 2 °C and

mixed depth decreased from 3 to 2 m. Reduced turbulence in the thermally stabilized water column probably contributed to these losses. But such rapid clearance of fine particles suggests an additional mechanism, perhaps co-flocculation with polysaccharides excreted by phytoplankton (AVNIMELECH et al. 1982, SØBALLE & THRELKELD 1988). SØBALLE & THRELKELD (1988) speculated that some circumstances might lead to preferential flocculation and loss of minerals rather than algal-mineral aggregates. Thus the rapid loss of TSS_{fit} during this bloom may have been a direct result of algal growth due to mineral particles co-precipitating with algal cells or being induced to precipitation by algal excretions.

Physiological processes contributing to rapid sedimentation of non-algal seston would be an advantageous adaptation for phytoplankton growing under light limitation in turbid lakes. During the June algal bloom transparency increased 20 % despite increased algal biomass. This episode may represent an example of phytoplankton contributing to their own well being through their effect on the light environment. Empirical evidence of a negative relation between phytoplankton and mineral turbidity (JONES & NOVAK 1981, WALKER 1982, AVNIMELECH et al. 1982, HOYER & JONES 1983, CUKER 1987, CARLSON 1991, JONES & KNOWLTON 1993) is usually assumed to result from adverse effects of turbidity on phytoplankton. But if phytoplankton growth is capable of reducing mineral turbidity directly then the cause-effect relations underlying these observed trends may be the reverse of that expected.

Light conditions

Vertical attenuation

Vertical diffuse attenuation of PAR (k_{par} , m^{-1}) ranged from 0.6/m to 18.4/m ($n=230$, $x=3.8$, median = 2.6) corresponding to photic depths (1 % incident PAR = $\ln 100/k_{par}$) of 0.25 to 7.8 meters. Secchi transparency ranged from 0.03 to 3.6 m ($n=672$, $x=0.66$, median = 0.45) and covaried strongly with photic depth. We used a regression model relating the two variables (\log_{10} photic depth = $0.863 \cdot \log_{10}$ Secchi depth + 0.464, $r^2=0.95$, $n=230$) to estimate photic depth and k_{par} for observations without light measurements ($n=417$).

Water in Mark Twain Lake is not strongly colored and thus light attenuation varies consistently with total seston concentration. In a regression with \log_{10} transformed data, ΣTSS accounted for >95 % of the variation in k_{par} . In contrast, k_{par} was not closely related to CHL except that scatter plots show a distinct "edge" (Fig. 7) indicating a lower limit to light attenuation at given CHL concentration (SMITH 1990).

Most observations near the "edge" of the CHL- k_{par} plot occurred during the preflood period in 1989 and 1990 or during subsequent surface blooms in up-

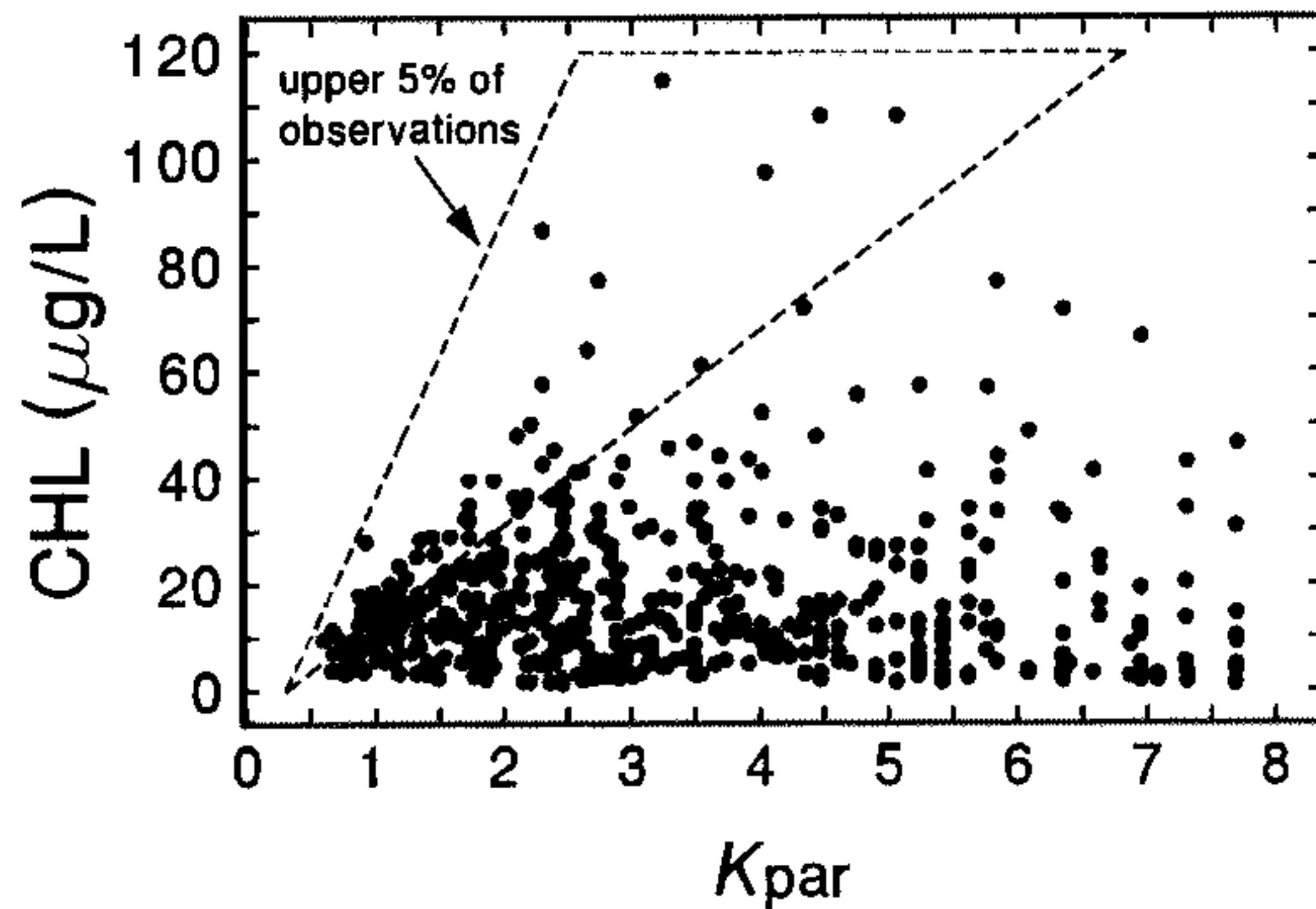


Fig. 7. Plot of chlorophyll concentrations (CHL) versus vertical extinction of PAR (k_{par}). Observations with $k_{\text{par}} > 8$ ($n = 83$) not shown.

lake areas. These observations represent conditions when phytoplankton regulation of light attenuation was maximal. It is likely, however, that non-algal materials had a large, and perhaps dominant influence on light conditions even for these selected observations. Specific attenuation of PAR by pigments of living phytoplankton center around a value of about $0.02 \text{ m}^2/\text{mg CHL}$ (KIRK 1983, REYNOLDS 1984). If this value is correct then light attenuation by phytoplankton ($k_{\text{chl}} = 0.02 \cdot \text{CHL}$) was 0.2% to 75.3% of k_{par} in this data set and averaged 12.3% ($n = 652$, median = 8.5%). Even among the 5% of observations nearest the “edge” in Fig. 7, $k_{\text{chl}} : k_{\text{par}}$ averaged only 43% ($n = 33$, median = 40.1%) suggesting an influence of non-algal materials. This conclusion is also indicated by seston composition. Among the 5% of observations with maximal $k_{\text{chl}} : k_{\text{par}}$, TSS_{filt} comprised an average 23% of ΣTSS ($n = 24$, median = 19.7%). Few if any phytoplankton are small enough to occur in the TSS_{filt} fraction and the low CHL content of TSS_{gff} (mean = 0.40%, median = 0.41%, $n = 32$) suggests that phytoplankton comprised a small part of this portion of the seston. The CHL content of living phytoplankton is usually in the range of 1–3% of dry weight (REYNOLDS 1984, RIEMANN et al. 1989). So it is likely that non-algal material or detritus made up a sizable fraction of total seston even during the preflood period and algal blooms that comprise this 5% of our observations. In the remaining 95% of our data set, the contribution of phytoplankton to total seston weight was probably quite small.

Mixed layer irradiance

Mixing depth, corrected for local basin morphology, ranged from $>18 \text{ m}$ at downlake sites during winter overturn, to near zero during periods of surface

stratification in calm, sunny weather ($n = 549$, $x = 5.4$, median = 4.6). In spring and summer the mixed zone was often poorly defined with near-surface gradients in temperature and dissolved oxygen. We made conservative estimates of underwater light intensities by calculating mixed depths based on maximum gradients in temperature or dissolved oxygen and ignored lesser, near surface gradients. Mean irradiance in this layer averaged 9.8 % of surface irradiance during the study ($n = 643$, median = 7.0 %, range 0.5 %–39.8 %) and only six of 643 observations showed mean irradiance less than 1 % of incident light. Light penetration and mixed depth contributed similarly to the overall variation in mean subsurface irradiance. In a multiple regression using \log_{10} transformed data, partial coefficients of determination for mixed depth and k_{par} were 55 % and 45 %, respectively.

Weekly mean irradiance ($\overline{\text{PAR}}_7$) estimated from a model using regional “minutes of sunshine” data ranged from 4.9 to 49.8 $\text{E m}^{-2} \text{d}^{-1}$ (Fig. 8). On the basis of average irradiance in the week ending on a given sample date, daily average irradiance in the mixed layer (\bar{I}_{mix}) ranged from 0.2 to 18.1 $\text{E m}^{-2} \text{d}^{-1}$ with a mean of 3.1 $\text{E m}^{-2} \text{d}^{-1}$ ($n = 643$, median = 1.8; Fig. 9). Variation in incident light, mixed depth, and turbidity contributed similarly to variation in \bar{I}_{mix} . Mean \bar{I}_{mix} declined 80–90 % from summer to winter in 1989 and 1991 (Fig. 9) due mostly to increased mixed depth and reduced incident light (Fig. 8). The several fold increase in turbidity following floods in winter 1990 (Fig. 3 c–d, 4) further reduced \bar{I}_{mix} by about half at most sites. On a proportional basis, high post-flood turbidity had its greatest effect during summer 1990 when mean \bar{I}_{mix} was usually <25 % of the values observed in summer 1989 and 1991.

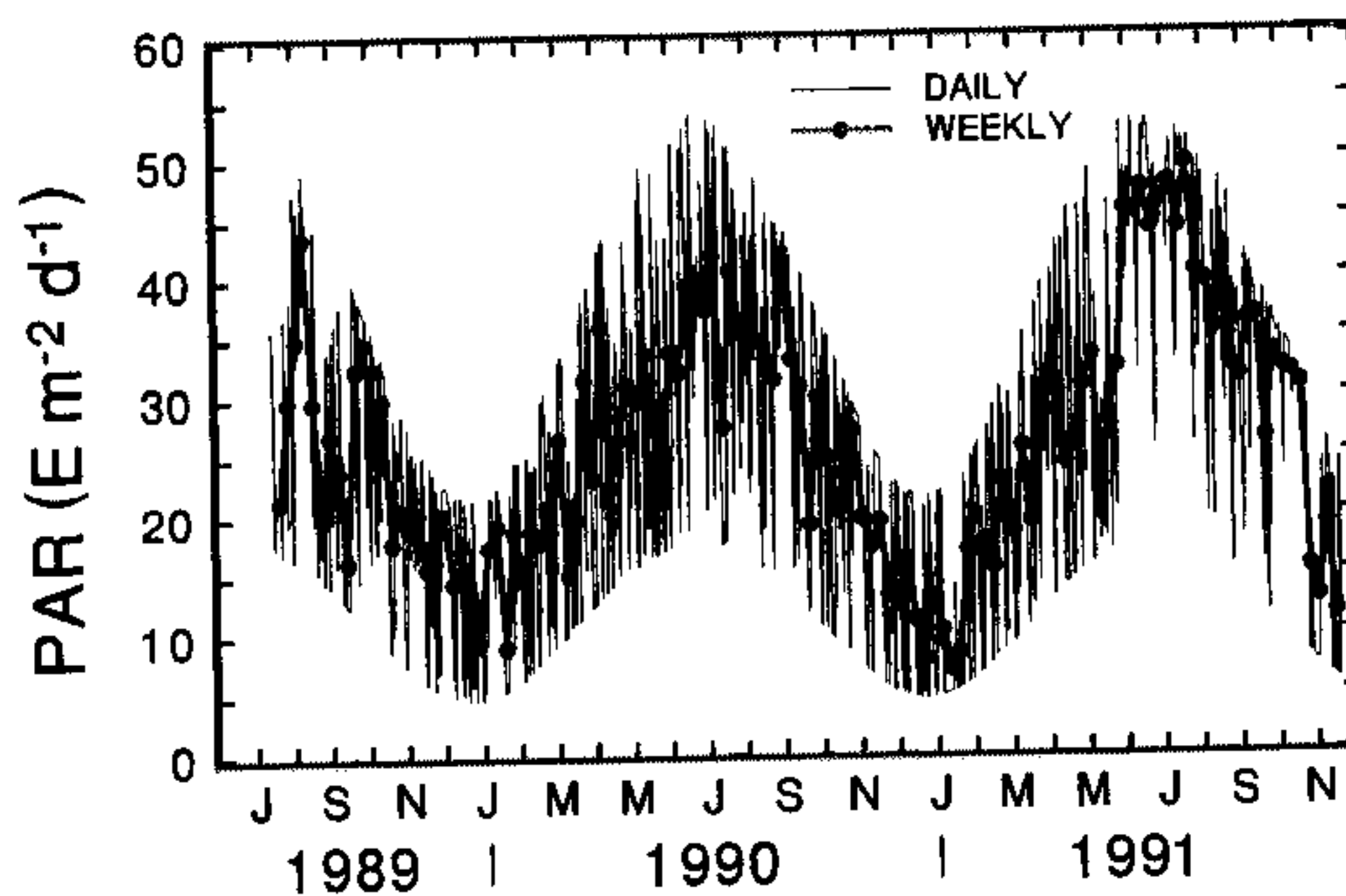


Fig. 8. Estimated daily total incident PAR and weekly mean PAR at Mark Twain Lake during this study.

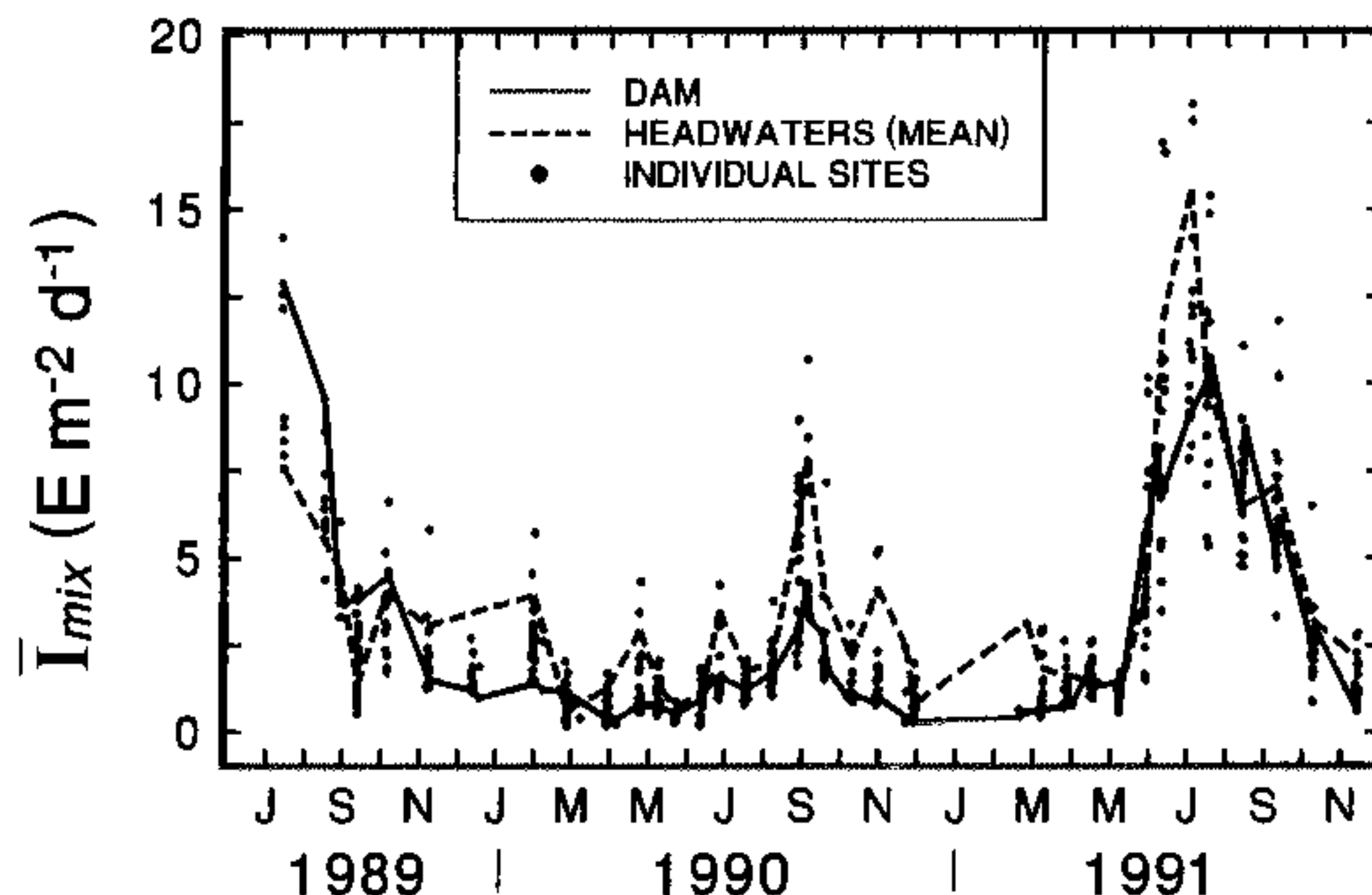


Fig. 9. Weekly mean mixed layer PAR (\bar{I}_{mix}) at routine sampling sites during this study (solid dots). Observations near the dam are connected by a solid line. A dashed line connects the mean for each sampling run of four headwater sampling sites (Lick Creek – 10 km, Middle Fork – 45 km, North Fork – 45 km and South Fork – 42 km).

Differences in light attenuation between headwaters and the dam proportionately matched differences in TSS between these locations. Nonetheless, \bar{I}_{mix} was usually higher at headwater sites (dashed line in Fig. 9) than at the dam (solid line in Fig. 9) because of the lesser mixed depths of shallow, protected areas uplake. This fact points to the counterintuitive conclusion that light conditions were occasionally more favorable for algal growth in extremely turbid locations as compared to areas with less turbidity, especially during winter when deep mixing limited \bar{I}_{mix} in downlake areas.

Nutrients and algal biomass

Phosphorus

Total phosphorus (TP) concentrations in surface water ranged from 16 to 929 $\mu\text{g/L}$ ($n=613$, $x=141$, median = 101) with an average of 39% ($n=602$, median = 39%, range 1–81%) retained by glass fiber filters. Total and filtrate TP (TP_{filt}) were highly correlated ($r \geq 0.88$) with their respective size fractions of TSS. Dissolved P was not separately measured in this study but it is likely that much of the TP in filtrates was bound to particles.

Total phosphorus in filtrates averaged 0.42% of TSS_{filt} by weight ($n=549$, median = 0.43%, range 0.17–5.36%). Total phosphorus retained by filters ($\text{TP} - \text{TP}_{\text{filt}}$) averaged 0.26% of TSS_{gff} ($n=593$, median = 0.23%, range = 0.02–0.97%). Due to the close association between P and suspended sediment, our earlier description of spatial and temporal dynamics of suspended sediment applies nicely to phosphorus dynamics. Fig. 10 shows the near syn-

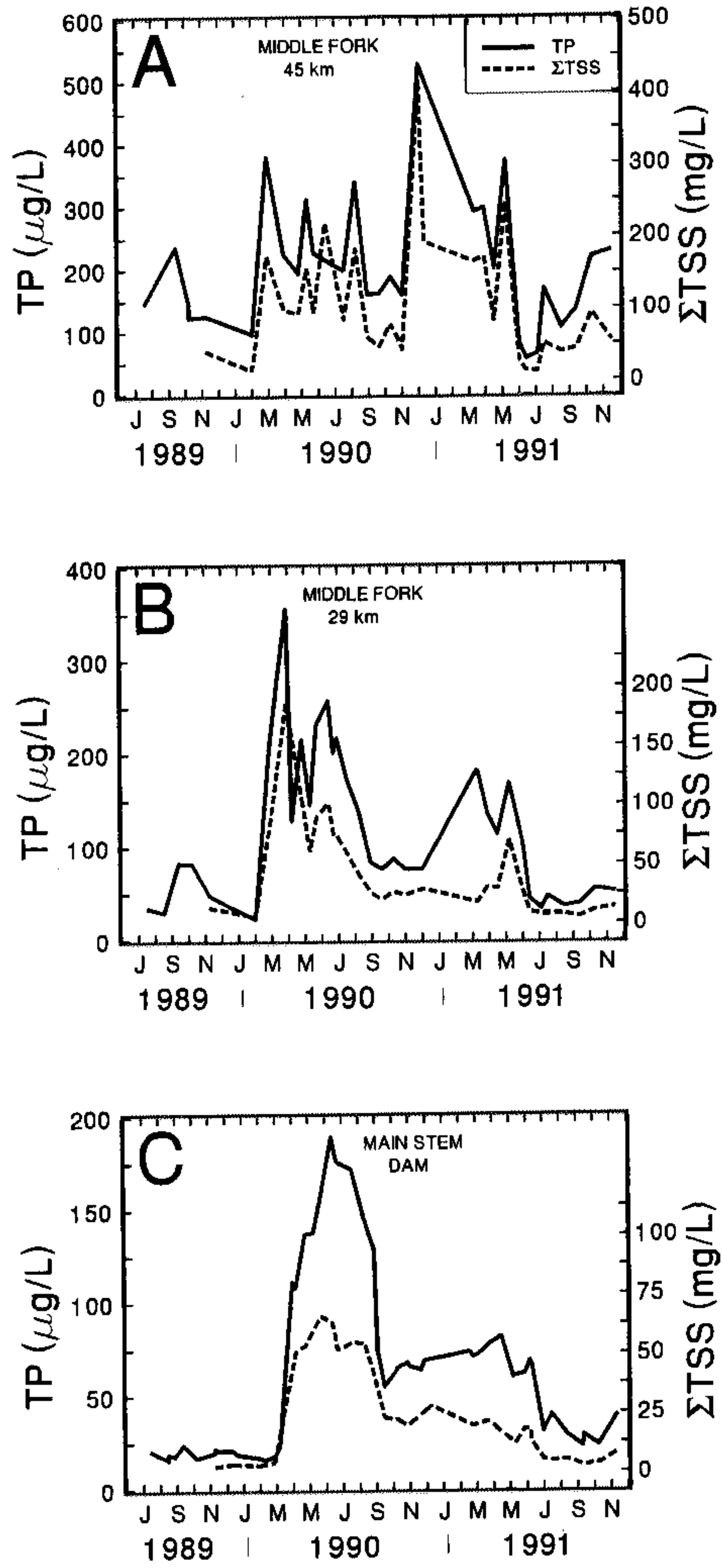


Fig. 10. Temporal variation in total phosphorus (TP) and total suspended solids (ΣTSS) in surface water at sites in the headwaters (A – Middle Fork, 45 km), middle reaches (B – Middle Fork, 29 km) and mainstem (C – dam) of Mark Twain Lake during this study.

chronous fluctuations of TP and Σ TSS at representative sites. TP declined by an average factor of ≈ 3 from the headwaters to the dam (e.g. Fig. 10 a versus Fig. 10 c). During periods marked by floods and extreme spatial variation in TSS (Fig. 3 c, 3 g), order of magnitude differences in TP among sampling sites were common (e.g. March and November 1990 – Fig. 10). And total and filtrate fractions of TP in flood inflows decreased rapidly as the water moved downlake.

Collectively, data from this study show that the timing of turbid, nutrient laden inflows relative to seasonal stratification can be as important as their volume in controlling sediment and phosphorus loading to surface water downlake. Thermal stratification “protects” the surface layer from sediment and nutrient inputs during late spring and summer. Thus surface water turbidity and TP downlake in late summer 1991 was similar to the minimal values observed during the drought year of 1989 despite a ≈ 5 fold difference in inflow between the two periods (Figs. 3, 4). The proportionately smaller difference in inflows between 1990 and 1991 ($< 50\%$) produced a far greater effect on turbidity and TP because a large proportion of the 1990 inflows occurred before stratification.

Previous work on midwestern reservoirs has suggested that open water phosphorus concentrations are less than would be expected from loading models based on natural lakes (JONES & BACHMANN 1978). This difference was attributed to rapid sedimentation of phosphorus from the water column and data from Mark Twain Lake support this hypothesis. Our data on inflow stratification also helps explain why simple application of loading data overestimates TP in some artificial lakes. For waterbodies such as these, loading models need to take into account the effects of inflow timing and flow stratification. Our data suggest the relative timings of runoff and stratification will vary from year to year and could make surface layer TP content unpredictable for a given lake except as a long term average.

Nitrogen

During the floods of early 1990 headwater sites in the four major arms exhibited concentrations of $\text{NO}_3\text{-N}$ between 2.4 and 3.5 mg/L and TN between 3.9 and 5 mg/L (Fig. 11 a). These N-rich inflows moved through the entire lake increasing surface water $\text{NO}_3\text{-N}$ to over 1 mg/L lakewide by the end of March 1990 (Fig. 11). Subsequent flood inflows carried less nitrogen, typically about 2 mg/L $\text{NO}_3\text{-N}$ and 3.5 mg/L TN in the South Fork arm and ≈ 1 mg/L $\text{NO}_3\text{-N}$ and 2-4 mg/L TN in the other arms sampled. Inflows in May–July 1990 increased TN and $\text{NO}_3\text{-N}$ in uplake areas (Fig. 11 a–b) but had no noticeable effect on sites in the reservoir mainstem (Fig. 11 c). And floods in May–July 1991 had little effect on nitrogen concentrations except at headwater sites.

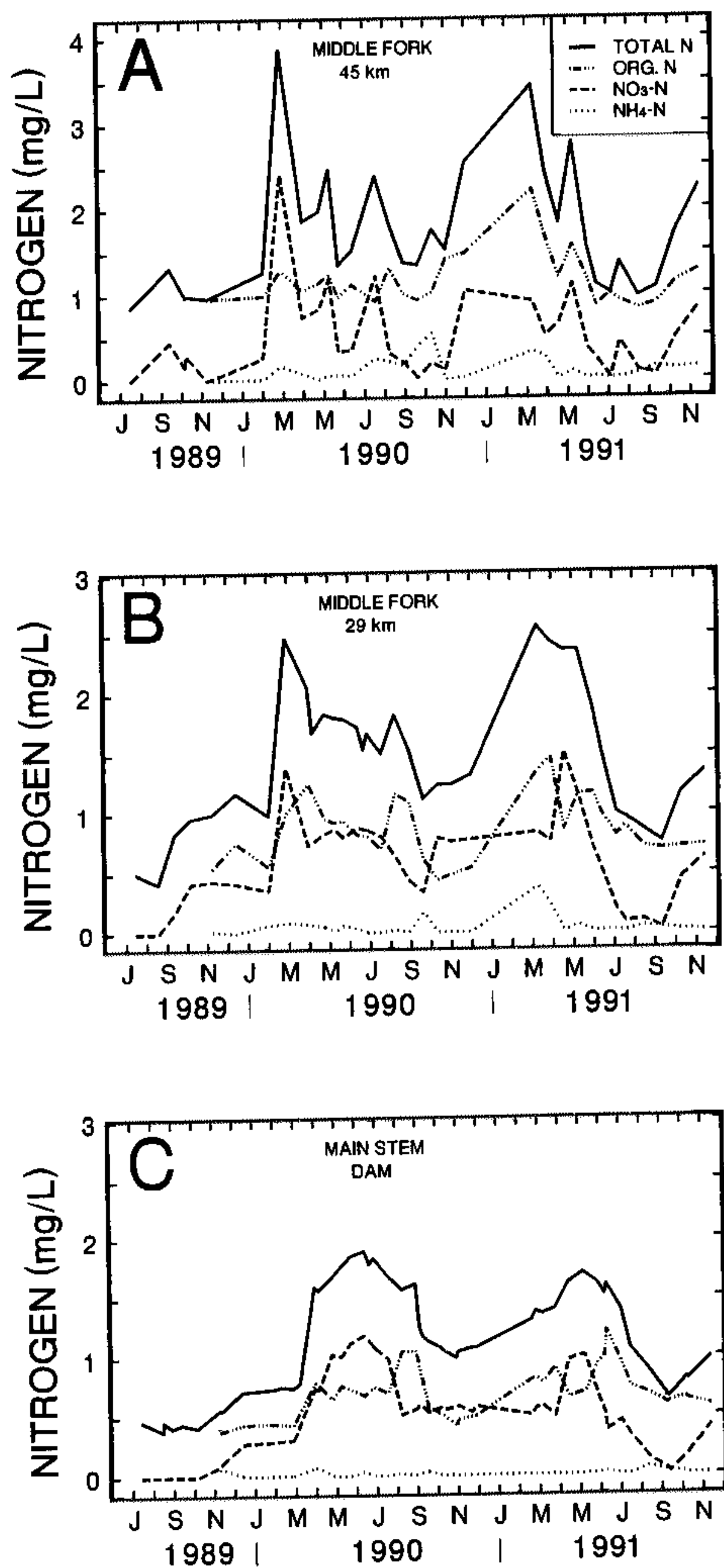


Fig. 11. Temporal variation in total nitrogen, organic nitrogen NO₃-N and NH₄-N in surface water at sites in the headwaters (A – Middle Fork, 45 km), middle reaches (B – Middle Fork, 29 km) and mainstem (C – dam) of Mark Twain Lake during this study.

Apart from the lake-wide increase from early 1990 inflows, nitrogen dynamics seem to have been largely the result of seasonal variation in stratification and mixing and accompanying biological phenomena rather than fluvial inputs.

When sampling began during summer stratification in 1989, $\text{NO}_3\text{-N}$ was below detection ($\approx 10 \mu\text{g/L}$) downlake and TN was less than 0.5 mg/L (Fig. 11). Subsequent periods of intense stratification in spring and summer 1990 and 1991 were accompanied by rapid losses of $\text{NO}_3\text{-N}$ and TN at all sites sampled which often coincided with large, ephemeral increases in organic nitrogen estimated as TN minus DIN ($\text{DIN} = \text{NO}_3\text{-N} + \text{NH}_4\text{-N}$). In downlake areas, $\text{NO}_3\text{-N}$ and TN decreased by $>1 \text{ mg/L}$ during summer in both 1990 and 1991 and uplake areas exhibited even larger declines. Near the end of summer 1991, $\text{NO}_3\text{-N}$ was once again near or below detection over most of the lake.

At most sampling sites, fall destratification in 1989, 1990 and 1991 produced brief pulses of $\text{NH}_4\text{-N}$ ($0.1\text{--}0.8 \text{ mg/L}$) followed by rapid increases in $\text{NO}_3\text{-N}$ and TN. During both winters sampled concentrations of organic nitrogen more than doubled at most sites. In 1989–1990 this increase can be attributed to external loading during floods. But external loading could not explain the large increase observed in winter 1990–1991 which occurred well after destratification during a period of low inflow when the lake was mostly ice covered. At present we have no conclusive data on the source of this nitrogen but it may have resulted from recycling of N from detritus lost to the sediments during the preceding summer.

In 1991, organic nitrogen was extensively mineralized during a period of rapid warming in late March and early April. This process produced a large pulse of $\text{NH}_4\text{-N}$ ($0.2\text{--}0.5 \text{ mg/L}$) at most sites, followed by a near doubling of $\text{NO}_3\text{-N}$. Due to the combined effects of autumnal mixing, internal loading, and nitrification, vernal concentrations of TN and $\text{NO}_3\text{-N}$ at most sites around the lake were as great or greater in 1991 as in 1990 (Fig. 11) despite reduced external loading in 1991.

Of the 0.4 to 4.9 mg/L TN measured in lake water, 0 to 51% ($n = 557$, $x = 11\%$, median = 8.8%) was retained by glass fiber filters. In the filtrate fraction (TN_{filt}), 0 to 75% (mean = 40%) was present as $\text{NO}_3\text{-N}$ and 0 to 46% (mean = 4%) as $\text{NH}_4\text{-N}$ with the remaining 20 to 63% (mean = 55%) in the form of dissolved and fine particulate organic materials. In comparison with phosphorus, total and filtrate fractions of organic N were less strongly correlated to their respective size fractions of TSS ($r = 0.61$ and 0.62 , respectively). Presumably, much of the filterable organic nitrogen was present as dissolved materials rather than fine particles.

Total nitrogen and TP were strongly correlated during the study ($r = 0.84$, \log_{10} transformed data) but did not vary in direct proportion. On average, surface samples contained 16.2 times more TN than TP by weight but this ratio declined with increasing concentrations of N and P and varied among size

fractions and sampling sites. TN:TP averaged 27.8 in samples in the lowest 10% of observations for both nutrients ($n=38$, TP $<28 \mu\text{g/L}$, TN $<0.77 \text{ mg/L}$) and averaged 7.9 among observations in the uppermost 10% for TN and TP ($n=30$, TP $>316 \mu\text{g/L}$, TN $>2.39 \text{ mg/L}$). In filtrates, N:P averaged 26.2 ($n=556$; median = 20.8, range 5.1–105.3) compared to a mean of 4.3 ($n=555$, median = 3.5, range 0–21.1) for particles retained by glass fiber filters. Ratios of N:P in all fractions tended to increase downlake from the headwaters to the dam. This trend probably occurred because of the large proportion of TP associated with particles and the consequent rapid sedimentary loss of TP as new inflows moved downlake.

Algal biomass

Time series of algal CHL at all sites were punctuated by brief blooms that produced maximum CHL ranging from 24 to 115 $\mu\text{g/L}$ (Fig. 12). Between blooms CHL fell as low as 1.5 $\mu\text{g/L}$. CHL peaks were mostly confined to the summer stratified period in deeper downlake areas but occurred in all seasons at shallow uplake sites. CHL $>70 \mu\text{g/L}$ was observed only at the four shallowest sites, but among the other 15 sites there was no consistent spatial pattern in maximum CHL. Among deepwater sites in the reservoir mainstem, peak CHL ranged up to 48 $\mu\text{g/L}$ with the largest blooms occurring during periods of shallow stratification in summer 1990 and 1991.

The onset of CHL peaks was probably rapid. In observations made near the dam in June 1991 CHL increased from 15.4 to 39.6 $\mu\text{g/L}$ over a three day period with an accompanying 161 $\mu\text{g/L}$ decline in DIN, a 14 $\mu\text{g/L}$ decline in TP_{filt}, and a 4 mg/L increase in surface dissolved oxygen. Volatile suspended solids increased from 1.8 to 3.5 mg/L. Algal growth measured in containers during this study (KNOWLTON & JONES, in press) frequently showed 100–300% increases in CHL over time spans of 3–8 days so the potential for rapid growth was often large (Fig. 13). We routinely sampled at intervals of about three weeks so our data provide little detail about specific conditions leading to the rise and decline of CHL peaks that could presumably appear and disappear in much less than three weeks. Nor do these data supply information on the precise duration or frequency of peaks.

In most observations photic depth was less than mixing depth so areal biomass can be conservatively estimated as the product of CHL and Z_{mix} . Overall, areal CHL ranged from 4 to 319 mg/m^2 during the study with a mean and median of 64 and 51 mg/m^2 , respectively. Lakewide and at individual sites, areal CHL was closely correlated with CHL concentration ($r=0.64$ to 0.98 at individual sites) so time series of areal biomass are similar to those for CHL (Fig. 12). Areal CHL did not, however, vary consistently with mixed depth despite the fact that Z_{mix} was used in its calculation. Lakewide, variation in Z_{mix} ac-

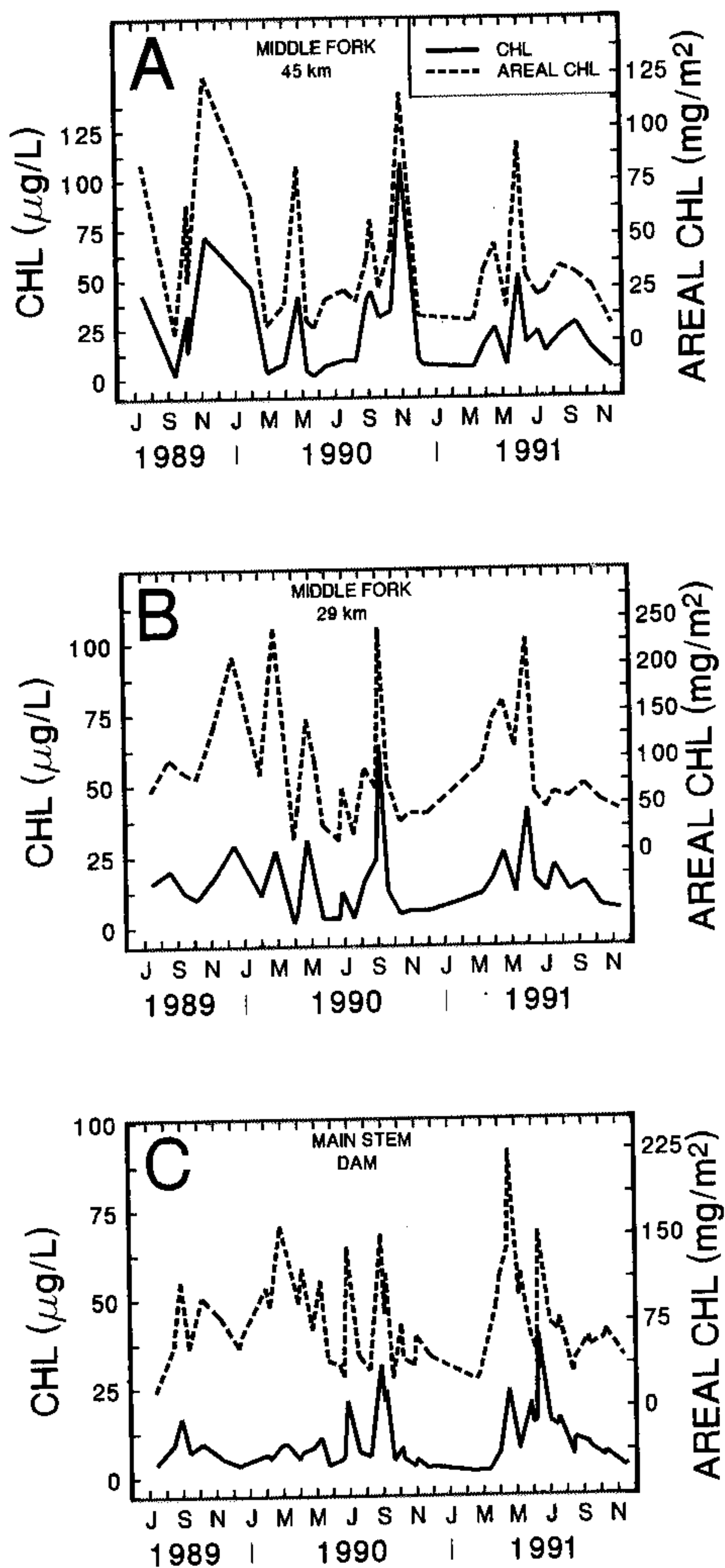


Fig. 12. Temporal variation in chlorophyll (CHL) concentration and areal CHL at sites in the headwaters (A – Middle Fork, 45 km), middle reaches (B – Middle Fork, 29 km) and mainstem (C – dam) of Mark Twain Lake during this study.

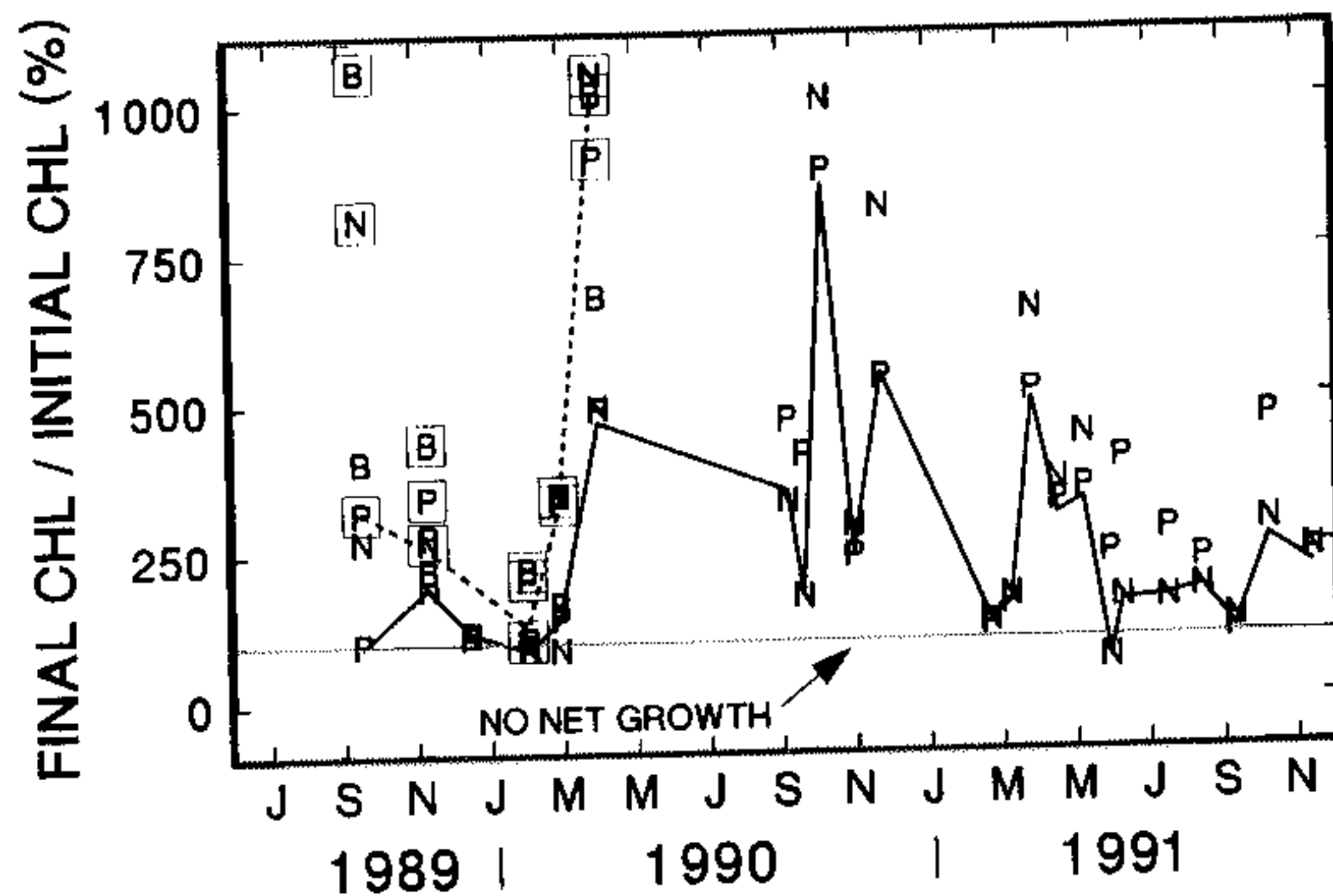


Fig. 13. Partial results from algal growth experiments run at the dam and near the confluence of the Middle and South Forks (KNOWLTON & JONES, in press). Data shown are maximum final CHL as percent of initial CHL in containers incubated 3–8 d at saturating irradiance in situ. Treatments were: P – Phosphate added, N – ammonium nitrate added, B – both P and N added. Data points from the uptake site are enclosed in boxes. Results for controls are connected by a line (solid – dam; dashed – uptake).

counted <5% of the variation in areal CHL (\log_{10} transformed data, $n=629$; $r^2=0.048$) and areal CHL was significantly ($p<0.05$) correlated to Z_{mix} at only two of 19 sampling sites.

Limiting factors

Nutrient limitation

Phosphorus seems likely to have limited algal biomass only sporadically during the study. Our algal growth experiments showed that phytoplankton were nearly always capable of substantial growth at ambient phosphorus concentrations and in situ CHL was not correlated with TP (Fig. 14). But in our experiments, which in some ways simulated the occurrence of algal blooms in situ, rapid growth of phytoplankton seems often to have produced a state of phosphorus limitation by the end of the incubation. Addition of P as phosphate significantly increased CHL yield in about half the experiments even though rapid growth in controls indicated P was not limiting when the experiments began.

Comparison of CHL:TP ratios between our experiments and the lake suggests that phosphorus may also have become limiting during in situ algal blooms and thus regulated the magnitude of CHL peaks. In growth experiments showing a significant effect of phosphate addition, maximum CHL:TP in controls was always ≥ 0.3 at some time during the incubation ($n=12$, $x=0.5$, range 0.3–1.0). Among the 133 observations corresponding to in situ

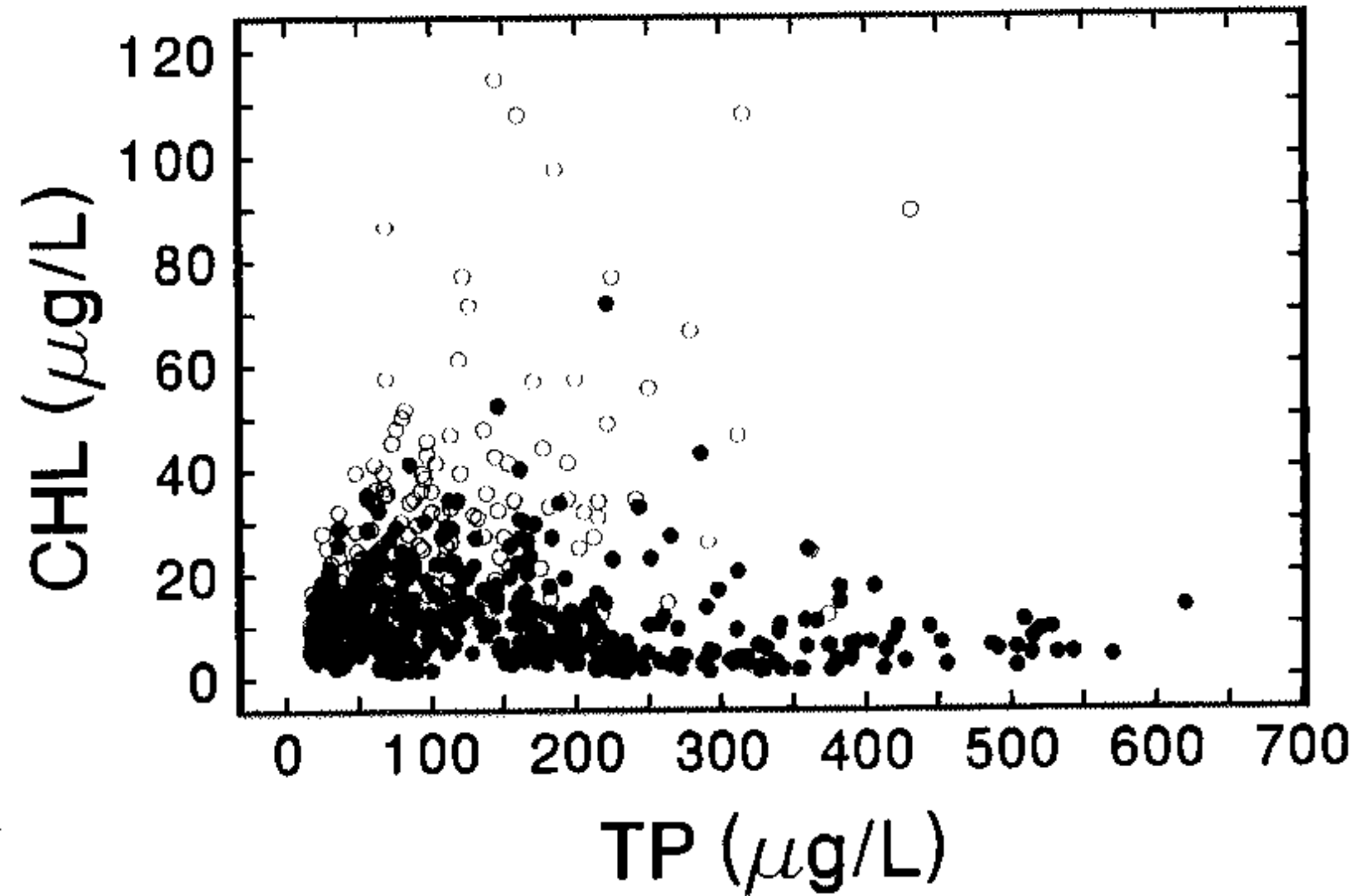


Fig. 14. Plot of chlorophyll (CHL) versus total phosphorus (TP) concentrations for surface water samples. Open circles represent “peak” CHL observations as described in the text.

CHL peaks (e.g. Fig. 12) 56 % had $\text{CHL} : \text{TP} > 0.3$. Given the long intervals between our sample visits it is unlikely that CHL peaks we observed represent the maximum biomass achieved in individual blooms. So it is possible that phosphorus may have transiently limited biomass during some, and perhaps a majority, of blooms observed during the study.

Nitrogen may also have limited maximum CHL in some cases. In one experiment from September 1989 when DIN was near zero, algal growth responded to N but not P and there was no growth in controls. Between fall overturn in 1989 and July 1991, DIN was always present in measurable concentrations but was sometimes nearly depleted during algal blooms at head-water sites (e.g. Fig. 11 a – November 1990). During summer 1991 DIN was usually less than $200 \mu\text{g/L}$ lakewide and fell below detection during some blooms (e.g. Fig. 11 a – July 1991). Algal growth experiments in summer 1991 showed no response to N, but CHL yield in response to P was correlated with ambient DIN ($r = 0.83$, $p = 0.08$, $n = 5$ experiments) and by the end of summer neither N or P produced a significant response. Growth in controls declined steadily in June–September (Fig. 13) in parallel with decreasing DIN (Fig. 11 c) and TP_{filt} . These results suggest phytoplankton were nearing the limits of available P and N during summer 1991. Maximum CHL in blooms may have been limited by either or both nutrients during that period.

Light limitation

Our experimental measurements of algal growth strongly suggested that light often limited phytoplankton biomass (Fig. 13). We usually observed rapid

growth ($>25\%/d$) in controls incubated at light intensities greater than ambient \bar{I}_{mix} . We estimated compensatory irradiance, the light intensity at which net growth was zero (TALLING 1971), from growth-irradiance curves and found values ranging from 0.1 to $7.1 \text{ E m}^{-2} \text{ d}^{-1}$ with most observations between 0.2 and $2 \text{ E m}^{-2} \text{ d}^{-1}$. Lakewide, \bar{I}_{mix} frequently fell in a similar range. For observations in which phosphorus and DIN were high relative to CHL (CHL:TP <0.3 , DIN $>200 \mu\text{g/L}$, $n=389$), 98% of the \bar{I}_{mix} measurements were $<7.1 \text{ E m}^{-2} \text{ d}^{-1}$ and 78% were $<2 \text{ E m}^{-2} \text{ d}^{-1}$. So irradiance may often have been near compensatory intensity and phytoplankton growth and biomass severely light-limited.

Algal growth rates are light limited whenever mixed layer irradiance is less than that required to saturate growth. But light limitation of **growth** does not necessarily result in reduced biomass because, in theory, even submaximal growth rates could eventually produce as much biomass as available nutrients could support. Light limitation of algal **biomass** implies that biomass cannot increase without an increase in ambient light availability as determined by incident irradiance, non-algal light attenuation and the specific absorption of PAR by phytoplankton. For biomass to be light limited, growth must balance losses so that net growth is zero. The irradiance at which this equilibrium occurs is called the compensatory irradiance (\bar{I}_{comp}) or "column compensation point" (TALLING 1971) and depends on the efficiency of algal growth and the intensity of loss factors such as algal respiration (WOLFSY 1983).

Based on growth irradiance curves from our experiments we estimated compensatory irradiances ranging from 0.1 to $7.1 \text{ E m}^{-2} \text{ d}^{-1}$ with most observations between 0.2 and $2 \text{ E m}^{-2} \text{ d}^{-1}$. Because these data are based on growth in enclosed containers they may misrepresent compensatory irradiance in situ. Field measurements of maximum areal CHL, however, point to similar conclusions about the approximate range of compensatory irradiance.

Maximum areal biomass will occur when nutrients are in excess and biomass is as great as can be supported with available light. So the range of \bar{I}_{mix} associated with maximum areal CHL provides an independent estimate of I_{comp} . In our data, areal CHL $>150 \text{ mg/m}^2$ occurred mostly between 0.4 and $4 \text{ E m}^{-2} \text{ d}^{-1}$ (Fig. 15) in reasonable agreement with our experimental estimates of I_{comp} .

Transitional conditions: light versus nutrients

In light-limited phytoplankton communities biomass should covary with light availability and our data show some evidence of this trend. A plot of our data (Fig. 16 a) shows a roughly dome-shaped relation between the highest values of areal CHL and \bar{I}_{avail} , an index of available PAR calculated by correcting \bar{I}_{mix} for light attenuation for algal pigments. Maximum CHL increased precipi-

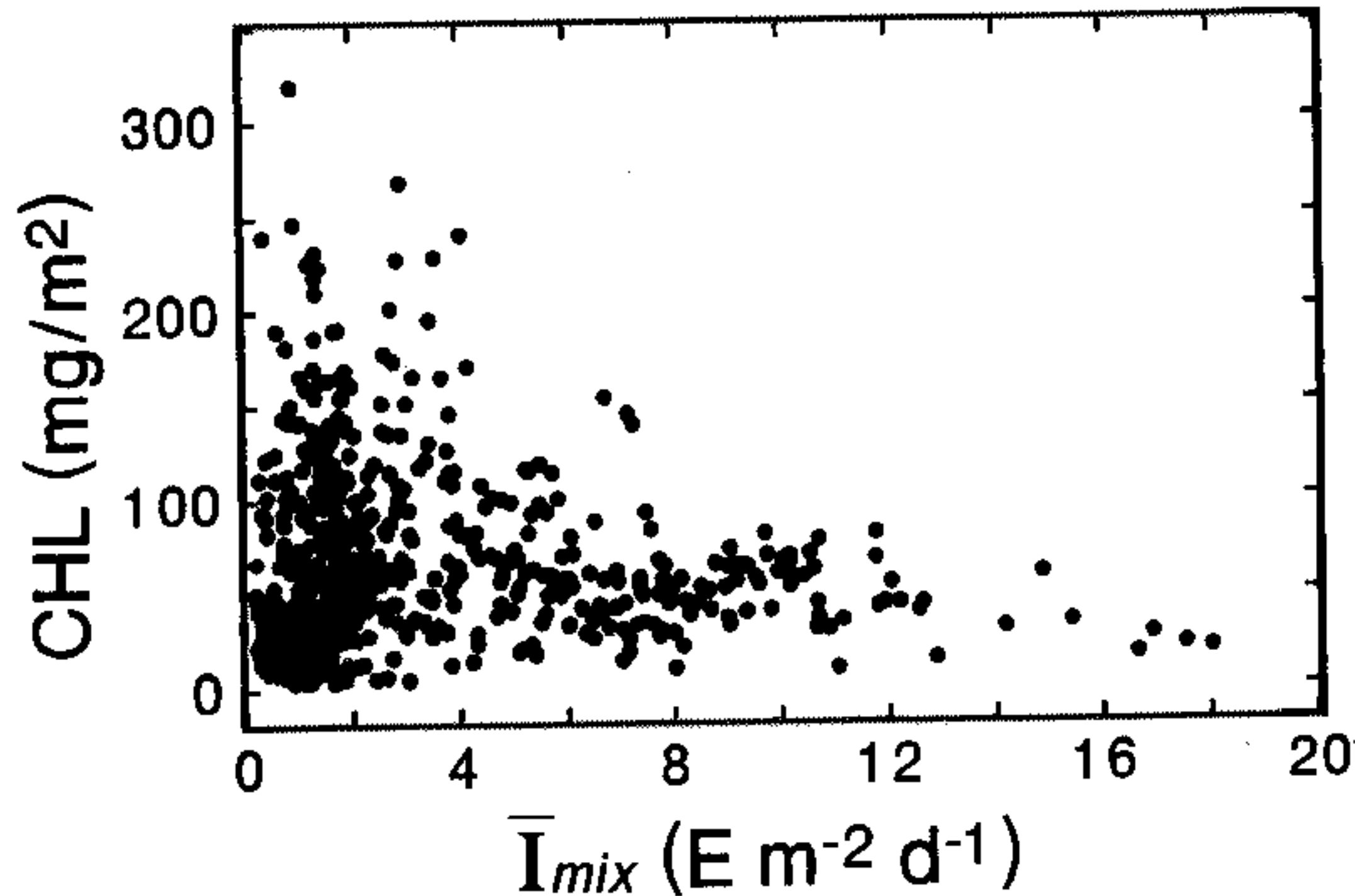


Fig. 15. Plot of areal chlorophyll (CHL) versus mean mixed layer PAR (\bar{I}_{mix}).

tously as \bar{I}_{avail} increased from near zero to about $2 \text{ E m}^{-2} \text{ d}^{-1}$. The majority of observations with areal CHL $> 100 \text{ mg/m}^2$ fell between 1.5 and $4.5 \text{ E m}^{-2} \text{ d}^{-1}$ and maximum biomass declined at higher values of \bar{I}_{avail} .

The decline in maximum biomass at high light availability was presumably influenced by nutrient limitation. The large biomass possible at high irradiances may have exceeded the limits of available nutrients. For example, in our experiments CHL:TP averaged 0.5 in the controls of trials showing significant effects of P addition, so this value is probably indicative of incipient phosphorus limitation. Fig. 16 b shows that maximum CHL:TP rose rapidly with light. Values exceeding 0.5 became common at values of $\bar{I}_{avail} > 1 \text{ E m}^{-2} \text{ d}^{-1}$. Thus nutrients may have quickly supplanted light as the principle factor limiting maximum biomass.

General models of the relation between algal biomass and TP predict that CHL will increase with TP until selfshading by phytoplankton produces a state of light limitation beyond which CHL is asymptotic with respect to TP (STRASKRABA 1980, STRASKRABA & GNAUCK 1985). Under this scenario CHL:TP is an asymptotic function of light availability as seems to be approximately the case in Mark Twain Lake (Fig. 16 b). But the relation between CHL and TP in Mark Twain Lake is not asymptotic, but dome-shaped with maximum CHL declining in the upper range of TP (Fig. 14). The reason for this trend is that in this reservoir light availability is an inverse function of nutrients. Both phosphorus and nitrogen in Mark Twain Lake are strongly correlated with non-algal light attenuation produced by mineral turbidity (Fig. 17). Thus light conditions vary systematically with nutrient supply rather than with algal biomass. In this situation maximum biomass should increase in more or less direct proportion to TP in the lower range of TP and decrease in the upper range as observed in this data set.

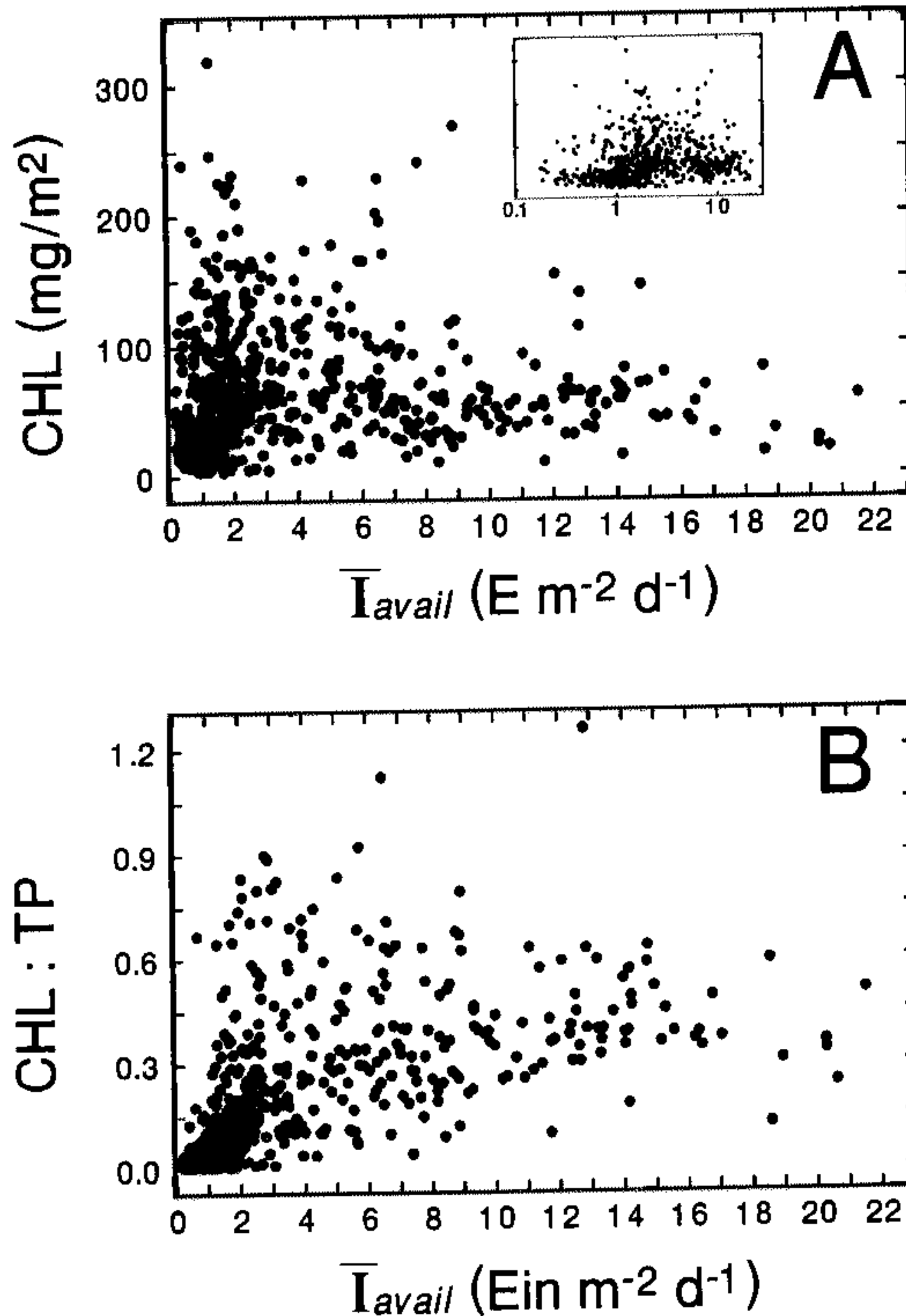


Fig. 16. Areal chlorophyll (CHL) concentration (A) and chlorophyll to total phosphorus (CHL : TP) ratio (B) versus “available” mixed layer PAR (\bar{I}_{avail}). The insert in panel A shows the data on semi-log axes to clarify the increase in areal CHL over the initial range of \bar{I}_{avail} .

Biomass versus growth rates

Maximum CHL and CHL : TP seem to vary predictably with light availability and TP but the majority of individual observations fall well below the upper limits of these relations (Figs. 14, 16). Under conditions of light limitation the fact that areal CHL did not co-vary closely with \bar{I}_{avail} (Fig. 16 a) is probably due to natural variation in conditions controlling biomass under light limitation. Maximum biomass is determined not only by light availability but also by the specific light attenuation, growth efficiency, and loss rates of phytoplankton all of which are highly variable (WOLFSY 1983). Scatter in this relationship may also be due to time lags in the response of growth to changing

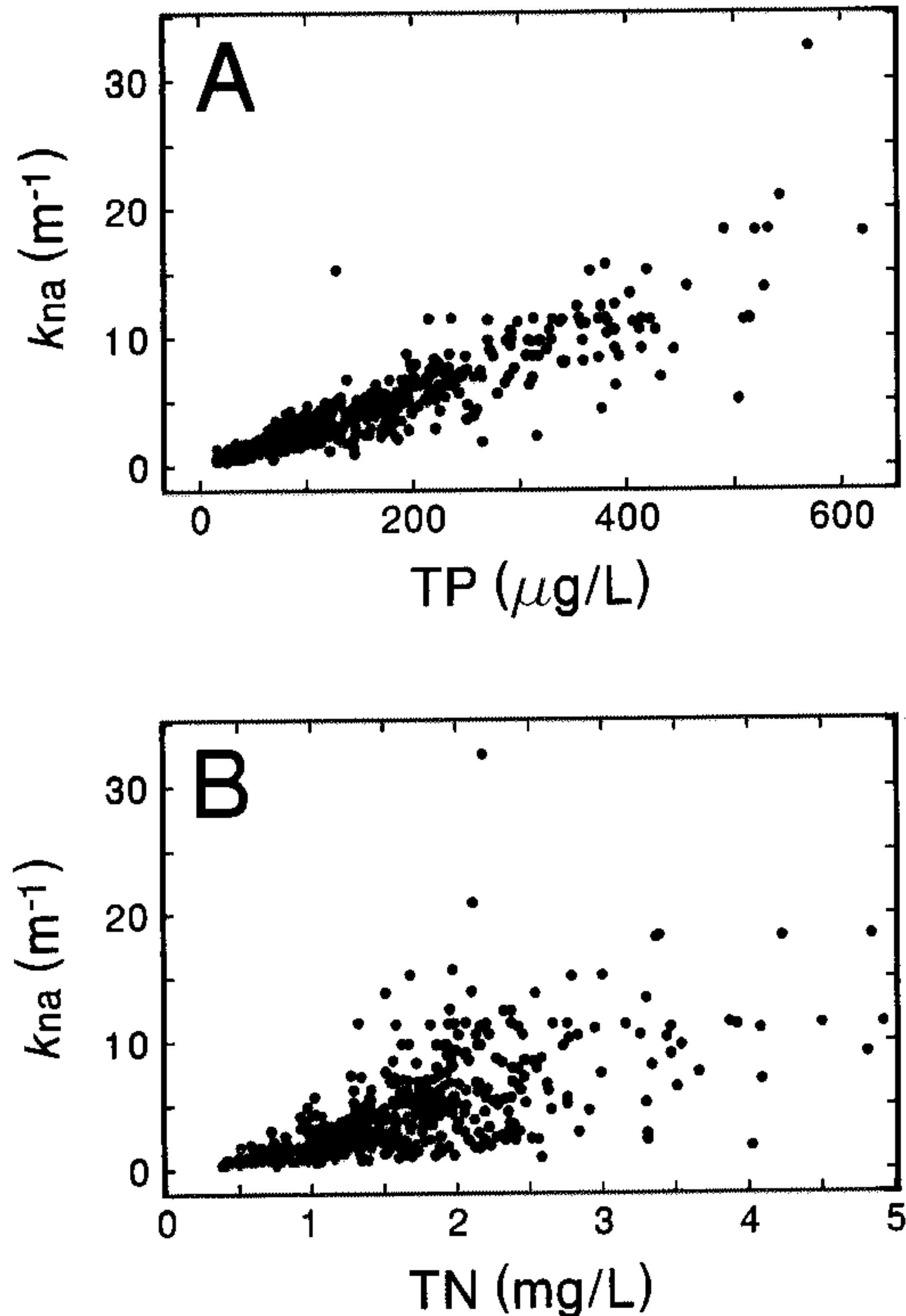


Fig. 17. Relation of non-algal light attenuation (k_{na}) to concentrations of (A) total phosphorus (TP) and (B) total nitrogen (TN).

light conditions. Small changes in light availability will have a proportionately greater effect on potential biomass than on growth rates, so biomass will usually lag behind changes in available light.

For example, median values from this data set describe a typical scenario in which CHL, mixed depth, $\overline{\text{PAR}}$, k_{na} , and \overline{I}_{mix} have respective values of about 12 μg/L, 4.5 m, 26 E m⁻² d⁻¹, 3.0/m, and 1.8 E m⁻² d⁻¹. If areal CHL (12 g/L · 4.5 m = 54 μg/m²) is initially in equilibrium with light at this ambient irradiance (i.e. $\overline{I}_{mix} = I_{comp} = 1.8 \text{ E m}^{-2} \text{ d}^{-1}$) and incident irradiance then doubled to 52 E m⁻² d⁻¹, total light attenuation would also have to double to reduce \overline{I}_{mix} back to compensating irradiance and restore equilibrium. If algal specific attenuation is 0.02 m²/mg CHL, then biomass would have to increase by more than an

order of magnitude to $174 \mu\text{g/L}$ (areal CHL = 783 mg/m^2) for this to be accomplished.

Factor of two and larger variation in incident irradiance is not uncommon. In the pyronometer data we used to calibrate our irradiance estimates, day to day variation of total irradiance in a typical week was >4 fold. But in our experimental data, I_{comp} was usually less than 10% of the irradiance producing maximum growth rates. So even quadrupling irradiance to 400% of I_{comp} would typically increase growth rate from zero to less than half of maximum. Despite greatly increasing potential biomass, even large increases in light availability would still leave growth rates well below maximum.

Under such conditions, biomass would lag well behind changes in light availability even if nutrient supplies were adequate to support such large changes in biomass. Thus the scatter in Fig. 16 a may well reflect the degree to which biomass and light fail to achieve equilibrium under temporally variable conditions. And because growth rates in situ may be very low, biomass might lag well behind its potential even when light conditions improve steadily over an extended period such as occurs during vernal stratification. In this circumstance biomass is not strictly light-limited insofar as areal CHL will increase without increasing irradiance. On the other hand, increasing irradiance will increase growth rates and lead to more rapid increase in biomass in which case CHL and \bar{I}_{mix} could be correlated as observed by OLIVER & GANF (1988) in a turbid Australian reservoir. The term "growth-rate limited" seems appropriate to describe the status of phytoplankton biomass under such circumstances.

Temporal variation in nutrient supply is probably much less than that of light availability which may explain why the variation of areal CHL seems greater in the lower range of \bar{I}_{avail} , where light limitation was likely, than in the upper range where nutrients probably limited biomass (Fig. 16). Nonetheless, ratios of CHL : TP at in the upper range of light availability covered a wide range and few observations were near the maximum values seen in the study (Fig. 16 b). This scatter may be due to variation in nutrient availability or phytoplankton community characteristics that produce differences in the range of CHL : TP where P limitation becomes important. In our growth experiments, maximum ratios of CHL : TP in controls ranged by a factor of 3 (from 0.3 to 1.0) in experiments showing a significant P-response. So CHL : TP is not a sensitive indicator of nutrient status.

Also our data suggest that biomass was not always nutrient limited when light availability was high. During summer 1991 \bar{I}_{mix} near the dam was usually greater than the irradiances that saturated growth in our experiments and yet phytoplankton biomass did not seem nutrient-limited in situ. We usually observed significant growth in controls without added P or N (Fig. 13). These data suggest biomass may have been limited by high loss rates rather than conditions limiting growth. Other biotic factors such as grazing and parasitism

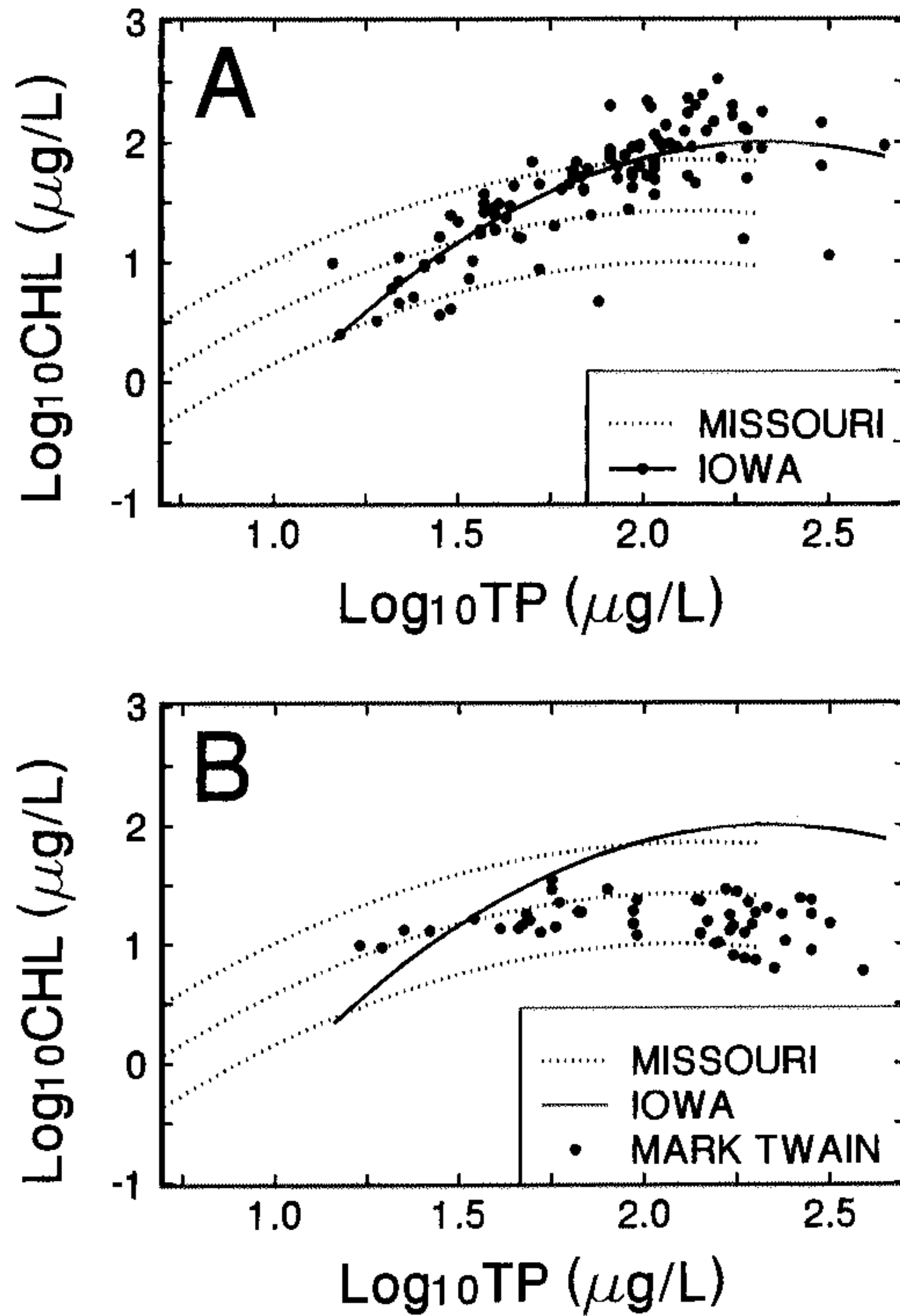


Fig. 18. Base 10 logarithmic plots of chlorophyll (CHL) and total phosphorus (TP). A) – Summer mean data for Iowa lakes (KNOWLTON et al. 1984, KNOWLTON & JONES 1993) with a fitted quadratic regression line (solid line) superimposed on the regression model and 95 % predictive confidence intervals for Missouri reservoirs from JONES & KNOWLTON (1993). – B) – May–September means for sampling sites on Mark Twain Lake superimposed on the Iowa and Missouri regressions from panel A.

were not considered in this study but undoubtedly influence algal dynamics to some extent. Thus the nutrient and light variables we measured provide some indication of potential biomass but do not clearly indicate when or if that potential will be reached.

Regional limnology and summer mean conditions

Most limnological data from lakes in the region encompassing Mark Twain Lake have been obtained in summer lake surveys and used as seasonal means,

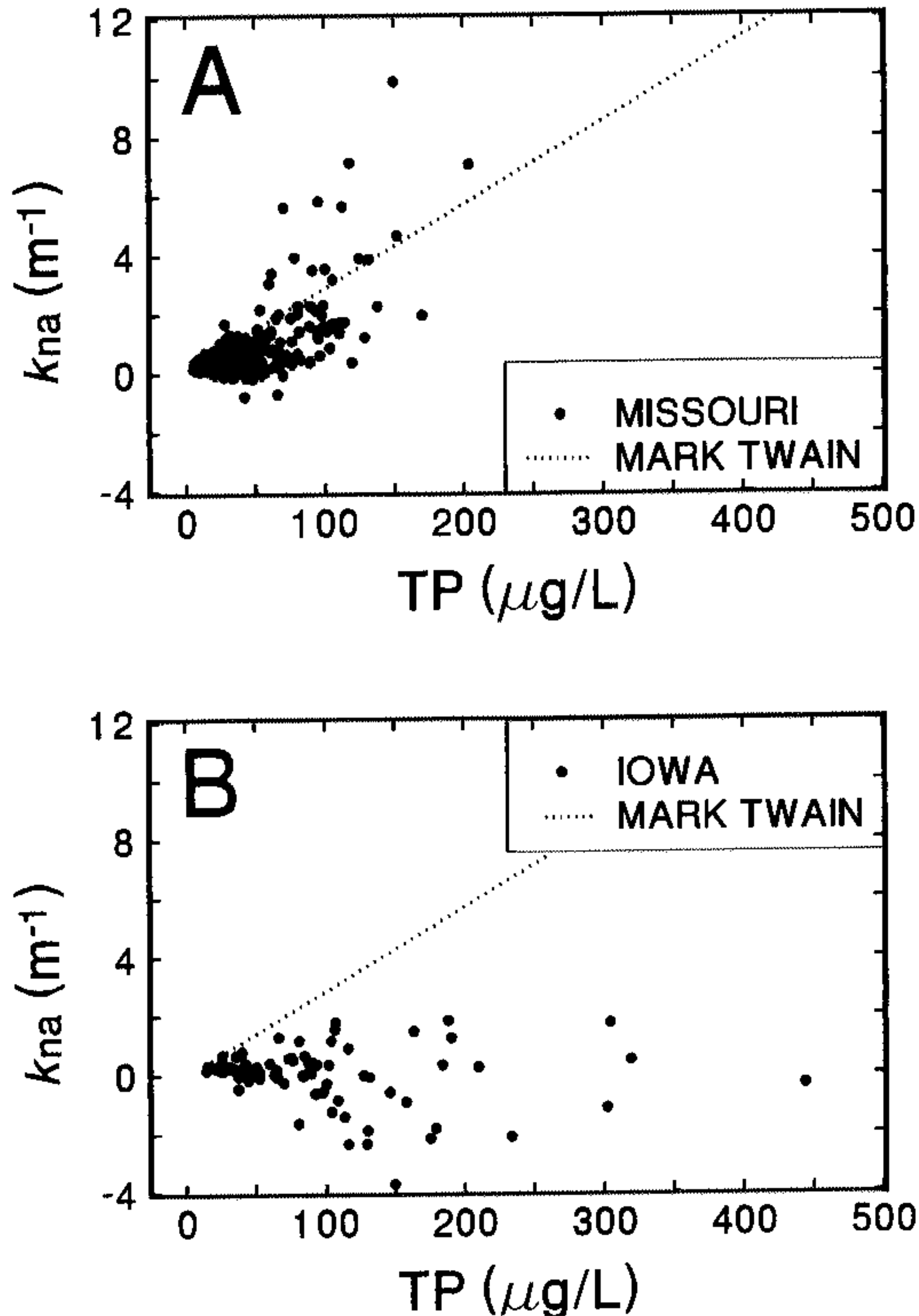


Fig. 19. Plots of total phosphorus (TP) and non-algal light attenuation estimated as $k_{na} = 1/\text{Secchi Depth} - 0.025 \cdot \text{CHL}$ (WALKER 1982). A) – Summer means from Missouri reservoirs (JONES & KNOWLTON 1993) superimposed on a regression model based on Mark Twain Lake data in Fig. 17 a ($k_{na} = 0.028 \cdot \text{TP} + 0.074$, $n = 604$; $r^2 = 0.82$). B) – Summer means from Iowa lakes (KNOWLTON et al. 1984, KNOWLTON & JONES 1993) superimposed on the Mark Twain Lake regression.

to describe variation in transparency and algal biomass (JONES & BACHMANN 1976, 1978; HOYER & JONES 1983, JONES & KNOWLTON 1993). JONES & KNOWLTON (1993) showed the summer mean CHL for lakes in Missouri increased with mean TP up to about $50 \mu\text{g/L}$ beyond which CHL seemed to plateau or decline. Data from Iowa lakes also show a significantly curvilinear response of CHL to TP (KNOWLTON & JONES 1993). Among Iowa lakes initial slope of the relationship is steeper than in Missouri and reaches an asymptote at much higher mean TP and CHL (Fig. 18 a).

Part of this regional difference in CHL-TP relations is that the two data sets cover a different range of TP. Missouri lakes are typically less enriched than those in Iowa. But May–September means of CHL and TP from Mark Twain Lake overlap most of the range of TP comprised by both Missouri and Iowa data sets and clearly conform with the pattern predicted by extrapolation of the Missouri model. Summer mean CHL in Mark Twain Lake peaked at TP between 50 and 100 $\mu\text{g/L}$ and showed a distinct, but gradual, decline over the upper range of TP (Fig. 18 b). Maximum mean CHL was less than half that occurring in Iowa lakes with TP > 100 $\mu\text{g/L}$.

An important factor explaining these differences is regional variation in the relation between TP and non-algal light attenuation. The strong relation between TP and k_{na} in Mark Twain Lake was shared to some extent by lakes in Missouri. In the JONES & KNOWLTON (1993) data set, TP is positively correlated to non-algal light attenuation estimated as inverse Secchi depth ($1/SD$) minus $0.025 \cdot \text{CHL}$ (WALKER 1982, Fig. 19 a). But the same trend does not hold for lakes and reservoirs in Iowa in which TP and k_{na} do not significantly covary (Fig. 19 b). In many Iowa lakes, light attenuation is low relative to CHL so non-algal light attenuation according the Walker (1982) index is estimated as less than zero. Low light attenuation in Iowa lakes means that light conditions favor higher maximum CHL than in Missouri lakes. Such regional differences in growth limiting conditions must be considered in assessing algal-nutrient relations (PREPAS & TREW 1983, DUARTE & KALFF 1989, JONES & KNOWLTON 1993).

References

- American Public Health Association (A.P.H.A.) (1980): Standard methods for the examination of water and wastewater, 15ed. – American Public Health Association, New York, NY, 1193 pp.
- AVNIMELECH, Y., TROEGER, B. W. & REED, L. W. (1982): Mutual flocculation of algae and clay: Evidence and implications. – *Science* **216**: 63–65.
- CARLSON, R. E. (1991): Expanding the trophic state concept to identify non-nutrient limited lakes and reservoirs, pp. 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, 112 pp.
- CRUMPTON, W. G., ISENHART, T. M. & MITCHELL, P. D. (1992): Nitrate and organic N analyses with second-derivative spectroscopy. – *Limnol. Oceanogr.* **37**: 907–913.
- CUKER, B. E. (1987): Field experiment on the influences of suspended clay and P on the plankton of a small lake. – *Limnol. Oceanogr.* **32**: 840–847.
- DUARTE, C. M. & KALFF, J. (1989): The influence of catchment geology and lake depth on phytoplankton biomass. – *Arch. Hydrobiol.* **115**: 27–40.
- FINNEY, V. L. (1986): Seasonal Sediment Yield to Mark Twain Lake, Missouri. – *Bull. Assoc. Engin. Geol.* **23**: 333–338.

- HERGENRADER, G. L. & HAMMER, M. (1971): Eutrophication of small reservoirs in the Great Plains. – *Geophys. Monogr. Ser.* **17**: 560–566.
- HOWARD-WILLIAMS, C. (1985): Suspensoids and Turbidity: Chairman's summary. – *Hydrobiologia* **125**: 243–245.
- HOYER, M. V. & JONES, J. R. (1983): Factors affecting the relation between phosphorus and chlorophyll-a in midwestern reservoirs. – *Can. J. Fish. Aquat. Sci.* **40**: 192–199.
- JAMES, W. F., KENNEDY, R. K., MONTGOMERY, R. H. & NIX, J. (1987): Seasonal and longitudinal variations in apparent deposition rates within an Arkansas reservoirs. – *Limnol. Oceanogr.* **32**: 1169–1176.
- JONES, J. R. & BACHMANN, R. W. (1976): Prediction of phosphorus and chlorophyll levels in lakes. – *J. Water Pollut. Control Fed.* **48**: 2176–2182.
- – (1978 a): Phosphorus removal by sedimentation in some Iowa reservoirs. – *Verh. Int. Verein. Limnol.* **20**: 1576–1580.
- – (1978 b): Trophic status of Iowa lakes in relations to origin and glacial geology. – *Hydrobiologia* **57**: 267–273.
- JONES, J. R. & KNOWLTON, M. F. (1993): Limnology of Missouri reservoirs: An analysis of regional patterns. – *Lake Reserv. Managem.* **8**: 17–30.
- JONES, J. R. & NOWAK, J. T. (1981): Limnological characteristics of Lake of the Ozarks, Missouri. – *Verh. Int. Verein. Limnol.* **21**: 919–925.
- KENNEDY, R. H., THORNTON, K. W. & CARROLL, J. H. (1981): Suspended-sediment gradients in Lake Red Rock. – In: STEFAN, H. G. (ed.): *Proceedings of the symposium on surface water impoundments.* – Amer. Soc. Civil Engr., New York, NY, pp. 1318–1328.
- KENNEDY, R. H. & WALKER, W. W. (1990): Reservoir nutrient dynamics. Chapter 5. – In: THORNTON, K. W. (ed.): *Reservoir Limnology: An ecological continuum.* – John Wiley & Sons, New York.
- KIMMEL, B. L., LIND, O. T. & PAULSON, L. H. (1990): Reservoir primary production. Chapter 6. – In: THORNTON, K. W. (ed.): *Reservoir Limnology: An ecological continuum.* – John Wiley & Sons, New York.
- KIRK, J. T. O. (1983): *Light & Photosynthesis in aquatic ecosystems.* – Cambridge University Press, Cambridge, 401 pp.
- KNOWLTON, M. F. (1984): Flow-through microcuvette for fluorometric determination of chlorophyll. – *Water Res. Bull.* **20**: 795–799.
- KNOWLTON, M. F., HOYER, M. V. & JONES, J. R. (1984): Sources of variability in phosphorus and chlorophyll and their effects on use of lake survey data. – *Water Resour. Bull.* **20**: 397–407.
- KNOWLTON, M. F. & JONES, J. R. (1993): Testing models of chlorophyll and transparency for midwest lakes and reservoirs. – *Lake Reserv. Managem.* **8**: 13–16.
- – (in press): Experimental evidence of light and nutrient limitation of algal growth in a turbid midwest reservoir. – *Arch. Hydrobiol./Suppl.*
- LIND, O. T. (1986): The effect depth to chlorophyll-a. – *Hydrobiologia* **140**: 27–35.
- National Oceanic and Atmospheric Administration (N.O.A.A.) (1991): *Local climatological data – Monthly summary.* Columbia, Missouri.
- OLIVER, R. L. & GANF, G. G. (1988): The optical properties of a turbid reservoir and its phytoplankton in relation to photosynthesis and growth (Mount Bold Reservoir, South Australia). – *J. Plankt. Res.* **10**: 1155–1177.

- PREPAS, E. E. & RIGLER, F. A. (1982): Improvements in quantifying the phosphorus concentration in lake water. – *Can. J. Fish. Aquat. Sci.* **39**: 82–829.
- PREPAS, E. E. & TREW, D. O. (1983): Evaluation of the phosphorus-chlorophyll relationship for lakes off the Precambrian shield in western Canada. – *Can. J. Fish. Aquat. Sci.* **40**: 27–35.
- REYNOLDS, C. S. (1984): *The ecology of freshwater phytoplankton*. – Cambridge University Press, Cambridge, 384 pp.
- RIEMANN, B., SIMONSEN, P. & STENSGAARD, L. (1989): The carbon and chlorophyll content of phytoplankton from various nutrient regimes. – *J. Plank. Res.* **11**: 1037–1045.
- RILEY, G. A. (1957): Phytoplankton of the north central Sargasso Sea. – *Limnol. Oceanogr.* **2**: 252–270.
- SARTORY, D. P. & GROBBELAAR, J. U. (1984): Extraction of chlorophyll-a from freshwater phytoplankton for spectrophotometric analysis. – *Hydrobiologia* **114**: 177–187.
- Soil Conservation Service (1988): *Upper Salt River Basin erosion and sediment inventory*. – U.S. Department of Agriculture, Soil Conservation Service, Columbia, Missouri.
- SMITH, V. H. (1990): Effects of nutrients and non-algal turbidity on blue-green algal biomass in four North Carolina reservoirs. – *Lake Reserv. Managem.* **6**: 125–131.
- SØBALLE, D. M. & KIMMEL, B. L. (1990): A large scale comparison of factors influencing phytoplankton abundance in rivers, lakes and impoundments. – *Ecology* **68**: 1943–1954.
- SØBALLE, D. M. & THRELKELD, S. T. (1988): Algal-clay flocculation in turbid waters: Variation due to algal and mineral differences. – *Verh. Int. Verein. Limnol.* **23**: 750–754.
- STANTON, M. P., CAPEL, M. S. & ARMSTRONG, F. A. J. (1977): *Chemical analysis of freshwater*. – 2nd ed. *Can. Fish. Mar. Serv. Misc. Spec. Publ.* **25**: 166 pp.
- STEFAN, H. G., CARDONI, J. J., SCHIEBE, F. R. & COOPER, C. M. (1983): Model of light penetration in a turbid lake. – *Water Resour. Res.* **19**: 109–120.
- STRASKRABA, M. (1980): The effects of physical variables on freshwater production: analyses based in models. Chapter 3. – In: LE CREN, E. D. & LOWE-McCONNELL, R. H. (eds.): *The functioning of freshwater ecosystems*. – Cambridge University Press, Cambridge, 588 pp.
- STRASKRABA, M. & GNAUCK, A. (1985): *Freshwater ecosystems – modeling and simulation*. – Elsevier, Amsterdam, 309 pp.
- TALLING, J. F. (1971): The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. – *Mitt. Int. 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.

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