

## Summer distribution of nutrients, phytoplankton and dissolved oxygen in relation to hydrology in Table Rock Lake, a large midwestern reservoir<sup>1</sup>

By MATTHEW F. KNOWLTON and JOHN R. JONES

With 13 figures and 4 tables in the text

### Abstract

Table Rock Lake is a large (17 km<sup>3</sup>) hydropower reservoir with hypolimnetic discharge. In summer, nutrient-poor hypolimnetic outflow from an upstream reservoir (Beaver Lake) flows as a density current into the hypolimnion of the White River arm of Table Rock Lake with little effect on surface water quality. Nutrient-rich inflow from other tributaries enters the epilimnion where dilution and sedimentation cause extreme longitudinal gradients. Downlake declines of >80% in concentrations of phosphorus and chlorophyll have been recorded in the James River and Long Creek arms in one or more years. In the White River arm local nutrient inputs from Leatherwood Creek cause similar, but much smaller gradients. Algal biomass throughout the White River arm and in other downlake areas is highly correlated to phosphorus concentration both in the mixed layer and metalimnion. Other uplake reaches may be nitrogen limited, especially in late summer. Metalimnetic chlorophyll maxima develop in summer in most parts of the lake with communities numerically dominated by diatoms, especially *Achnanthes minutissima*, in downlake areas and bluegreens, flagellates and photosynthetic bacteria in headwater reaches. Oxygen depletion is most rapid near the sediments and in the lower metalimnion and is faster in headwater areas than near the dam. Discharge for power generation causes rapid replacement of hypolimnetic water near the dam increasing the temperature and decreasing oxygen concentrations. Discharge volume accounts for >80% of interannual variation in hypolimnetic warming and oxygen depletion in summer.

### Introduction

Many large reservoirs exhibit complex spatial variation in the distribution of nutrients and phytoplankton (BAXTER 1977, JONES & NOVAK 1981, KENNEDY et al. 1982, THORNTON et al. 1982). Inputs from rivers create gradients in advective movement, turbulence, and suspended and dissolved materials along the axis of the former river channel. The magnitude of gradients depends on the volume and water quality of inflows and morphology of the basin. These gradients vary over

<sup>1</sup> Contribution of the Missouri Agricultural Experiment Station Journal Series No. 10506.

time and among different arms in the same lake (JONES & NOVAK 1981, KENNEDY et al. 1982). In large impoundments, sedimentation of influent materials can limit nutrient loading to downlake areas and produce great longitudinal variation in trophic state characteristics such as transparency, algal standing crop and oxygen depletion rates (CARMACK & GRAY 1982, HANNAN et al. 1981, JONES & NOVAK 1981, JAMES et al. 1987, THORNTON, in press). Spatial variation in trophic state features may also include gradients in the vertical distribution of phytoplankton with metalimnetic or hypolimnetic production increasing downlake along gradients in nutrients and transparency (KIMMEL et al., in press).

Table Rock Lake in southern Missouri and northern Arkansas is a large, complex waterbody which impounds waters of the White River, James River, Kings River and several lesser tributaries. Since completion of Table Rock Dam in 1959, the reservoir has been operated for flood control and hydropower generation and is presently one of four hydropower reservoirs in series on the White River lying immediately below Beaver Lake (completed in 1963) and above Lake Taneycomo (1913) and Bull Shoals Lake (1951). Data collected during the National Eutrophication Survey in 1974–1975 show extreme variation in nutrient loading among the several arms of Table Rock Lake (U.S. Environmental Protection Agency 1977) resulting from point source inputs to the James River and other tributaries and removal of nutrients from the White River by sedimentation in Beaver Lake (WALKER 1981). These data also show great spatial variability in nutrient concentrations, algal standing crops and oxygen depletion. But vertical distribution of phytoplankton was not measured and other data were collected at widely spaced locations and do not show details of longitudinal gradients.

Reservoir surveys conducted by the University of Missouri during 1978–1984 show Table Rock Lake at the dam is the least fertile large reservoir in Missouri and the only one where metalimnetic chlorophyll peaks are common (KNOWLTON & JONES 1989). Trophic characteristics of the lake are important because of exceptional transparency in downlake areas and because the temperature and oxygen content of hypolimnetic releases from Table Rock Lake influence a valuable trout fishery in Lake Taneycomo immediately downstream (WEITHMAN & HASS 1984). Rapid population growth and urban development are occurring near the lake which will result in increased nutrient loading. Our aim in this paper is to document trophic state characteristics of Table Rock Lake at this time and describe the spatial distribution of phytoplankton and dissolved oxygen in relation to nutrient inputs and hydrology.

### Data base

Data were collected in 1976–1988 by the University of Missouri, U.S. Army Corps of Engineers (Little Rock District, Little Rock, Arkansas), and U.S. Geological Survey (Rolla, Missouri and Little Rock, Arkansas). Data include daily records of water level, discharge and inflow from the White and James Rivers and monthly profiles of temperature

and dissolved oxygen taken near the dam by the Corps of Engineers or U.S.G.S. Also included are monthly records of several water quality variables (total phosphorus, sodium, specific conductance, calcium, iron) collected from the James River at a site 47 km upstream from the reservoir and, in some years, from sites on the White River, Kings River and Long Creek. Other records include measurements of temperature, dissolved oxygen (DO), specific conductance, chlorophyll and total phosphorus concentration (TP) taken three times a year during 1985–1987 by the U.S. G.S. from two depths at 7 locations. Morphometric measurements were obtained from the U.S. Army Corps of Engineers or were determined by planimetry using pre-impoundment topographic maps.

In 1978, 1981, 1982–1984 and 1987–1988, we measured chlorophyll (CHL), total phosphorus (TP), and total nitrogen (TN) concentrations and Secchi transparency at one or more locations on 1–5 dates during summer. Other measurements (silica, alkalinity, specific conductance, volatile and non-volatile suspended solids, nitrates) were made occasionally. We measured CHL spectroscopically or fluorometrically using acetone, acetone-dimethyl sulfoxide or ethanol extracts of algae concentrated on glass fiber filters (A.P.H.A. 1976, BURNISON 1980, SARTORY & GROBBELAAR 1984, KNOWLTON 1984). Total phosphorus was measured after persulfate digestion (MENZEL & CORWIN 1965) according to A.P.H.A. (1976) or PREPAS & RIGLER (1983) and TN was measured according to D'ELIA et al. (1977). We made other determinations according to A.P.H.A. (1976).

In 1982 we took temperature, DO, and *in vivo* fluorescence (chlorophyll) profiles on four dates at six locations in the lower reaches of Long Creek and James River arms. Fluorometric measurements were taken as described by KNOWLTON & JONES (1989). During one additional visit in 1982, we sampled at 21 locations in the White River, Long Creek and lower James River arms. In 1983, we took profiles on four dates at six locations and on one occasion, collected profiles at 13 locations.

In August 1987, we took temperature, DO, and specific conductance profiles at approximately 8 km intervals over the entire James River, White River and Long Creek arms. We collected surface samples at 16 km intervals and from inflowing streams for analysis of CHL, TP, TN, silica (SiO<sub>2</sub>), alkalinity, calcium, sodium, chloride and volatile and non-volatile suspended solids (VSS, NVSS). Similar data were collected from 7 sites on the James River arm on 17 May 1988, and from 14 sites on the White River arm on 13–14 September 1988. The latter included one collection from the Leatherwood Creek arm – a small embayment of the White River arm. Additionally, vertical profiles of CHL, TP, TN, VSS and NVSS were collected near the dam in August 1987 and on 5 dates between 2 June and 28 September 1988. Samples taken in 1988 were also analyzed for nitrate-N.

Phytoplankton counts from surface or metalimnetic samples were made on several occasions in 1982 and 1983. Counts were made on samples preserved with acid Lugol's iodine using an inverted microscope technique (LUND et al. 1958).

## Results

### Morphometry, hydrology and temperature regime

Table Rock Lake is located about 10 km west of Branson, Missouri in the rugged White River Hills region of the Ozark Plateau. The lake drains 10,412 km<sup>2</sup> (Fig. 1) most of which is forested with thin soils, underlain by limestone bedrock (THOM & WILSON 1980). Table Rock Lake is the deepest waterbody in Missouri. At the average surface elevation of 278 m MSL it has mean and maximum depths

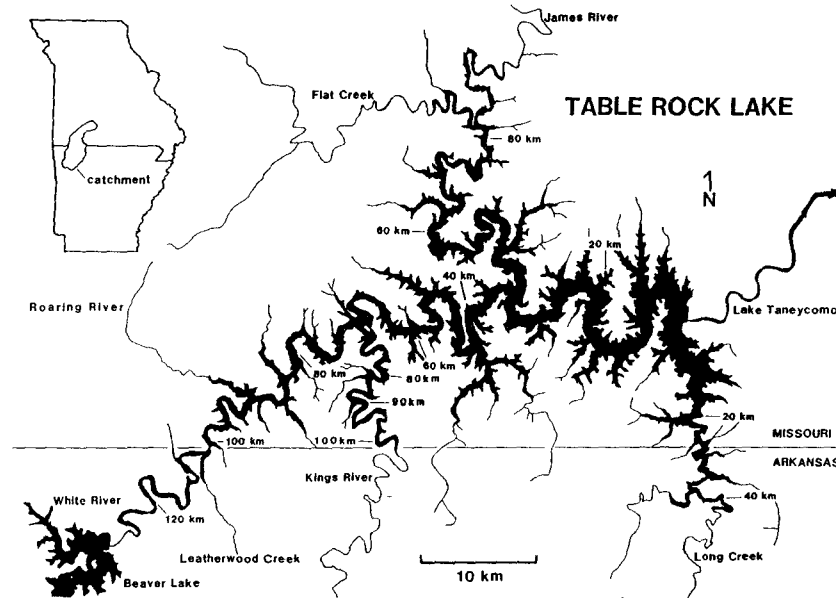


Fig. 1. Table Rock Lake and major tributaries. Lake surface is shown at 279 m MSL. Distances shown adjacent to shore were measured from the dam along former river channels.

of 18.9 m and 66 m respectively and a surface area of 167 km<sup>2</sup>. The basin is highly serpentine and dendritic with major arms formed by the White River, Kings River, James River and Long Creek (Fig. 1). At average lake level the White River arm extends 120 km uplake from the dam. Over half of the total lake volume, however, occurs within 30 km of the dam in lower reaches of the White River and Long Creek arms (Fig. 2).

Table Rock Lake is operated for power generation and flood control in concert with other reservoirs in the White River system. Water levels fluctuate about 5 m in an average year (mean = 4.8 m, range 2.6–7.0 m for 1976–1986) typically peaking in winter or spring and declining in summer. Large water level fluctuations, however, may occur any time of the year in response to run-off. Inflow from the White River is regulated by Beaver Lake immediately upstream. Both Table Rock and Beaver lakes are used principally to meet peaking power, demand so major water releases in summer are usually restricted to short periods (4–12 h/d). Discharge from Beaver Lake often peaks during spring or summer while inflow from the James River and other unregulated tributaries are usually greatest in spring and minimal in summer. During 1976–1986 inflow from the White and James rivers comprised about 26% and 30%, respectively, of total inflow to the lake. Based on proportional flow estimates made by the U.S.E.P.A. (1977), inflows from the Kings River and Long Creek comprised about 14% and 3% of total inflow. Other major tributaries

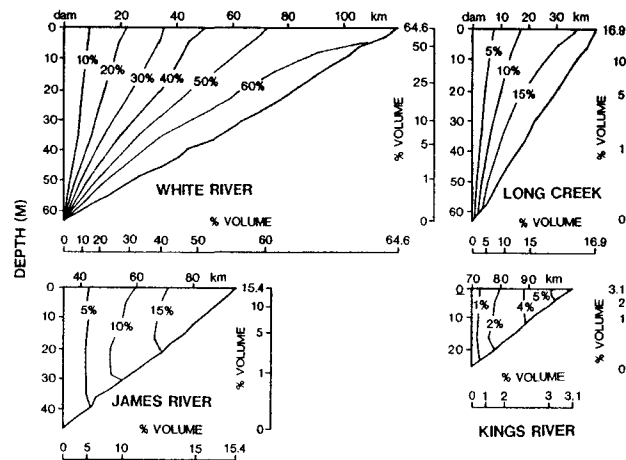


Fig. 2. Volume distribution in major arms of Table Rock Lake at lake level = 277 m MSL. Vertical bars show cumulative volume below the indicated depth and horizontal bars show cumulative volume downlake for distances measured along former river channels. Volumes are given as a percent of total lake volume (3.04 km<sup>3</sup>). Isopleths show cumulative volume downlake calculated at 3 m depth intervals. Values were obtained by planimetry from pre-impoundment topographic maps and are not corrected for sedimentation.

include Flat Creek on the James River arm (5% of annual inflow), Yokum Creek on the Long Creek Arm (0.9%) and Roaring River on the White River arm (0.9%).

In 1976–1986 theoretical residence times for Table Rock Lake varied from 216 days in 1985 to 1287 days in 1981 using the lake volume on 1 January as the reference. The median value for the period was 333 days in 1982. Residence times vary greatly throughout the year and among different arms. For the James River arm theoretical residence time in an average year ranges from 107 days in April–June to 321 days in July–September (Table 1).

Values for the upper portion of the White River arm (above the James River) are similar but are less seasonally variable because of regulation by Beaver Dam. Other tributaries are not gauged but assuming their monthly inflows are proportional to the annual flow estimates made by the U.S.E.P.A. in 1974–1975, average annual residence times range from 62 days for the Kings River arm to 838 days for the Long Creek arm with seasonal variation like that of the James River arm.

Patterns of water movement suggested by differences in residence times among arms are further complicated by thermal stratification and density currents in inflows and discharge. Table Rock Lake is usually stratified from March through November or December and develops a sharp thermocline (ca. 2–3 C/m) in summer at 7–12 m (e.g. Fig. 3). Water is released from the dam through openings centered about 42 m below the average lake surface so the withdrawal layer is

Table 1. Quarterly and annual mean inflow and outflow for 1976–1986 and mean theoretical residence times (time period  $\times$  mean volume/total inflow) for major parts of Table Rock Lake. Flow data are from U.S.G.S. records (U.S.G.S., 1977–1987). Total inflow was calculated as outflow plus net volume change without adjustment for evaporation. Residence times were estimated from average monthly water levels and inflow data and volumes computed by planimetry using preimpoundment topographic maps. Inflows from specific ungauged sources and direct run-off were estimated as a percentage of the inflow from the James River using proportions estimated during the National Eutrophication Survey in 1974–1975 (E.P.A., 1977).

	mean flow (km <sup>3</sup> )				
	Jan–Mar	Apr–Jun	Jul–Sep	Oct–Dec	annual
Inflow					
White River	0.23	0.30	0.28	0.19	1.01
James River	0.26	0.31	0.10	0.21	0.87
Total	0.93	1.15	0.43	0.81	3.33
Outflow	0.85	1.06	0.66	0.73	3.31

area	mean residence time (days)				
	Jan–Mar	Apr–Jun	Jul–Sep	Oct–Dec	annual
White River Arm <sup>1</sup>					
upper	157	131	149	192	165
lower	124	104	209	153	138
Long Creek Arm	699	607	1823	864	838
James River Arm	122	107	321	151	147
Kings River Arm	51	46	136	63	62
Table Rock Lake	294	248	661	344	338

<sup>1</sup> The White River arm was divided into upper and lower segments at the mouth of the James River, 34 km above the dam (Fig. 1).

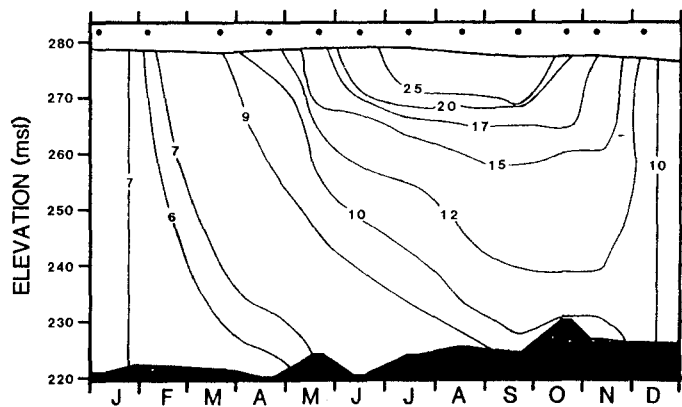


Fig. 3. Temperature regime of Table Rock Lake – 1983. Isotherms were interpolated from monthly temperature profiles taken near the dam (U.S.G.S. 1984). Closed circles show sampling dates. Profile depths (shown by darkened area at the bottom) varied due to small variations in sampling location with respect to the thalweg.

restricted by thermal density gradients to the hypolimnion and lower metalimnion. These have not been measured directly but a selective withdrawal model developed by the Corps of Engineers (DAVIS et al. 1987) predicts a fairly thick withdrawal zone that entrains water from the lake bottom to the bottom of the metalimnion.

Figure 4 is a model of water movement in the lake during an average summer month which shows the extent of the withdrawal zone as predicted from a one-dimensional model (DAVIS et al. 1987) and temperature data from 17 August 1983 (Fig. 3). In this simulation we assumed that each depth stratum (initially tabulated at 3 m intervals) moves as a discrete plug flow changing in elevation, thickness and longitudinal position as water is withdrawn from its downlake terminus or added uplake. As shown by the arrows in the hypolimnion, withdrawal currents

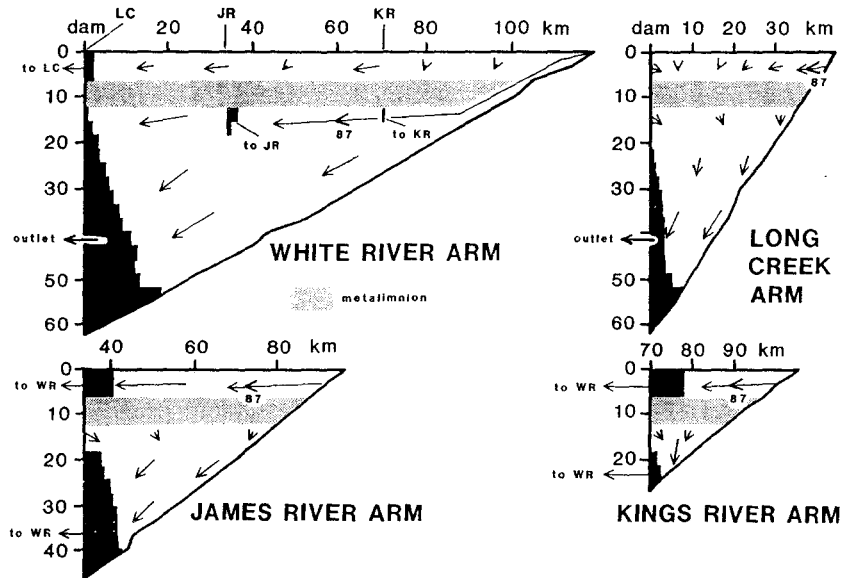


Fig. 4. Hypothetical net water movements in Table Rock Lake during an average summer month. Arrows show the positions of water masses in 3 m depth strata at the beginning and end of the month. Bold arrows denoted by the number 87 show similar estimates for July 1987. Solid areas show water masses discharged during the average month or lost from one arm to another. Results are based on a multiple layer plug flow model which estimates water movements in 3 m depth strata as a function of inflows and outflows. Outflows were calculated using a one dimensional selective withdrawal model (DAVIS et al. 1987) using average or July 1987 outflow estimates and temperature profiles from August 1983 (for the average month) or July 1987. White River and James River inflows were estimated from U.S.G.S. records. Inflow from other tributaries was estimated as a percentage of the James River inflow using annual flow measurements made by the E.P.A. (1977). It is assumed that inflow from the White River enters the 12–18 m depth stratum and all other inflow enter the surface layer (0–6 m). Vertical water movements are estimated by calculating volumes of depth strata (initially 3 m thick) after addition of inflows and subtraction of outflows and summing from the bottom using the depth-volume data in Figure 2. Horizontal movements are estimated by calculating cumulative volumes downlake in each stratum at the start and end of the month (see isopleths in Fig. 2). This model assumes no vertical mixing between strata.

pull hypolimnetic strata downlake. These layers also sink as volume is removed from underlying strata. These water movements cause a net warming of the hypolimnion during summer as cooler, deep water is removed and replaced by warmer water from above. This movement can be traced in temperature profiles as a steady deepening of hypolimnetic isotherms through summer (e.g. Fig. 3). Discharge currents probably also increase turbulence and vertical mixing by eddy diffusion (HUTCHINSON 1957, FORD, in press). Because these processes depend mostly on water releases there is a strong correlation between discharge volume and the amount of warming in the hypolimnion during summer. For example, during 1976–1986, temperature increase at the outlet depth between 1 June and 30 September varied from 1.2 C in 1980 when discharge was unusually low to 6.0 C in 1976 when discharge was above average. Overall, discharge volume accounts for 90% of the interannual variation in these data (Fig. 5). Hydrologic simulations which ignore vertical mixing (e.g. Fig. 4) predict a first order (linear) relation between discharge and warming through isothermal sinking of water masses. The upward curvature in the observed relation (Fig. 5) is probably due to the additional effects of turbulence. Similar effects may be common in other reservoirs with hypolimnetic outlets (STRASKRABA et al. 1973, FRUH & CLAY 1973; FORD, in press).

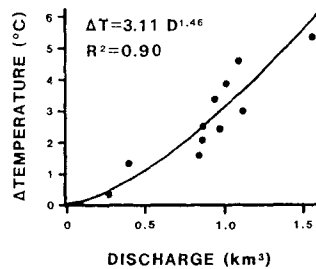


Fig. 5. Hypolimnetic warming at the depth of the penstock intake (236 m MSL) as a function of discharge volume, 1976–1986. Data represent the 1 June – 30 September period. Temperature changes were interpolated from monthly profiles taken near the dam (U.S.G.S. 1977–87).

Thermal stratification also controls the distribution of inflows into the lake. Temperatures in the James River and other unregulated tributaries are usually within 2 C of lake surface temperature and probably enter the mixed layer except during short periods in spring and fall when the rivers cool or warm earlier than the reservoir. As shown in our simulation, this results in short residence times for surface water in uplake areas. For example, in August 1987 inflow to James River and Long Creek arms was only 1–2 C cooler than surface temperatures downlake and probably entered the mixed layer after warming in the riverine reaches of these arms (Fig. 6a). Stream flows at this time were below average but downlake move-



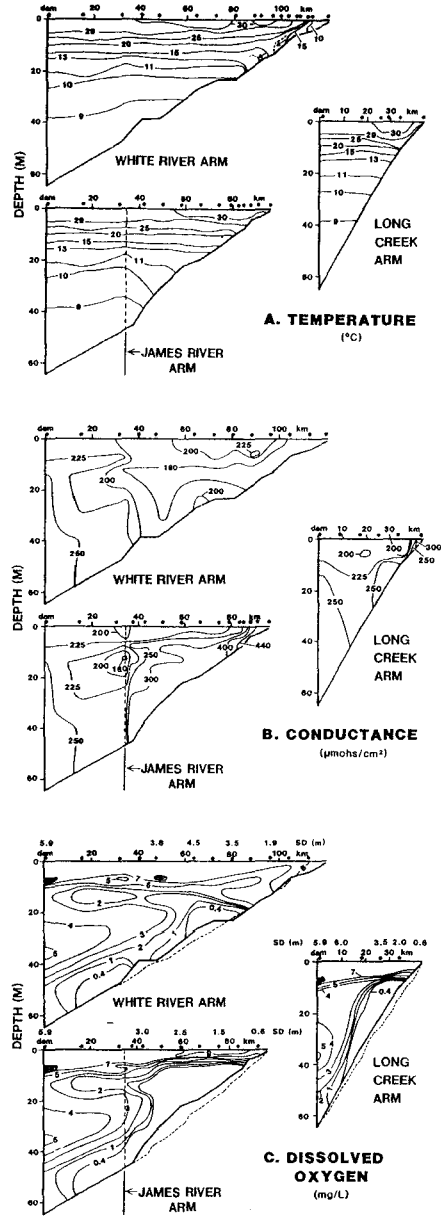


Fig. 6. A – Temperature, B – specific conductance (@ 25 C), C – dissolved oxygen distribution and Secchi depth (SD) in Table Rock Lake 3–9 August 1987. Solid circles above the surface show sampling sites. In a), dashed lines in upper White River arm show movement of 15 C isotherm in profiles taken ca. 20 hours apart. In c), shaded areas show oxygen supersaturation in the metalimnion and dashed lines along the lake bottom show original lake depth as determined from preimpoundment maps. Note that data from the lower White River arm was appended to the James River arm to show continuity between these water masses.

ment was still extensive in headwater areas. As shown by bold arrows in Figure 4 our simulation model suggests a residence time of one month for water in the upper 20 km of the James River arm and in the upper 20 km and 6 km, respectively, of the Kings River and Long Creek arms in July 1987.

Inflow from the White River usually enters the lake as an underflow or interflow (WUNDERLICH 1971, FORD & JOHNSON 1981). Beaver Dam has a hypolimnetic outlet and outflow temperatures seldom exceed 10 C. In summer, surface temperatures in Table Rock Lake are usually 15–20 degrees greater. In August 1987, water released from Beaver Lake entered the headwaters of the White River arm at 9 C and flowed about 8 km in the riverine zone before plunging below the surface as an underflow (Fig. 6a) which compressed metalimnetic strata for about 40 km downlake. On the day before these data were collected peaking power generation at Beaver Dam was increased 3 fold over the preceding two days and our data record the downlake movement of this new inflow plume. In temperature profiles collected 20 hours apart the 15 C isotherm at the leading edge of the inflow moved about 5 km downlake (dashed isotherms in Fig. 6a). The compressed portion of the metalimnion, represented in Figure 6a by the downlake warping of the 15 C isotherm, moved a similar distance.

Temperature data do not record the fate of the White River inflow, but conductance and DO profiles taken concurrently suggest that previous inflows entered the lower metalimnion (Fig. 6b–c). Dissolved solids in the water discharged from Beaver Lake are usually 20–30% less than at the surface in Table Rock Lake so inflows from the White River can be traced in conductance profiles. These data show a layer of low conductance water at 12–18 m in the lower metalimnion from the White River inflow extending through a large portion of the White River arm. Oxygen concentrations in the inflow drop rapidly downlake but show a peak at these depths just downlake from the point oxygenated water from the White River entered the lower metalimnion as an interflow. These plus similar data collected in 1988 and in June and September 1974 by the U.S.E.P.A. (1977) suggest that the White River interflow travels as a relatively discrete water mass through most of the White River arm and probably causes an uplake movement of metalimnetic water in the lower part of the James River arm. This pattern is also predicted by our plug flow simulations (Fig. 4) in which we assumed White River inflow enters the 12–18 m stratum. This model is not formulated to account for mixing between the interflow and other strata and may overestimate downlake movement of the interflow. Regardless, downlake movement in the lower metalimnion is rapid in the White River arm with accompanying effects on water quality variables downlake. Inflow density currents are a major hydrologic feature of many large reservoirs and are an important consideration in evaluating potential effects of nutrient loading (WUNDERLICH 1971, PAULSON & BAKER 1981, KENNEDY & WALKER, in press).

### Phosphorus loading and spatial distribution

Most phosphorus entering Table Rock Lake comes from point sources some distance away. Most important of these is the Southwest Treatment Plant near Springfield, Missouri which releases treated domestic waste into a tributary of the James River about 67 km above Table Rock Lake. This outfall contributes about 75% of annual phosphorus loading (U.S.E.P.A. 1977). About one third of the remaining phosphorus input comes from small municipal treatment plants on Flat Creek, Leatherwood Creek and tributaries of Long Creek, Kings River and James River. Other inputs are from more diffuse sources and direct precipitation.

In the past 11 years, TP in James River has averaged 1195 µg/L at a site sampled monthly by the U.S.G.S. 47 km above the lake (Table 2). Concentrations are

Table 2. Average TP at U.S.G.S. sampling sites upstream from Table Rock Lake. Measurements were made in 1979–1985 (U.S.G.S., 1980–1986).

	n	TP (µg/L)	
		mean	range
White River <sup>1</sup>	17	<15 <sup>2</sup>	0–60
Long Creek	20	34	10–130
James River	115	1195	50–8000
Kings River <sup>3</sup>	52	115	20–550

<sup>1</sup> Site below Beaver Dam

<sup>2</sup> Six of 17 values were recorded as 0 or as <10 µg/L (detection limit)

<sup>3</sup> Includes data from a site on the Kings River (October 1979–October 1983) and a major tributary (Osage Creek, November 1983–December 1985)

substantially diluted by tributary inflows before water enters the lake, but during low flow periods TP in the James River inflow is sometimes >500 µg/L. Concentrations in other streams with point sources are far less. In 1974–1975, the U.S.E.P.A. measured annual mean TP ( $\pm$ SD) of  $67\pm 96$ ,  $25\pm 14$  and  $13\pm 3$  µg/L respectively in Kings River, Long Creek and Flat Creek compared to  $245\pm 142$  µg/L in the James River. For seven other tributaries without point sources averages ranged from  $<11\pm 4$  µg/L to  $25\pm 31$  µg/L (overall mean = 16 µg/L) and the White River between Beaver and Table Rock Lakes averaged  $<15\pm 10$  µg/L with 5 of 11 monthly samples containing <10 µg/L. Values published recently by the U.S.G.S. (1981–1985) for sites on Long Creek, Kings River and White River are similar (Table 2).

Spatial distribution of TP in the lake shows the influence of inflow concentrations. In August 1987, epilimnetic TP below the James River was 459 µg/L

compared to 35  $\mu\text{g/L}$  in the headwaters of the Long Creek arm and 5  $\mu\text{g/L}$  below the inflow of the White River (Fig. 7a). These data show steep gradients in TP downlake in the Long Creek and James River arms and a peak in the White River arm near the mouth of Leatherwood Creek. Similar patterns were observed in 1988 (Fig. 7b) when additional samples from the upper White River arm confirmed Leatherwood Creek as the source of elevated TP in that portion of the lake.

Phosphorus gradients in 1987 occurred in locations with theoretical residence times of 30–60 days as predicted by our hydrologic simulations (bold arrows in Fig. 4) in areas where advective flow decreases rapidly downlake because of

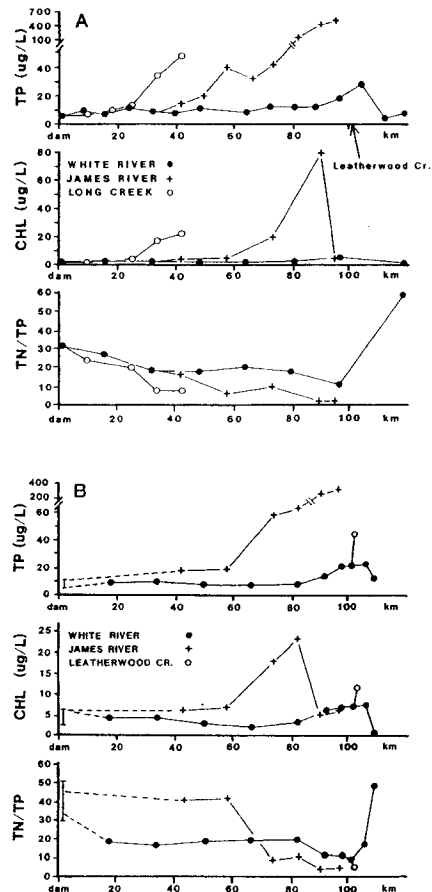


Fig. 7. Gradients of TP, CHL and ratios of TN to TP in the epilimnion of Table Rock Lake, A) 3–9 August 1987; B) 17 May 1988 (James River arm), 13–14 September 1988 (White River arm and Leatherwood Creek arm). Vertical bars show range of values observed near the dam in 1988. May and September values are interpolated (dashed lines) to closest sampling dates at the dam.

increasing volume (Fig. 2). Minimum TP values, lake-wide, occur in areas which experience minimal advective movement during summer such as downlake portions of the Long Creek arm and in the White River arm above the James River. Maximum TP occurs below major inflows except in the upper White River arm where the inflow from Beaver Lake plunges below the epilimnion. Dye tracer studies of other lakes have shown some mixing between plunging inflows and the surface layer (KENNEDY et al. 1982, FISCHER & SMITH 1983). Because water from Beaver Lake is relatively phosphorus-poor, mixing with surface waters may dilute phosphorus inputs from other sources. Nonetheless, our data suggest that loading from relatively minor tributaries such as Leatherwood Creek substantially increases surface water TP in this part of the lake.

In the James River arm a relatively steep downlake gradient in TP concentration persists throughout the year as the result of sedimentary losses and dilution of phosphorus inputs from the James River and Flat Creek. The magnitude and shape of this gradient varies over time, depending on hydrologic conditions. For example, following a month of above average inflow in June 1983 the TP gradient was relatively flat in headwaters of the arm but steepened rapidly near the mouth (Fig. 8). Later that summer, following a month of low flow, concentrations dropped

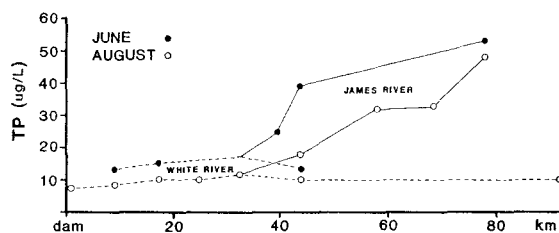


Fig. 8. Gradients of TP in Table Rock Lake, 6 June and 15–17 August 1983.

rapidly below the point of inflow. The steep gradients observed in August 1987 and May 1988 (Fig. 7) also followed periods of below-average flow. We presently do not have enough data to determine if variation in the location of TP gradients is consistently related to differences in water residence times but this hypothesis seems likely (KENNEDY et al. 1982, THORNTON, in press).

James River water is diluted about 25% by other inflows as it moves through the arm. Wind currents probably cause some longitudinal mixing within and between arms. These processes probably contribute to the formation of gradients in the lake. Variable amounts of dilution also occur before inflows reach the lake. Point source inputs to the James River are relatively constant over time so TP is greatly diluted by tributary inflows to the James River during high flow. For example, in 1980–1986 TP at the U.S.G.S. sampling site averaged 2375 µg/L when

flow was  $<2.5 \text{ m}^3/\text{s}$  ( $n=16$  monthly observations) and only  $215 \text{ }\mu\text{g/L}$  when flow was  $>15 \text{ m}^3/\text{s}$  ( $n=10$ ). Thus, downlake declines in TP could occur when inputs of dilute water during high flow are followed by more concentrated inputs during low flow. KENNEDY et al. (1981) found such processes responsible for nutrient and turbidity gradients in Red Rock Reservoir, Iowa. Inflow variation may be a major source of spatial variation in many lakes with large fluvial inflows (CARMACK & GRAY 1982, KENNEDY & WALKER, in press).

Rough estimates of the relative effects of dilution versus sedimentation in forming gradients can be obtained from the spatial distribution of conservative elements. In our 1987 and 1988 data, concentrations of Cl and Na declined 42–50% in the upper third of the James River arm (Table 3). These elements would presumably be unaffected by sedimentation so changes in their concentrations downlake show the effect of dilution. Because of the dominance of point source inputs in the James River, ratios of Na and Cl to TP are relatively constant over the range of flow. At the U.S.G.S. sampling site, TP/Na ( $\times 10^3$ ) by weight averaged 27 in 1980–1986 ( $n=23$ ) with a coefficient of variation of only 30%. Thus spatial differences in relative concentrations of these elements can be used to estimate TP sedimentation. In 1987 TP at the inflow and a site 21 km downlake were 538 and 43  $\mu\text{g/L}$ , respectively (Table 3). If dilution over this distance was 50%, as suggested by Na and Cl values, TP at the downlake site would have been 269  $\mu\text{g/L}$  ( $538 \mu\text{g/L} \times 0.5$ ) in the absence of sedimentation. The difference between this value and the observed TP indicates that 84% of the TP input sedimented from the epilimnion between the two sites (e.g.  $(269 - 43)/269 = 0.84$  – Table 3). In May 1988, changes in Na and TP over approximately the same distance suggest sedimentary loss of 65% of inflow TP (Table 3). Similar calculations for other sites on the arm in both years suggest that about 90% of James River phosphorus input sediments from the epilimnion before reaching the White River arm (Table 3).

The sedimentary loss of TP in the James River arm is probably affected by both purely physical and biologically mediated sedimentation. In August 1987, inflowing water contained 17.8 mg/L NVSS which declined by 87% in the upper 21 km of the arm (Table 3). For lakes in this region, TP and NVSS are highly correlated (HOYER & JONES 1983), so it's likely that physical sedimentation of inflowing particulates contributed to the downlake decline in TP (e.g., GREEN et al. 1978).

It is probable, however, that the main route of TP sedimentation is through the in-lake production and loss of seston and photosynthetic precipitation of calcite. In both August 1987 and May 1988, uplake reaches of the James River arm exhibited high concentrations of CHL and VSS as well as substantial downlake declines in Ca, alkalinity (ALK),  $\text{SiO}_2$  and  $\text{NO}_3$  (Table 3). These data suggest intense photosynthesis in this part of the lake and sedimentary loss of calcium carbonate (OTSUKI & WETZEL 1972). Also, most of the TP entering the James River arm is in dissolved form. In May 1988 only about 5% of influent TP was retained by a  $0.45 \text{ }\mu\text{m}$  filter

Table 3. Water quality gradients and estimated TP sedimentation in the James River arm of Table Rock Lake, 3–7 August 1987 and 17 May 1988. Values are in mg/L. Sampling sites are noted by distance from the dam measured along the former river channel.

August 1987	inflow	James River arm			
	95 km	90 km	74 km	58 km	42 km
TP	0.538	0.459	0.043	0.040	0.015
NVSS	17.8	9.9	2.4	1.7	0.9
SiO <sub>2</sub>	13.7	13.0	2.8	1.7	0.4
TN	1.41	1.32	0.43	0.28	0.23
CA	62.2	60.1	20.0	22.3	24.9
ALK <sup>1</sup>	146	148	56	58	71
VSS	2.8	6.7	4.1	2.0	1.5
CHL	0.005	0.079	0.019	0.005	0.004
NA	18.3	15.6	9.0	6.4	4.2
CL	21.0	19.5	12.0	9.5	6.0
TP/NA ( $\times 10^3$ )	29	29	5	6	4
TP sedimentation <sup>2</sup>	0%	0%	84%	82%	90%

May 1988	97 km	90 km	74 km	58 km	42 km
TP	0.317	0.289	0.058	0.019	0.018
dTP <sup>3</sup>	0.306	0.273	0.021	0.010	0.012
NVSS	3.9	—	3.0	—	1.2
TN	1.68	1.48	0.55	0.83	0.74
NO <sub>3</sub>	0.81	0.73	0.18	0.47	0.43
CA	56.4	57.6	31.6	29.6	29.6
ALK	288	282	182	162	144
VSS	0.8	—	2.7	—	1.2
CHL	6.4	5.1	17.9	6.8	6.3
NA	13.0	13.1	6.7	4.1	3.1
CL	15.6	16.1	9.1	6.4	4.9
TP/NA ( $\times 10^3$ )	24	22	9	5	6
TP sedimentation	0%	0%	64%	81%	76%

<sup>1</sup> As calcium carbonate

<sup>2</sup> Estimated from TP/Na as described in text

<sup>3</sup> TP passing through 0.45  $\mu$ m glass fiber filter

(Table 3). Dissolved phosphorus was not measured in 1987 but a published regression relating TP to NVSS in other midwest lakes (HOYER & JONES 1983: 198, Fig. 6) predicts TP in this inflow of 108  $\mu$ g/L — only 20% of the observed TP. If this regression applies to conditions in the James River then sediment-bound TP may usually comprise a small fraction of the total. If so, then purely physical sedimentation may play a relatively minor role in the loss of TP from inflowing water.

Unfortunately, we do not have the data to evaluate TP sedimentation during periods of high flow. Presumably, much of the phosphorus loading to downlake areas of the James River arm occurs during such periods when inflow causes downlake extension of the riverine zone and impedes sedimentation (KENNEDY & WALKER, in press). Large run-off events are usually brief, however, so it seems likely that most of the annual phosphorus input is lost to the sediments of the James River arm. Soundings taken during the 1987 survey, shown in Figure 6c, suggest extensive sedimentation in this part of the reservoir.

Downlake reaches of large reservoirs are more lake-like than the headwaters (GOLDMAN & KIMMEL 1978, JONES & NOVAK 1981, WHALEN et al. 1982). If so, then phosphorus budgets in downlake areas of Table Rock Lake may be more influenced by vertical mixing and exchange with the sediments (e.g. FEE 1979, PREPAS & VICKERY 1984) than by the advective processes that control TP in headwater areas. More must be known about these spatial differences before we can accurately predict the effects of increased nutrient loading to the lake.

### Phytoplankton

Phytoplankton abundance in Table Rock Lake generally follows the spatial and temporal variability in TP both in the epilimnion and illuminated portions of the metalimnion. In August 1987 and May 1988, epilimnetic CHL in the James River arms peaked near the inflow. This also occurred in the Long Creek arm in 1987. In the Long Creek arm, however, epilimnetic CHL was less than in the inflowing stream (Fig. 7). In the White River arm CHL values in both years peaked near the mouth of Leatherwood Creek in response to local nutrient inputs. Secchi transparency varied inversely with CHL in both years ranging from <1 m in headwater areas of the James River and Long Creek arms to 6 m near the dam (Fig. 6c – 1987 data only). In summer 1982 and 1983 we found similar gradients in transparency and both epilimnetic and metalimnetic CHL. Metalimnetic CHL was usually several times greater than in the mixed layer (e.g. Fig. 9). Metalimnetic CHL in August 1983 showed a clear continuity between the James River arm and downlake areas of the White River arm in parallel with a gradient in metalimnetic TP (Fig. 10). This TP gradient is similar to that observed in the epilimnion earlier that year (Fig. 8) suggesting that it formed by sedimentation of phosphorus from the mixed layer. Overall, regressions of CHL to TP are similar for both strata. For epilimnetic data, TP explains about 81% of variation in CHL if one 1987 datum from the headwater site in the James River arm is excluded (Fig. 11a). The relation is weaker in the metalimnion (Fig. 11b) but has a similar slope.

Although phytoplankton abundance mimics the distribution of TP in Table Rock Lake, nutrient ratios suggest that portions of the reservoir are not always phosphorus limited. In headwater areas of the James River and Long Creek arms TN/TP ratios (by weight) are often less than 12, suggesting nitrogen limitation



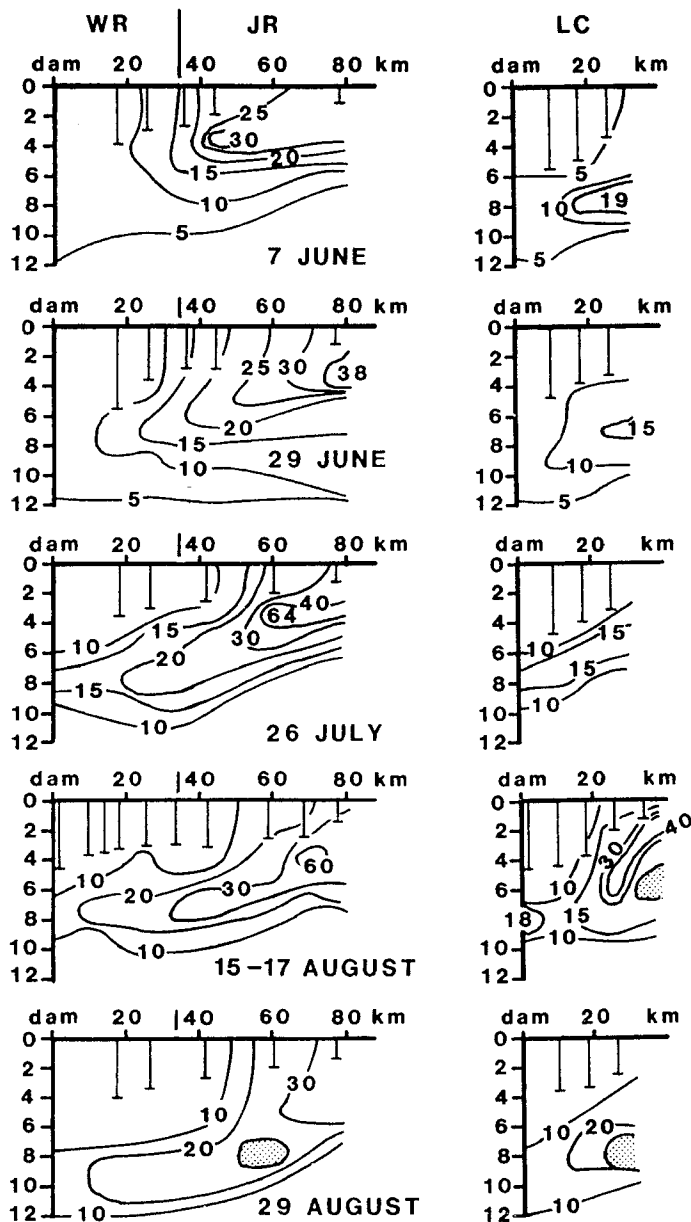


Fig. 9. Chlorophyll distribution and Secchi depths in summer, 1983, in the Long Creek arm (LC), James River arm (JR) and lower White River arm (WR). Isoleths were drawn from *in vivo* fluorescence profiles calibrated to discrete chlorophyll measurements at 1-3 depths. Shaded areas show observed locations of green sulfur bacteria as determined by pigment analysis (KNOWLTON & JONES 1989). Other data not shown were collected at 1-2 locations in the White River arm uplake from the James River. Chlorophyll concentrations at these sites were always equal to, or less than, those just downlake from the mouth of the James River arm.

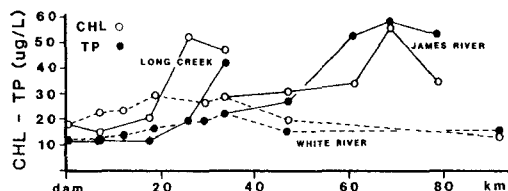


Fig. 10. Metalimnetic CHL and TP gradients in Table Rock Lake 15–17 August 1983.

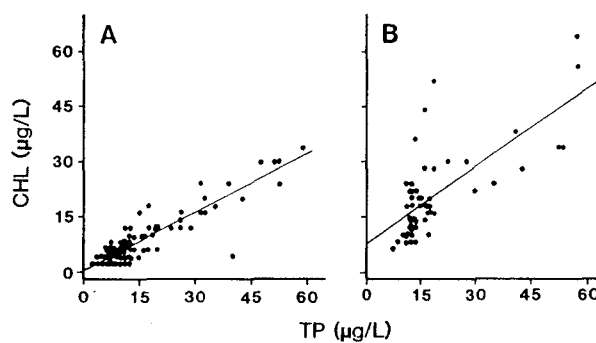


Fig. 11. Relation of CHL to TP in the epilimnion (a) and metalimnion (b) of Table Rock Lake. Data were collected in summer 1982, 1983, and 1987. An outlying data point from the upper James River arm (TP = 459 µg/L, CHL = 79 µg/L – Fig. 7) was omitted from analysis. Regression models fitted by least squares are: epilimnion – CHL =  $0.51 \times \text{TP} + 0.61$ ,  $n = 96$ ,  $R^2 = 0.80$ ,  $p < 0.0001$ ; metalimnion – CHL =  $0.71 \times \text{TP} + 7.52$ ,  $n = 52$ ,  $R^2 = 0.51$ ,  $p < 0.0001$ .

(FORSBERG & RYDING 1980). In August 1987, TN/TP ranged from less than 3 below the James River inflow to  $>30$  near the dam (Fig. 7). The ratio of TN/TP in the White River inflow was 60. In May 1988 TN/TP in the James River arm ranged from 5.1 to 43.7 along a downlake gradient. In September 1988 TN/TP in the White River arm ranged from 9.5 near the mouth of Leatherwood Creek to 47 just below the White River inflow. In the Leatherwood Creek arm TN/TP was 6.2. Near the dam, TN/TP in 1988 ranged from 33 in mid-August to 52 in mid-June (Fig. 7b).

Seasonally, nitrogen limitation seems most important in late summer. In 1983, TN/TP ratios in the upper James River arm declined from 18 in early June to 6 in late August. Near the dam TN/TP dropped from 71 to 28 during the same period. Similar trends were also observed by the U.S.E.P.A. in 1974 (U.S.E.P.A. 1977) and probably recur annually because of the rapid loss of TN from the epilimnion in the summer. Total nitrogen dropped an average of about 25% per month in the June–August of 1983 period at six locations sampled in Table Rock Lake. Phosphorus also declined at most stations (Fig. 8) but by a smaller percentage than TN resulting in decreased TN/TP.

Most of the decline in TN may be due to exhaustion of epilimnetic  $\text{NO}_3$ . Between 2 June and 28 September 1988, epilimnetic  $\text{NO}_3$  near the dam declined from 333  $\mu\text{g/L}$  to <10  $\mu\text{g/L}$  (mean = 132  $\mu\text{g/L}$  for five sampling dates) while non- $\text{NO}_3$  nitrogen remained nearly constant at 165  $\mu\text{g/L}$  to 223  $\mu\text{g/L}$  (mean = 203  $\mu\text{g/L}$ ). Similar trends have been observed in reservoirs on the Colorado River (BAKER & PAULSON 1981, PRISCU et al. 1981) and seem typical of reservoirs in Missouri and surrounding states. This apparent exhaustion of readily available N may contribute to a condition of N-limitation in late summer in these lakes.

The seasonal decline of nutrient concentrations at the surface is paralleled by a decline in phytoplankton biomass in the mixed layer and an increase in the metalimnion. As shown in Figure 9, epilimnetic CHL in the lower reaches of the James River arm dropped from >20 to <10  $\mu\text{g/L}$  during summer 1983. Transparency increased from 2 m to 3 m, with an accompanying increase in metalimnetic CHL from <10 to >30  $\mu\text{g/L}$ . Similar changes occurred in the White River arm. By late August metalimnetic CHL maxima were present throughout the White River, James River and Long Creek arms (Fig. 9). We observed similar development of the metalimnetic phytoplankton in 1982. In early September 1982, metalimnetic CHL in some downlake areas of the White River arm exceeded 60  $\mu\text{g/L}$  compared to about 6  $\mu\text{g/L}$  in the epilimnion. A much smaller metalimnetic peak was observed in 1987 when a single profile taken near the dam showed a peak concentration of 6  $\mu\text{g/L}$  in the metalimnion compared to 1.6  $\mu\text{g/L}$  at the surface. In five profiles taken in 1988, metalimnetic CHL peaked in mid-August at a concentration of 17.2  $\mu\text{g/L}$  compared to 6  $\mu\text{g/L}$  in the epilimnion.

Several factors are involved in development of metalimnetic CHL peaks in Table Rock Lake. In the James River arm summer declines in epilimnetic phytoplankton increases light transmission to the metalimnion, in some cases resulting in a depression of the previously established oxycline as the trophogenic zone thickens. In 1982, for example, Secchi transparency in the lower James River arm went from 1.8 m in late June to 4 m in early August with a corresponding deepening of the oxycline from 3 to 6 m and development of a metalimnetic CHL peak at 7 m. In productive areas of the reservoir where the upper metalimnion becomes anoxic we have found large populations of photosynthetic sulfur bacteria in the metalimnion lying beneath accumulations of algae (Fig. 9 – August data). Similar accumulations of sulfur bacteria occur in several reservoirs in the region which do not develop persistent phytoplankton peaks (KNOWLTON & JONES 1989). These bacteria have not been thoroughly studied but seem to dominate primary production in the metalimnia of productive reservoirs.

In August 1983 metalimnetic phytoplankton communities in transparent areas of Table Rock Lake were dominated numerically by *Achnanthes minutissima* which comprised 36–84% of total cell counts (Table 4). We did not measure cell volume in these samples, but it is likely that this small diatom (ca. 10  $\mu\text{m}$  maximum length) comprised a relatively small fraction of total biomass. Metalimnetic phytoplankton

Table 4. Dominant phytoplankton taxa in the metalimnion of Table Rock Lake, 15–17 August, 1983. Data are presented as percents of total counting units. One counting unit equal: one frustule or cell for diatoms or unicells, four cells for colonies (50 cells for some colonial bluegreens), or, for filaments, each 100  $\mu\text{m}$  of filament length.

White River – 9 km <sup>1</sup>	42 km	88 km
<i>Achnanthes</i> <sup>2</sup> (83%)	<i>Achnanthes</i> (49%)	<i>Achnanthes</i> (36%)
<i>Pediastrum</i> (3%)	<i>Synedra</i> (17%)	<i>Melosira</i> (14%)
<i>Chlamydomonas</i> (3%)	<i>Fragilaria</i> (6%)	<i>Dictyosphaerium</i> (7%)
<i>Synedra</i> (2%)	<i>Dictyosphaerium</i> (6%)	<i>Synedra</i> (7%)
total:		
diatoms (89%)	(77%)	(69%)
bluegreens (1%)	(6%)	(6%)
flagelates (3%)	(4%)	(3%)
others (7%)	(14%)	(21%)
Long Creek – 10 km	19 km	26 km
<i>Achnanthes</i> (49%)	<i>Achnanthes</i> (44%)	<i>Achnanthes</i> (84%)
<i>Synedra</i> (10%)	<i>Dictyosphaerium</i> (13%)	coccoid BG (4%)
<i>Dictyosphaerium</i> (7%)	<i>Lyngbya</i> (11%)	<i>Dictyosphaerium</i> (4%)
<i>Peridinium</i> (4%)	<i>Anabena</i> (5%)	<i>Synedra</i> (1%)
total:		
diatoms (65%)	(48%)	(88%)
bluegreens (11%)	(16%)	(4%)
flagelates (6%)	(10%)	(1%)
others (17%)	(26%)	(6%)
James River – 44 km	69 km	77 km
<i>Lyngbya</i> (26%)	<i>Merismopedia</i> (12%)	<i>Merismopedia</i> (35%)
centric diatoms (13%)	<i>Dictyosphaerium</i> (11%)	centric diatoms (13%)
<i>Dictyosphaerium</i> (9%)	<i>Cryptomonas</i> (10%)	<i>Dictyosphaerium</i> (8%)
coccoid BG (7%)	<i>Ceratium</i> (9%)	<i>Stephanodiscus</i> (6%)
<i>Achnanthes</i> (6%)	<i>Chlamydomonas</i> (9%)	filamentous BG (5%)
<i>Merismopedia</i> (6%)	centric diatom (7%)	<i>Peridinium</i> (4%)
total:		
diatoms (25%)	(17%)	(28%)
bluegreens (45%)	(20%)	(45%)
flagelates (5%)	(38%)	(7%)
others (26%)	(25%)	(21%)

<sup>1</sup> Distance from dam measured along former river channel

<sup>2</sup> Dominant species included *Achnanthes minutissima*, *Synedra delicatissima*, *S. radians*, *Melosira ambigua*, *Dictyosphaerium pulchellum*, *Fragilaria crotonensis*, *Lyngbya limnetica*, *L. spiralinoides*, *Merismopedia tenimissima*, *Pediastrum simplex*, *Ceratium cornutum*, and *Stephanodiscus astraea*

communities in all parts of the lake comprised a diverse assemblage of taxa, unlike the nearly monospecific metalimnetic peaks observed in some lakes (e.g. BROOK et al. 1971, FEE 1976, PICK et al. 1984). Metalimnetic chlorophyll peaks can form in a variety of ways and should be expected in lakes where the euphotic zone extends below the mixed layer (CULLEN 1982, MOLL & STOERMER 1982, PRISCU & GOLDMAN 1983, COON et al. 1987). Such conditions probably exist in many reservoirs, but metalimnetic CHL maxima have seldom been studied in artificial lakes (KIMMEL et al., in press) and we presently have too few data to distinguish those factors most important to the origin and maintenance of these peaks in Table Rock Lake.

### Dissolved oxygen

In downlake areas of Table Rock Lake seasonal changes in dissolved oxygen concentrations (DO) follow a similar pattern from year to year. In summer, DO depletion is most rapid near the bottom and in the lower metalimnion so DO profiles in late summer usually show a peak at mid-depth in the hypolimnion (Fig. 12). In most years, DO peaks also occur just below the mixed layer because

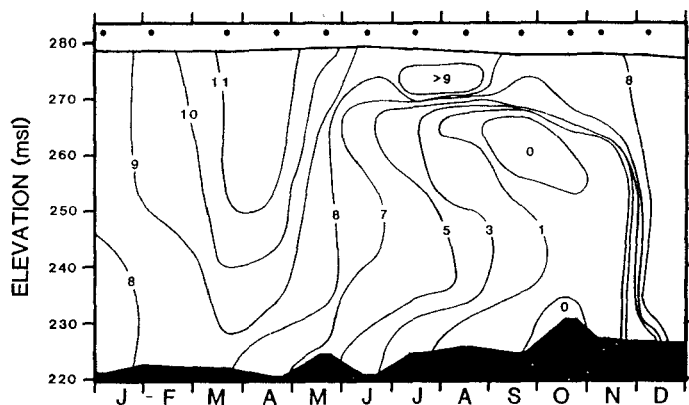


Fig. 12. Dissolved oxygen regime of Table Rock Lake - 1983. Isopleths were interpolated from monthly oxygen profiles taken near the dam (U.S.G.S. 1984). Closed circles show sampling dates. Profile depths (shown by darkened area at the bottom) varied due to small variations in sampling location with respect to the thalweg.

of metalimnetic photosynthesis. In 1982 and 1983 DO values were at 100–175% saturation above metalimnetic CHL peaks in the White River and Long Creek arms. Monthly DO profiles taken near the dam have recorded supersaturation in the upper metalimnion in 9 of the past 11 years.

Oxygen measurements made in 1974 by the U.S.E.P.A. and in 1985–1987 by the U.S.G.S. suggest that DO depletion is most rapid near the sediments in

productive areas of the lake. Our data from 1982–1983 and 1987–1988 show strong downlake gradients in DO paralleling the TP and CHL gradients in the surface waters. In 1987 and 1988 we found oxyclines all over the lake at roughly twice the Secchi depth (Fig. 6c – 1987 data only). In productive areas of the James River and Long Creek arms, sharpest vertical gradients in DO occurred just below the mixed layer. A similar oxycline was present beneath the interflow in the White River arm. These areas had extensive anoxic zones which extended downlake along the bottom. The continuity of anoxic zones between uplake and downlake areas, particularly that between the James River arm and the downlake portion of the White River arm, strongly suggests downlake flow of hypolimnetic water. In the lower metalimnion, longitudinal gradients in DO also suggest an influence of advective processes. In the White River interflow, DO at 15 m dropped 3 mg/L past the mouth of the Kings River arm, probably because of the input of DO depleted water from this source. An in situ cause seems unlikely because the interflow may require as little as 3 days to travel between the two points. Also, concentrations showed no further decline downlake until reaching the mouth of the James River where another slight decline occurred, perhaps also because of advective movements.

Withdrawal currents and downlake flow from productive areas of Table Rock Lake have a major influence on DO depletion rates near the dam. For the period of record, interannual variation in discharge accounts for 86% of observed variation in DO depletion at the outlet depth during June–September and 45% of the variation in DO depletion in the lower metalimnion (Fig. 13). A close dependency of oxygen depletion on discharge has previously been observed in Slapy Reservoir (STRASKRABA et al. 1973).

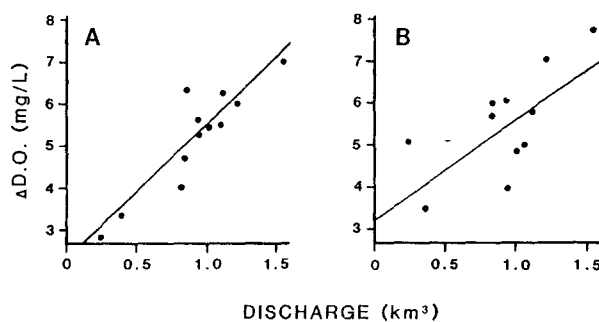


Fig 13. Relation of hypolimnetic and metalimnetic oxygen depletion to discharge volume for Table Rock Lake – 1976–86. Data represent the 1 June – 30 September period. Net change in dissolved oxygen was interpolated from monthly profiles taken near the dam (U.S.G.S. 1977–87). Hypolimnetic depletion was calculated at the depth of the penstock intake (236 m MSL). Metalimnetic depletion was calculated at the depth of the metalimnetic DO minimum which varied among and within years. Regression models fitted by least squares are: hypolimnion –  $DO = 3.25 \times \text{Discharge} + 2.24$ ,  $n = 11$ ;  $R^2 = 0.93$ ,  $p < 0.0001$ ; metalimnion –  $DO = 2.33 \times \text{Discharge} + 3.28$ ,  $n = 11$ ;  $R^2 = 0.67$ ,  $p < 0.0001$ .

Hypolimnetic water in downlake areas is completely replaced in most summers so the relation of oxygen depletion to discharge probably depends mostly on advective transport. Because of the relatively rapid oxygen depletion in shallow, uplake areas, discharge and downlake water movement in summer results in the replacement of relatively oxygen-rich water near the dam by oxygen-depleted water from uplake. Advection may also stimulate oxygen depletion in situ by increasing contact between water and bottom sediments. In natural lakes, a large proportion of total oxygen consumption in the hypolimnion occurs at the sediment-water interface (CORNETT & RIGLER 1987). It is possible that respiration and chemical oxidation at this boundary are increased by water movement and turbulence in the same way that stirring increases oxygen consumption of sediments in the laboratory (HARGRAVE 1972).

### Discussion

Table Rock Lake exhibits an unusual degree of spatial variability, both longitudinally and vertically. Over 95% of the 433 reservoirs sampled in the National Eutrophication Survey had mean TP and CHL within the range of values observed among sampling sites in Table Rock Lake in our 1987 survey (CANFIELD & BACHMANN 1981). On the basis of TP, sampling sites in the Long Creek and James River arms comprise the most and least fertile large expanses of water in Missouri covering a range of over 70 fold (HOYER & JONES 1983, JONES & KNOWLTON, in prep.). Vertically, we have measured differences of >10 fold between CHL in the epilimnion and metalimnion. In a recent survey of 48 lakes in Iowa, Missouri, Kansas, Oklahoma and Arkansas only Table Rock Lake consistently showed metalimnetic phytoplankton peaks (KNOWLTON & JONES 1989).

Monthly temperature and oxygen profiles taken near the dam by the Corps of Engineers and U.S.G.S. provide a comprehensive picture of some conditions in this part of the lake. They clearly record the recurrent patterns in metalimnetic and hypolimnetic oxygen depletion (e.g. Fig. 12) and the strong dependence of hypolimnetic temperature and oxygen on outflow (Fig. 5 and 13) — conditions commonly observed in reservoirs with hypolimnetic outlets (STRASKRABA et al. 1973, HANNAN & COLE, in press). But our present records of the spatial and temporal variation in other parts of the lake are inadequate to answer important questions concerning nutrient loading to downlake areas and the effects of water movement on the distribution of oxygen and phytoplankton. In addressing such questions the size and temporal dynamics of large reservoirs present serious obstacles to collection of adequate data (THORNTON et al. 1982, KNOWLTON et al. 1984).

Questions about nutrient loading seem particularly pertinent. Downlake areas of the reservoir are relatively unproductive because most of the annual phosphorus load sediments from the mixed layer far uplake. The relatively minor influence of

high phosphorus loads from the James River on conditions downlake suggest that nutrient loads in other major inflows could increase substantially without changing surface water quality near the dam. But this might not be true of smaller tributaries whose embayments lack the residence time required for efficient sedimentation (THORNTON, in press). More information on the effects of local inputs will be needed to assess this question.

Other questions concern factors controlling phytoplankton distribution and abundance. Our present data show clear trends relating algal biomass estimates to nutrient distribution in the surface layer and metalimnion (Fig. 11) but we have too few data to determine specific features of nutrient limitation and the relative importance of advection and in situ production in creating the spatial patterns observed. Our 1987 data suggest some influence of allochthonous import. In the James River arm, inflowing algae seems to have contributed little to the intense bloom immediately downlake (Fig. 7). But high CHL in the Long Creek inflow suggests an important role of stream inputs. Such effects have previously been observed in Saylorville and Red Rock reservoirs in Iowa where most of the suspended algae in headwater areas originates in inflows (SOBALLE & BACHMANN 1983).

Of particular interest is the occurrence of metalimnetic phytoplankton and bacteria maxima in the lake. Metalimnetic phytoplankton have been studied recently in oceans and natural lakes (e. g. FEE 1976, CULLEN 1982, MOLL & STOERMER 1982, COON et al. 1987) but have received little attention in reservoirs (KIMMEL et al., in press). The gradation of metalimnetic communities we observed in 1983 (Fig. 9, Table 4), from obligately anaerobic bacteria in headwater areas to aeophylic diatoms downlake follows the trophic continuum of metalimnetic production hypothesized by MOLL & STOERMER (1982). In Table Rock Lake extreme gradients in nutrient concentrations mimic, in situ, trophic differences among lakes in creating a continuum of light penetration, algal abundance and oxygen regime. In eutrophic, uplake areas, the metalimnion is anoxic by early summer and provides a suitable habitat for photosynthetic bacteria after seasonal decreases in epilimnetic nutrients and phytoplankton allow sufficient light penetration. Downlake from the headwaters, metalimnetic oxygen depletion is not as rapid and there is less temporal variation in transparency. In downlake areas and in the middle reaches of the White River arm, the upper metalimnion remains well illuminated and near oxygen-saturated all summer.

Photosynthetic sulfur bacteria are obligately phototrophic and anaerobic (PFENNIG 1978) so metalimnetic bacteria peaks must form by in situ growth. But metalimnetic phytoplankton peaks in Table Rock Lake may depend on production in the surface layer. There is currently a question about the relative importance of in situ production versus migration or cell capture in the formation of metalimnetic CHL maxima (PICK et al. 1984). The longitudinal gradients in communities forming metalimnetic peaks in Table Rock Lake and possible gradients in relative importance



of different formation processes may make this and similar reservoirs advantageous sites for the study of metalimnetic CHL maxima.

An important concern regarding water quality in Table Rock Lake is the effect of DO in outflows on the trout fishery in Lake Taneycomo immediately downstream (WEITHMAN & HAAS 1984). In autumn, outflow from Table Rock Lake is sometimes nearly anoxic. The outflow is partially re-aerated through the penstocks and in riverine areas below the dam but DO in Lake Taneycomo occasionally drops below 5 mg/L, causing physiological stress to the trout and decreasing angler catch rates (WEITHMAN & HAAS 1984). Various measures have been attempted to ameliorate this problem and the Corps of Engineers is presently studying the efficacy of adding multi-level outlets or a depth-diversion weir to the dam to limit outflow to strata with higher DO (Gordon Proctor, U. S. Army Corps of Engineers, pers. comm.). From our present understanding of DO dynamics in the lake, we expect such measures will be ineffective unless provision is made to draw water from the epilimnion. Selective withdrawal from deeper strata would speed the movement of DO-depleted water from uplake thus increasing oxygen depletion in that layer. The relation of DO to outflow shown in Figure 13 suggests that DO depletion could be reduced by limiting summer discharge. Also, the present spillway gates can be used to release epilimnetic water when outflow DO reaches critical levels. But these practices conflict with the principal role of the reservoir as a power generating facility and will probably receive limited use. We presently know too little about production and oxygen depletion in the lake to know whether other measures, such as reducing nutrient loading, would improve DO conditions in Lake Taneycomo.

### Summary

Summer nutrient concentrations, algal biomass and oxygen depletion in Table Rock Lake exhibit order of magnitude variation along longitudinal gradients resulting from variation in inflow hydrology and water quality. Sedimentation of influent material and intense algal production in headwater areas results in >85% loss of surface water TP during downlake flow of water in the James River and Long Creek arms (Fig. 7). Subsurface inflow of nutrient-poor water from Beaver Lake has little effect on nutrient concentrations in the upper White River arm which are controlled by local inflows. Chlorophyll concentrations follow the distribution of TP in the surface waters and the metalimnion (Fig. 7, 10, 11) but metalimnetic CHL is often several times greater than in the mixed layer (Fig. 9), especially in relatively transparent downlake areas. Metalimnetic communities in productive areas of the James River and Long Creek arms sometimes include large populations of photosynthetic sulfur bacteria (Fig. 9). Oxygen depletion is rapid in shallow uplake areas (Fig. 6c). Inter-annual variation in oxygen depletion near the dam is highly correlated with discharge volume (Fig. 13), perhaps because of downlake transport of oxygen depleted water and stimulating effect of hypolimnetic turbulence on oxygen uptake by bottom sediments.

### Acknowledgments

Support for this study was provided by the Missouri Agricultural Experiment Station, Sport Fishing Institute, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri Research Council and PAUL K. WEIHMILLER Fellowship, Missouri Department of Conservation, Missouri Water Resources Research Center. We gratefully acknowledge KENT THORNTON who let us read a prepublication copy of "Reservoir Limnology: An ecological continuum" and the U.S. Geological Survey and U.S. Army Corps of Engineers who supplied published and unpublished data used herein. Thanks to GREG BUTHOLD and TIMOTHY CANFIELD for help in data collection, to ANN PAMPERL who counted our phytoplankton samples and to BILL and RACHEL BARKLEY who provided space, food, and friendship at Table Rock Lake.

### References

- American Public Health Association (1976): Standard methods for the examination of water and wastewater, 14ed. — Amer. Publ. Health Assoc., New York, NY., 1193 p.
- BAKER, J. R. & PAULSON, L. J. (1981): Influence of Las Vegas Wash density current on nutrient availability and phytoplankton growth in Lake Mead. [In:] STEFAN, H. G. (ed.): Proceedings of the symposium on surface water impoundments: 1638–1646. — Amer. Soc. Civ. Engng., New York.
- BAXTER, R. M. (1977): Environmental effects of dams and impoundments. — *Ann. Rev. Ecol. Syst.* 8: 255–283.
- BROOK, A. J.; BAKER, A. L. & KLEMER, A. R. (1971): The use of turbidimetry in studies of the population dynamics of phytoplankton populations with special reference to *Oscillatoria agardhii* var. *isobrix*. — *Mitt. Internat. Verein. Limnol.* 19: 244–252.
- BURNISON, B. K. (1980): Modified dimethyl sulfoxide (DMSO) extraction for chlorophyll analysis of phytoplankton. — *Can. J. Fish. Aquat. Sci.* 37: 729–733.
- CANFIELD, D. E. & BACHMANN, R. W. (1981): Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. — *Can. J. Fish. Aquat. Sci.* 38: 414–423.
- CARMACK, E. C. & GRAY, C. R. J. (1982): Patterns of circulation and nutrient supply in a medium residence-time reservoir, Kootenay Lake, British Columbia. — *Can. Wat. Res. J.* 7: 51–69.
- CORNETT, R. J. & RIGLER, F. H. (1987): Decomposition of seston in the hypolimnion. — *Can. J. Fish. Aquat. Sci.* 44: 146–151.
- COON, T. G.; LOPEZ, M.; RICHESON, P. J.; POWELL, T. M. & GOLDMAN, C. R. (1987): Summer dynamics of the deep chlorophyll maximum in Lake Tahoe. — *J. Plank. Res.* 9: 327–344.
- CULLEN, J. J. (1982): The deep chlorophyll maximum: Comparing vertical profiles of chlorophyll *a*. — *Can. J. Fish. Aquat. Sci.* 39: 791–803.
- DAVIS, J. E.; HOLLAND, J. P.; SCHNEIDER, M. L. & WILHELMS, S. C. (1987): Select: A numerical, one-dimensional model for selective withdrawal. Environmental and Water Quality Operational Studies. — Instructional Rep. E-87-2 U.S. Army Eng. Waterways Exper. Stat., Vicksburg, Miss., 94 pp.
- D'ELIA, C. F.; STEUDLER, P. A. & CORWIN, N. (1977): Determination of total nitrogen in aqueous samples using persulfate digestion. — *Limnol. Oceanogr.* 22: 760–764.
- FEE, E. J. (1976): The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: Implications for primary production estimates. — *Limnol. Oceanogr.* 21: 767–783.

- FEE, E. J. (1979): A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. — *Limnol. Oceanogr.* 24: 401–416.
- FISCHER, H. B. & SMITH, R. D. (1983): Observations of transport to surface waters from a plunging inflow to Lake Mead. — *Limnol. Oceanogr.* 28: 258–272.
- FORD, D. E. (in press): Reservoir transport processes. [In:] THORNTON, K.W. (ed.): *Reservoir Limnology: An ecological continuum*, Chap. 2. John Wiley & Sons, New York.
- FORD, D. E. & JOHNSON, M. C. (1981): Field observations of density currents in impoundments. [In:] STEFAN, H. G. (ed.): *Proceedings of the symposium on surface water impoundments*: 1239–1248. — Amer. Soc. Civil Engng., New York.
- FORSBERG, C. & RYDING, S. (1980): Eutrophication parameters and trophic state indices in 30 Swedish waste-receiving lakes. — *Arch. Hydrobiol.* 89: 189–207.
- FRUH, E. G. & CLAY, H. M. JR. (1973): Selective withdrawal as a water quality management tool for southwestern impoundments. [In:] ACKERMANN, W. C.; WHITE, G. F. & WORTHINGTON, E. B. (eds.): *Man-made lakes: Their problems and environmental effects*. — Amer. Geophys. Union, Washington D.C., 847 pp.
- GOLDMAN, C. R. & KIMMEL, B. L. (1978): Biological processes associated with suspended sediment and detritus in lakes and reservoirs. [In:] CAIRNS, J.; BENEFIELD, E. F. & WEBSTER, J. R. (eds.): *Current perspectives on river-reservoir ecosystems*: 19–44. — North Amer. Benth. Soc. Publ. No. 1, 85 pp.
- GREEN, D. B.; LOGAN, T. J. & SMECK, N. E. (1978): Phosphate adsorption-desorption characteristics of suspended sediments in the Maumee River Basin of Ohio. — *J. Environ. Qual.* 7: 208–212.
- HANNAN, H. H.; BARROWS, D. & WHITENBERG, D. C. (1980): The trophic status of a deep-storage reservoir in central Texas. [In:] STEFAN, H. G. (ed.): *Proceedings of the symposium on surface water impoundments*: 425–434. — Amer. Soc. Civil Engng., New York.
- HANNAN, H. H. & COLE, T. M. (in press): Dissolved oxygen dynamics. [In:] THORNTON, K.W. (ed.): *Reservoir Limnology: An ecological continuum*, Chap. 4. — John Wiley & Sons, New York.
- HARGRAVE, B. T. (1972): Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. — *Limnol. Oceanogr.* 17: 583–596.
- 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.
- HUTCHINSON, G. E. (1957): *A Treatise on Limnology. I. Geography, Physics, and Chemistry*. — John Wiley & Sons, New York, 1015 pp.
- JAMES, W. F.; KENNEDY, R. K.; MONTGOMERY, R. H. & NIX, J. (1987): Seasonal and longitudinal variations in apparent deposition rates within an Arkansas reservoir. — *Limnol. Oceanogr.* 32: 1169–1176.
- JONES, J. R. & NOVAK, J. T. (1981): Limnological characteristics of Lake of the Ozarks, Missouri. — *Verh. Int. Verein. Theor. Angew. 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*: 1318–1328. — Amer. Soc. Civ. Engng., New York.
- KENNEDY, R. H.; THORNTON, K.W. & GUNKEL, R. C. (1982): The establishment of water quality gradients in reservoirs. — *Can. Water Resour. J.* 7 (1): 71–87.
- KENNEDY, R. H. & WALKER, W.W. (in press): Reservoir nutrient dynamics. [In:] THORNTON, K.W. (ed.): *Reservoir Limnology: An ecological continuum*, Chap. 5. — John Wiley & Sons, New York.

- KIMMEL, B. L.; LIND, O. T. & PAULSON, L. J. (in press): Reservoir primary production. [In:] THORNTON, K. W. (ed.): Reservoir Limnology: An ecological continuum, Chap. 6. — John Wiley & Sons, New York.
- 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. (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 (2): 175–196.
- LUND, J. W. G.; KIPLING, C. & LECREN, E. D. (1958): The inverted microscope methods of estimating algal numbers and the statistical basis of estimates by counting. — *Hydrobiol.* 11: 143–170.
- MENZEL, D. W. & CORWIN, N. (1965): The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. — *Limnol. Oceanogr.* 10: 280–282.
- MOLL, R. A. & STOERMER, E. F. (1982): A hypothesis relating trophic status and subsurface chlorophyll maxima of lakes. — *Arch. Hydrobiol.* 94: 425–440.
- OTSUKI, A. & WETZEL, R. G. (1972): Coprecipitation of phosphate with carbonate in a marl lake. — *Limnol. Oceanogr.* 17: 763–767.
- PAULSON, L. J. & BAKER, J. R. (1981): Nutrient interaction among reservoirs on the Colorado River. [In:] STEFAN, H. G. (ed.): Proceedings of the symposium on surface water impoundments: 1647–1667. — Amer. Soc. Civ. Engng., New York.
- PFENNIG, N. (1978): General physiology and ecology of photosynthetic bacteria. [In:] CLAYTON, R. & SISTROM, W. (eds.): The Photosynthetic Bacteria: 3–18. — Plenum Press, New York.
- PICK, F. R.; NALEWAJKO, C. & LEAN, D. R. S. (1984): The origin of a metalimnetic chrysophate peak. — *Limnol. Oceanogr.* 29: 125–134.
- PREPAS, E. E. & RIGLER, F. A. (1982): Improvements in quantifying the phosphorus concentration in lake water. — *Can. J. Fish. Aquat. Sci.* 39: 822–829.
- PREPAS, E. E. & VICKERY, J. (1984): Seasonal changes in total phosphorus and the role of internal loading in Western Canadian lakes. — *Verh. Internat. Verein. Limnol.* 22: 303–308.
- PRISCU, J. C. & GOLDMAN, C. R. (1983): Seasonal dynamics of the deep-chlorophyll maximum in Castle Lake, California. — *Can. J. Fish. Aquat. Sci.* 40: 208–214.
- PRISCU, J. C.; VERDUIN, J. & DECON, J. E. (1981): The fate of biogenic suspensoids in a desert reservoir. [In:] STEFAN, H. G. (ed.): Proceedings of the symposium on surface water impoundments: 1657–1667. — Amer. Soc. Civ. Engng., New York.
- SARTORY, D. P. & GROBBELAAR, J. U. (1984): Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. — *Hydrobiol.* 114: 177–187.
- SOBALLE, D. M. & BACHMANN, R. W. (1984): Influence of reservoir transit on riverine algal transport and abundance. — *Can. J. Fish. Aquat. Sci.* 41: 1803–1813.
- STRASKRABA, M.; HRBACEK, J. & JAVORNICKY, P. (1973): Effect of an upstream reservoir on the stratification conditions in Słapy Reservoir. — *Hydrobiol. Stud.* 2: 7–82.
- THOM, R. H. & WILSON, J. F. (1980): The natural divisions of Missouri. — *Proc. Mo. Acad. Sci.* 14: 9–23.
- THORNTON, K. W. (in press): Sedimentary processes. [In:] THORNTON, K. W. (ed.): Reservoir Limnology: An ecological continuum, Chap. 3. — John Wiley & Sons, New York.

- THORNTON, K. W.; KENNEDY, R. H.; MORGAN, A. D. & SAUL, G. E. (1982): Reservoir water quality sampling design. — *Water Res. Bull.* **18**: 471–480.
- U.S. Environmental Protection Agency — National Eutrophication Survey (1977): Report on Beaver, Table Rock, and Bull Shoals reservoirs, Arkansas and Taneycomo Reservoir, Missouri. Working paper No. 480. — Off. Res. Dev., U.S. Environ. Prot. Agency, 40 pp.
- U.S. Geological Survey (1977–1987): Water Resources Data for Missouri. U.S. Geological Survey Water-Data Reports MO-76-1 — MO-86-1. — U.S. Geol. Surv., Water Res. Div., Rolla, Missouri.
- (1981–1987): Water Resources Data for Arkansas. U.S. Geological Survey Water-Data Reports AR-80-1 — AR-86-1. — U.S. Geol. Surv., Water Res. Div., Little Rock, Arkansas.
- WALKER, W. W., Jr. (1981): Analysis of water quality variation in reservoirs: Implications for monitoring and modelling efforts. [In:] STEFAN, H. G. (ed.): Proceedings of the symposium on surface water impoundments: 472–481. — Amer. Soc. Civ. Engng., New York.
- WEITHMAN, A. S. & HAAS, M. A. (1984): Effects of dissolved-oxygen depletion on the Rainbow Trout fishery in Lake Taneycomo, Missouri. — *Trans. Am. Fish. Soc.* **113**: 109–124.
- WHALEN, S. C.; LEATHE, S. A.; GREGORY, R. W. & WRIGHT, J. C. (1982): Physiochemical limnology of the Tongue River Reservoir, Montana. — *Hydrobiol.* **89**: 161–176.
- WUNDERLICH, W. O. (1971): The dynamics of density-stratified reservoirs. [In:] HALL, G. E. (ed.): Reservoir Fisheries and Limnology: 219–231. — Spec. Pub. No. 3, Amer. Fish. Soc., Washington D. C.

Address of the authors:

MATTHEW F. KNOWLTON and JOHN R. JONES, School of Forestry Fisheries and Wildlife, 112 Stephens Hall, University of Missouri, Columbia, Missouri 65211 USA.