Trophic Conditions and Gradients of the Headwater Reaches of Beaver Lake, Arkansas

Brian E. Haggard
Department of Biosystems and Agricultural Engineering, Oklahoma State University, Stillwater, OK 74078.

Philip A. Moore, Jr.
USDA-ARS, University of Arkansas, Fayetteville, AR, 72701.

Tommy C. Daniel
Department of Crops, Soils and Environmental Science, University of Arkansas, Fayetteville, AR, 72701.

Dwayne R. Edwards
Department of Agricultural Engineering, University of Kentucky, Lexington, KY, 40546-0276.

Water samples were taken at 10 sampling sites on Beaver Lake, Arkansas, from August 1993 to July 1995 approximately bi-monthly, starting 1 m below the surface and continuing every other meter to the lake bottom. Chlorophyll *a* concentrations were compared to a study conducted 20 yr earlier. Chlorophyll *a* concentration in year 1 significantly increased compared to levels 20 yr ago. However, chlorophyll *a* levels significantly decreased from years 1 to 2. The decrease in primary production could be related to increased lake levels and suspended sediments caused by episodic flood events. The decrease in chlorophyll *a* was accompanied with an increase in total phosphorus from years 1 to 2 throughout the reservoir. The trophic status throughout the reservoir indicated by chlorophyll *a*, total phosphorus, and Secchi depth varied spatially (longitudinal gradients) and temporally. The relationship between chlorophyll *a* and phosphorus was weakened because other factors were controlling phytoplankton growth. The dynamic nature of this reservoir can undermine traditional relationships between nutrients and primary production from year to year.

INTRODUCTION

The trophic state of a fresh water system is defined by its degree of eutrophication. Carlson (*1*) defined trophic state in terms of chlorophyll *a* (Chl*a*), total P (TP) and Secchi transparency depth in a quantitative trophic state index (TSI). Typical models of the process of eutrophication describe a scenario in which P inputs control phytoplankton productivity. Increasing P causes an increased Chl*a* concentration, reflecting increased algal biomass. This in turn results in a decreasing Secchi transparency depth. In many lakes, the basis for TSI is that the degree of eutrophication is largely a function of nutrient concentration. Trophic state indices provide a quantitative assessment of changing lake conditions related to eutrophication (*1*). To quantify the rate of eutrophication, primary productivity and standing crop are frequently measured and chlorophyll concentration is an indirect measure of productivity and standing crop (*2*, *3*).

Chl*a* analysis is considered a sensitive measure of algal biomass (*4*). Smith (*5*) found a direct relationship between mean Chl*a* and mean TP in lakes over a range of latitudes, whereas Brylinski and Mann (*3*) concluded nutrient conditions combined with energy conditions provided a better estimator of phytoplankton productivity. Several researchers (e.g., *1*, *2*, *6*-*8*) also found a log-linear relationship between Chl*a* and TP within and among lakes of different latitudes. However, Walker (*9*, *10*) reported that northern lake models tend to overestimate Chl*a* sensitivity to P in some reservoirs where light is limiting algal growth. Smith (*5*) found that when fresh water systems are limited by a factor other than P, particulate P (PP) displays a stronger relationship to Chl*a*.

Although reservoirs are similar to lakes in many aspects (11), reservoirs consist of different processes, such as profound external loading, that alienate them from lakes. Watershed land use often leads to increased nutrient and sediment loading. These sediments not only fill the reservoir, but can cause light limitation to primary production (*12*). Thus, the factors controlling phytoplankton growth are conditioned by the characteristics of the inflow of the primary sources of the reservoir (*13*). Longitudinal changes in reservoir morphology and velocity produce longitudinal gradients in water quality and trophic conditions (*12*). Reservoirs possess three distinct zones: the riverine zone, which is directly impacted from the primary sources and is often light limited; the lacustrine zone, which is similar to lakes and is affected by internal nutrient loading; and the transitional zone, which may be impacted from external and internal sources (*14*). The riverine zone is located furthest up-reservoir, the lacustrine furthest down-reservoir, and the transitional is in between.

Beaver Lake is the first and youngest impoundment in a chain of four reservoirs on the White River in Arkansas. This impoundment was established in 1964 and was constructed for purposes of flood control, hydropower generation, and water supply. The reservoir reached conservation-water supply capacity in 1968. White River, War Eagle Creek, and Richland Creek are the three primary inflows into Beaver Lake, with additional input from smaller creeks and tributaries. The primary sources of Beaver Lake converge to produce a transitional and a lacustrine zone. Bennett (*15*) reported that the water in the lotic zone of Beaver Lake had a retention time < 1 month, the transitional zone retention time > 2 months, and the lacustrine zone had a retention time > 10 months. The mean hydraulic retention time reported in the National Eutrophication Survey (*16*) was 1.5 yr for the entire reservoir. A history of areal hypolimnetic O_2 depletion, collected at the Beaver Lake dam, revealed a decreasing trend from 1974 to 1994 (*17*).

We conducted a water quality assessment of the headwaters of Beaver Lake from August 1993 to July 1995. The objectives of this study were (a) to provide baseline data on the physico-chemical and biological characteristics of the headwater reaches of the reservoir, (b) to determine the trophic status and gradients in Beaver Lake from the parameters measured, and (c) to determine if any relationship exists between primary productivity and the analytes measured.

MATERIALS and METHODS

Sampling Date, Site Selection and Description: Sampling dates and sites corresponded to the dates and locations sampled by Meyer (*18*) 20 yr earlier (Fig. 1, Table 1). We started collecting samples in the beginning of August 1993 and continued through July 1995. Sampling occurred twice a month at approximate equal intervals in August, September, March, April, May, June, and July. The months of October, November, December, and February were represented by one sampling, whereas no samples were collected in January. The exact days corresponded as closely to those of Meyer (*18*) as environmental conditions would permit. The intent of this replication was to allow statistical comparison between our chlorophyll data and the levels of 20 yr ago. The first sampling year (hereafter Year 1) comprises all sampling dates from August 1993 through July 1994, and the second sampling (Year 2) from August 1994 through July 1995.

We used the global positioning system (GPS) to find the location of the 10 sampling sites used by Meyer (*18*) 20 yr ago. Seven of these 10 sites were located in the lotic zone, two sites were located in the transitional zone and one in the lacustrine zone. Three of the lotic zone sites were within the War Eagle Creek arm of Beaver Lake, and four were on the White River arm. All the lotic zone locations were similar in flow and profile characteristics, but were dissimilar in that the White River drains a basin containing agricultural lands, suburban development, and the effluent of the City of Fayetteville's secondary sewage treatment plant, whereas War Eagle Creek drains agricultural and forested land with some developing suburban areas. All lake sampling stations within the White River reach were below Fayetteville's sewage treatment facility. Two sites were located in the transitional zone, where the flow characteristics change from lotic to lentic. One of these sites was located at the water intake of the City of Fayetteville's water treatment plant. The final site was located within the upper lacustrine zone of Beaver Lake to insure one sampling site was representative of a true lake system (*18*).

Sampling Procedure: Water samples were taken by using an Alpha style horizontal sampler starting 1 m below the surface and continuing in 2-m intervals to the lake bottom. Approximately 500 mL of water was collected at each sampling

TABLE 1. Reservoir sampling stations on Beaver Lake.

Lake Stations	Distance (km)	Zone	Latitude	Longitude
Prairie Creek (PCK)	00	Lacustrine	36%20'45.7"N	94%59'56.4"W
Water Works (WWK)	22	Transitional	36%15'35.9"N	94%04'09.8"W
Hickory Creek (HCK)	30	Transitional	36%14'24.1"N	94%01'37.0"W
White River (WTR)	37	Riverine[a]	36%13'50.5"N	94%00'15.6"W
Friendship Creek (FCK)	45	Riverine[a]	36%11'37.6"N	94%00'43.2"W
Blue Springs (BSP)	50	Riverine[a]	36%09'13.6"N	94%00'02.8"W
Angle (ANG)	63	Riverine[a]	36%06'48.5"N	94%02'04.4"W
Hoffman's Point (HPT)	34	Riverine[b]	36%13'28.6"N	93%59'50.3"W
War Eagle Creek (WEC)	40	Riverine[b]	36%12'41.1"N	93%39'27.9"W
War Eagle Inlet (WEI)	45	Riverine[b]	36%13'27.4"N	93%57'56.4"W

[a] White River arm of Beaver Lake.

[b] War Eagle Creek arm of Beaver Lake.

depth. To mimic the study 20 yr before all samples were collected, and parameters were determined by using the same, or the closest procedure available.

Field Determinations: Temperature and dissolved O_2 (DO) were determined (YSI Model 51B Oxygen Meter) starting 1 m below the surface and continuing at 2 m intervals to the lake bottom. Light extinction was measured with a Protomatic Meter at the same depths as for temperature and DO measurements and also 0.15 m below the surface. Secchi transparency depth was determined by using an alternating black and white quartered disc at each sampling location.

Electrical conductivity (EC) and pH were determined by using a 25 mL aliquot of each water sample immediately after collection (Orion Model 122 Conductivity Meter and Orion Model 230A pH Meter, respectively). A 25 mL portion of each water sample was filtered on site (0.45 m membrane) and acidified to pH 2 with 6 N HCl. The remaining sample was stored on ice for further biological and chemical analyses.

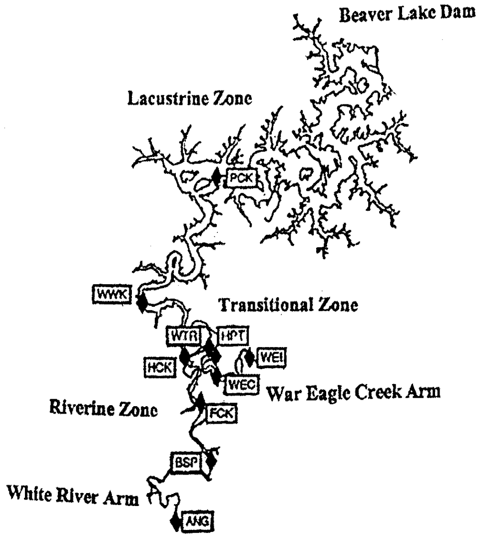

Figure 1. Beaver Lake and sites of sampling stations.

Laboratory Procedures: A 250 mL portion of each water sample was filtered through a glass fiber filter (Whatman GF/F), and the filter was frozen for chlorophyll analysis. The filters were ground with a tissue grinder in a solution of aqueous acetone, poured into conical tubes, and centrifuged at 500xG for 25 min. The supernatant was analyzed for Chl*a*, *b*, and *c* with the use of the trichromatic method (*19*) by using a DU-640 UV Spectrophotometer. An unfiltered, 20 mL portion of each sample was used for alkalinity determinations by the titration method (*19*). A 100 mL portion of each sample was acidified to pH 2 with 6 N HCl and frozen for total nutrient determinations.

Soluble reactive P (SRP) concentration was determined on the filtered, acidified samples by using the automated ascorbic acid reduction method (*19*). Also, inorganic N (NH_4^+-N and NO_3^--N) was determined on the filtered, acidified samples using a modified microscale determination method described by Sims and coworkers (*20*). The filtered, acidified samples were also used to determine soluble metals by inductively coupled plasma emission spectrometry on a Spectro Model D ICP (Spectro Analytical Instruments, Fitchburg, MA).

A 25 mL portion of each acidified, unfiltered water sample was digested for total Kjeldahl N (TKN) and TP by using H_2SO_4 with mercuric sulfate as a catalyst (*21*). TKN was determined colorimetrically on digests by using the automated salicylate-nitroprusside method (*22*). TP was measured by using the automated split reagent ascorbic acid method (*21*). PP was calculated as the difference between TP and SRP. Because SRP was determined on filtered, acidified (pH 2) water samples, the amount of P colorimetrically measured represented the acid hydrolyzed fraction. This fraction would most likely include the rapidly mineralized dissolved organic P (DOP) pool and best represents the bioavailable fraction of the dissolved P. However, the stability of DOP compounds is highly variable (*23*), and our technique may overestimate the amount of PP.

RESULTS

Data Analysis: Lake levels were estimated by individual date sampling depths at all 10 sampling locations. The epilimnion zone was determined by individual date analysis of the vertical profile of temperature, DO, and light extinction at each sampling site. The use of all three parameters worked quite well in distinguishing the mixed layer (epilimnion) from the hypolimnion during stratification, but under mixis the profiles of temperature and DO provided little information and separation of the epilimnion relied only on the measurements of light extinction with depth. Annual mean chlorophyll, TP and TN values were compared by using ANOVA (*24*). Linear regression of log-transformed parameters was used to derive relationships between Chl*a* and the other parameters.

TABLE 2. Annual mean chlorophyll *a* concentrations for the upper reaches of Beaver Lake and only the lacustrine zone.

	Chl*a* Concentrations (g L^{-1})[a]			
	Reservoir		Lacustrine	
	Mean	Median	Mean	Median
Meyer[b]	4.98[b]	3.36	3.28[a,b]	2.23
Year 1	6.99[a]	5.11	3.99[a]	3.67
Year 2	3.29[c]	1.73	2.23[b]	1.19

[a] Different letters within a column denote significant differences (α= 0.05).

[b] Values from 1974 data of Meyer (*18*).

TABLE 3. Annual mean TP and TN for the photic zone of the upper reaches of Beaver Lake and only the lacustrine zone. Meyer (*18*) did not report TP in his study.

	Reservoir Mean Concentration[a]			
	TP (g L^{-1})		TN (mg L^{-1})	
	Mean	Median	Mean	Median
Year 1	34[b]	28	1.29[a]	0.93
Year 2	42[a]	30	1.21[b]	0.91
	Lacustrine Zone Mean Concentration			
	TP (g L^{-1})		TN (mg L^{-1})	
	Mean	Median	Mean	Median
Year 1	19[b]	16	1.22[a]	0.89
Year 2	27[a]	20	1.19[a]	0.87

[a] Different letters within a column denote significant differences (α=0.05)

Primary Productivity: In Year 1, the overall annual mean lake Chl*a* concentration significantly increased over that of 20 yr ago (Table 2). Chl*a* concentrations significantly decreased in Year 2, compared to Year 1 and to Meyer (*18*). The accessory pigments (Chl*b* and *c*) also significantly increased in Year 1 compared to the levels measured 20 yr ago, whereas no difference was detected in Year 2. Comparing the chlorophyll concentrations from only the lacustrine zone sampling site, Prairie Creek, produced similar results.

Mean annual site Chl*a* concentrations decreased with distance throughout Beaver Lake, with the lotic zone having the highest concentrations and the lacustrine zone having the lowest levels (Fig. 2). According to Carlson's TSI, Chl*a* levels from Year 1 indicated that Beaver Lake was eutrophic in the lotic and upper transitional zones, while the lower transitional and lacustrine zone appeared mesotrophic. However, the Year 2 Chl*a* levels indicate that Beaver Lake was mesotrophic throughout the upper reaches of the impoundment. Seasonal assessment of Chl*a* gradients in the Beaver Lake headwaters displayed decreasing gradients of different magnitude in the summer of both sampling years, whereas the results varied for winter, spring and fall between sampling years.

The average euphotic zone Chl*a* levels, by date, for the headwaters of Beaver Lake displayed a bimodal distribution in both sampling years (Fig. 3). Chl*a* was greatest in the late summer growing season, and the second peak growth occurred in the spring season around mid-May

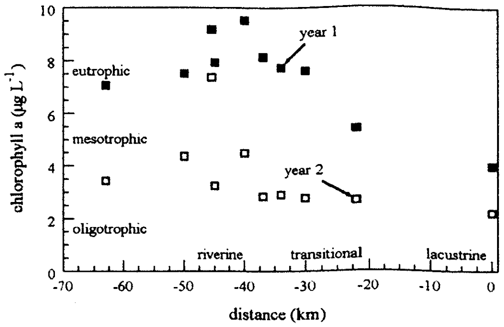

Figure 2. Annual mean chlorophyll *a* as a function of distance accross Beaver Lake. Negative distance denotes km upstream from furthest down-reservoir sampling site (PCK).

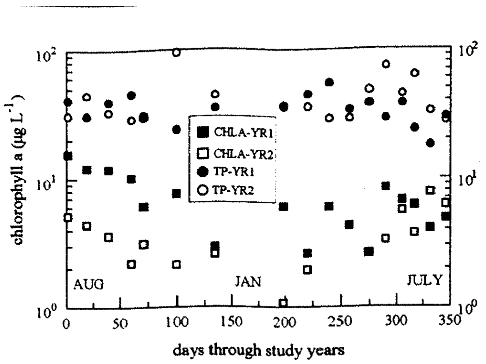

Figure 3. Temporal distribution of mean chlorophyll *a* and TP in the upper reaches of Beaver Lake.

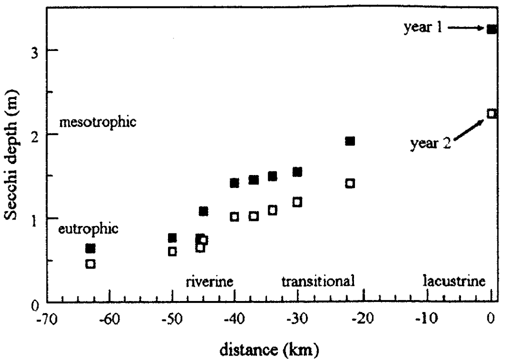

Figure 4. Annual mean Secchi transparency depth as a function of distance across Beaver Lake. Negative distance denotes km upstream from furthest down-reservoir sampling site (PCK).

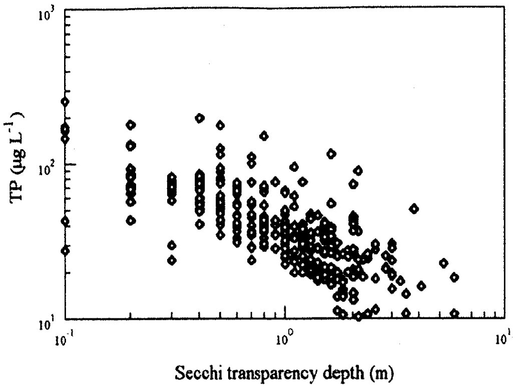

Figure 5. Relationship between Secchi depth and mean site TP in the euphotic zone.

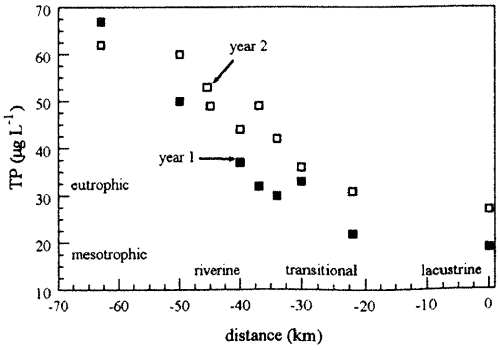

Figure 6. Annual mean TP as a function of distance across Beaver Lake. Negative distance denotes km upstream from furthest down-reservoir sampling site (PCK).

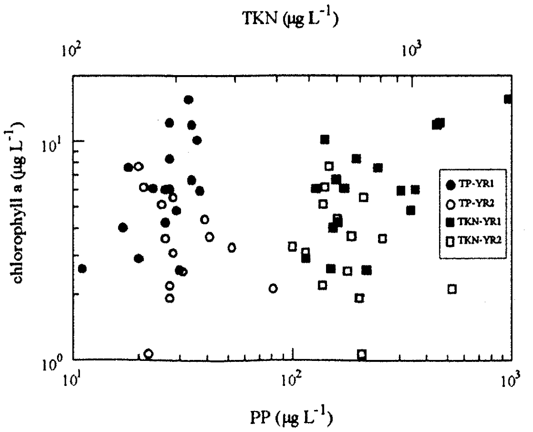

Figure 7. Mean chlorophyll *a* as a function of TKN and PP by date.

through early June. Levels in Year 1 were eutrophic during the bimodal peaks and were mesotrophic the rest of the year. In contrast, Year 2 levels were eutrophic during the summer peak, mesotrophic during fall and spring, and oligotrophic during the winter season.

Secchi Disc Transparency: Secchi depths from both Years 1 and 2 indicated that Beaver Lake was eutrophic in the lotic and transitional zones (Fig. 4). The one sampling site in the lacustrine zone would be classified mesotrophic by Secchi transparency depth standards. Secchi depths decreased between the two sampling years throughout Beaver Lake and increased along a down-reservoir gradient. The use of Secchi depth to determine trophic status might give erroneous values in lakes or reservoirs containing high amounts of suspended sediments or other abiotic particulate matter, but this measurement does describe the photic zone. Relating TP to Secchi depth transparency yielded a log-linear relationship (Fig. 5). The highest amount of TP occurred when the Secchi transparency was the lowest and vice versa.

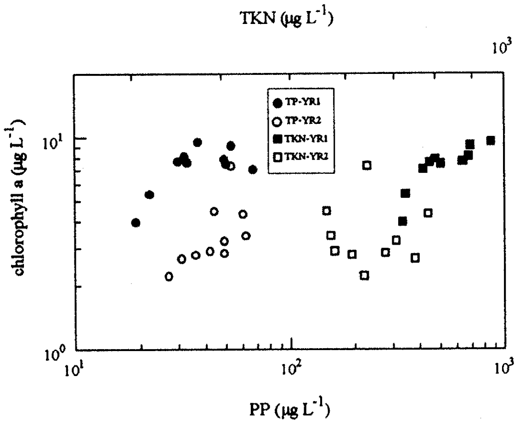

Figure 8. Mean chlorophyll *a* as a function of TKN and TP by site.

Phosphorus Concentrations: A significant increase in TP levels in the epilimnion was evident between sampling Years 1 and 2 throughout the upper reaches and was limited to the lacustrine zone (Table 3). The median value of both sampling years was also slightly higher in Year 2.

TABLE 4. Log-linear relationships between mean site by date nutrients and chlorophyll *a* in the epilimnion of the upper reaches of Beaver Lake.

	Chlorophyll *a*		
	Overall	Year 1	Year 2
SRP	$r = -0.22^{\dagger}$ $y = -0.18x + 0.71$	$r = -0.28^{\ddagger}$ $y = -0.17x + 0.87$	NS
NO_3^--N	$r = -0.31^{\ddagger}$ $y = -0.16x + 0.94$	$r = -0.31^{\ddagger}$ $y = -0.11x + 0.97$	$r = -0.13^{*}$ $y = -0.11x + 0.66$
NH_4^+-N	$r = 0.19^{\dagger}$ $y = 0.12x + 0.33$	$r = 0.27^{\ddagger}$ $y = 0.13x + 0.49$	$r = 0.18^{\dagger}$ $y = 0.12x + 0.15$
TP	NS	$r = 0.13^{*}$ $y = 0.16x + 0.51$	$r = 0.14^{\#}$ $y = 0.24x - 0.01$
PP	$r = 0.20^{\dagger}$ $y = 0.24x + 0.23$	$r = 0.33^{\ddagger}$ $y = 0.32x + 0.31$	$r = 0.20^{\dagger}$ $y = 0.26x + 0.01$
TKN	$r = 0.22^{\dagger}$ $y = 0.46x - 0.73$	$r = 0.35^{\ddagger}$ $y = 0.65x - 1.13$	NS
TN	NS	$r = 0.15^{\#}$ $y = 0.25x - 0.01$	NS

Chlorophyll is the dependent (y) variable and the nutrients are the independent (x). NS = not significant, * denotes $P = 0.10$, # denotes $P = 0.05$, † denotes $P < 0.01$, and ‡ denotes $P < 0.001$

Annual site means of TP concentration displayed decreasing gradients in Beaver Lake from the headwaters to the lacustrine zone during both Years 1 and 2 of the study, and the magnitude of TP was greatest during the second year (Fig. 6). SRP levels displayed similar annual gradients, with distance across Beaver Lake, but the overall proportion of TP as SRP increased in the second sampling year. Decreasing gradients in TP with distance were present during all seasons except the winter of the second sampling year. Analysis of the temporal distribution of TP over both sampling years displayed peak TP concentrations during the spring runoff events of both sampling years and another peak during the fall (November) episodic events of the second sampling year (Fig. 3).

Nitrogen Concentrations: A significant decrease in epilimnion TN was evident between sampling Years 1 and 2 (Table 3). No gradients were evident in any of the N measurements on a seasonal basis, except for a slight, decreasing, longitudinal gradient in TKN during the summer (Year 1) from the riverine zone toward the dam. Annually, only TKN produced decreasing levels with distance throughout the impoundment. Temporal distribution of N exhibited spring peaks in both sampling years, most prominently in NO_3^--N. Year 2 displayed a second peak in concentration during the fall.

Parameter-Chlorophyll Relationships: Mean site by date (site*date) Chl*a* data from the epilimnion of Beaver Lake was not significantly related to TP (Table 4). Relating PP to Chl*a* produced a significant, positive, log-linear relationship ($P < 0.001$) but PP explained only a small portion of the variance in chlorophyll levels. Year 1 TP and PP data displayed significant, positive relationships to Chl*a*, whereas Year 2 results produced a weaker relationship between PP and Chl*a*. Soluble nutrients, SRP and NO_3^--N, produced decreasing log-linear trends whereas NH_4^+-N was positively related to Chl*a*. Relating mean PP and Chl*a* by date yielded a significant, positive, log-linear relationship ($r = 0.55$, $P < 0.05$, Chl*a* = 0.93PP - 0.53) for Year 1 (Fig. 7). Mean TP also produced a significant, positive relationship with mean Chl*a* for the first sampling year, but PP displayed the strongest relationship. The increasing relationship between mean PP and Chl*a* was not observed in the second sampling year. Mean Chl*a* by site produced significant, log-linear relationships with PP in Year 1 ($r = 0.70$, $P < 0.05$, Chl*a* = 0.46PP + 0.19) and in year 2 ($r = 0.66$, $P < 0.05$, Chl*a* = 0.77PP - 0.64). Of all the nutrients, TKN explained a greater portion of the variance in Chl*a* concentrations than any form of P in Year 1 (Table 4). Mean site and date TKN produced significant, log-linear trends with Chl*a* in Year 1 [($r = 0.85$, $P < 0.01$, Chl*a* = 2.36TKN - 6.02) and ($r = 0.63$, $P < 0.01$, Chl*a* = 0.90TKN - 1.81), respectively], but not in Year 2.

DISCUSSION

Trophic Conditions and Gradients: The decrease in chlorophyll concentrations from Years 1 to 2 may be explained by the atypical lake levels experienced during the second sampling year. In Year 2, Beaver Lake recorded some of the highest lake levels in all its 30 yr impoundment. The magnitude of the discharge from episodic events was much greater in Year 2 compared to Year 1 [as indicated by hydrograph comparison of the primary sources of Beaver Lake (*25*)] and the increased depth to the benthos at the sampling sites. The effect was most profound in the White River arm of Beaver Lake. The episodic flood events that produced the high lake levels also increased the amount of suspended sediments throughout the lake. The increase in suspended sediments was detected via a decrease in the average Secchi depth, used to measure the photic zone, for all 10 sampling sites during Year 2. Phytoplankton productivity and chlorophyll production are light dependent; therefore, decreased light penetration and reduced photic zone may have resulted in lower total algal productivity. Light limitation by non-biotic particulate matter and a weak P-chlorophyll relationship have been previously reported in reservoirs across the world and in downstream impoundments on the White River (e.g., *12, 14, 26-29*).

Separation of trophic status by primary production between sampling years is possibly caused by an increase in lake levels and the influence abiotic turbidity has on phytoplankton productivity. James and coworkers (*30*) reported that reservoir turbidity was greatest in the upper reaches and decreased toward the dam. The influence from nonbiotic particulate matter on Chl*a* levels was also observed in Beaver Lake from the upper reaches of the reservoir through the lacustrine zone. Beaver Lake exhibited marked annual longitudinal gradients in Chl*a* levels with the riverine zone possessing the highest levels. Walker (*29*) reported similar gradients, but our study shows that the level of eutrophy in the riverine zone has increased in the last 10 yr. Similar longitudinal gradients in chlorophyll levels have also been reported in Degray Lake, Arkansas (*31*), and in downstream reservoirs on the White River (*29*). These peaks in primary production are probably influenced by episodic events and nutrient loading from the primary sources, because the riverine zone is directly impacted from external nutrient loading (*14*). The flood events may not affect down-reservoir primary production as drastically because of the increased sedimentation and removal of nutrient sources from the epilimnion (*30, 32*). As suspended sediment-laden water moves through the riverine zone in the transitional zone, sedimentation increases as advective velocity decreases and settling sediments may scavenge available nutrients from the mixed layer (*33, 34*). Nutrients may be removed from bioavailability temporarily, thus decreasing the immediate effect of elevated nutrient loading on down-reservoir primary production (*30*). Because of the sedimentation of particulate matter and nutrients, measurement of annual and seasonal chlorophyll levels in the upper reaches of reservoirs may be a means of assessing watershed nutrient management and reduced nutrient losses from upland areas.

The seasonal evaluation of the longitudinal gradients in phytoplankton production in Beaver Lake suggests it is similar to other reservoirs in Arkansas. Thorten and coworkers (*31*) reported longitudinal gradients in DeGray Lake, Arkansas, that were prominent in the summer and fall, but winter levels were lower and similar throughout the reservoir. In Year 1 of our study no longitudinal gradients were evident in the winter season and trophic conditions were oligotrophic with the exception of a eutrophic site in the transitional zone. The upper reaches of Beaver Lake were not as profoundly impacted in Year 1 (as Year 2) by high flow events, and eutrophic conditions may have persisted with advective transport down-reservoir. The progression of high summer chlorophyll levels were observed through the fall and winter of Year 1. Spring conditions produced higher primary productivity than did winter in general, especially in Year 1 when a marked decreasing gradient was observed. Summer gradients produced elevated primary productivity and eutrophic conditions in the riverine zone. The eutrophic conditions persisted throughout the transitional zone in Year 1, whereas only the riverine zone was eutrophic in Year 2. Seasonal variation of Chl*a* existed in the longitudinal gradients, but in general the riverine zone was the most productive as reported in DeGray Lake (*31*). The peak in primary production found in the riverine zone is in contrast to the typical reservoir gradients that culminate in the transitional zone (*12, 35*).

Assessment of mean date chlorophyll production produced a bimodal peak with maximum chlorophyll production during the summer. This is common in many reservoirs and lakes throughout North America and the world (*28, 36, 37*). The upper reaches of the reservoir were highly eutrophic (Chl*a* >15g L^{-1}) in August of Year 1. The levels remained eutrophic until fall mixis occurred in late November (*38*). After the mixing of the epilimnion and hypolimnion, the euphotic zone remained mesotrophic for the rest of the year except for a spring eutrophic peak during mid-May. Chlorophyll production again decreased and mesotrophic conditions prevailed, with chlorophyll levels peaking in late summer. The primary production of the upper reaches declined to oligotrophic conditions in the winter of Year 2 after extreme episodic events in late fall and early winter. The phytoplankton appeared to recover from the light-limiting conditions as algal biomass as indicated by Chl*a*, increased through the summer to the last sampling date of Year 2. The effects of nonalgal particulate matter are influential in the decrease in magnitude of mean chlorophyll levels by date from Years 1 to 2 by producing light-limiting conditions.

Examination of the temporal distribution of TP showed annual spring and fall peaks and summer lows. Typical northern lakes display bimodal TP distribution similar to phytoplankton production of northern lakes (*36, 37*). In Beaver Lake, TP peaks were not synonymous with the peaks in primary production but were synonymous with peaks in episodic loading. Elser and Kimmel (*39*) reported that nutrient inputs to reservoirs are often seasonal and associated with high precipitation events. In the current study, the highest mean sampling date TP level was actually recorded in the fall of the second sampling year. This peak in TP concentration corresponded to the beginning of the episodic events that would eventually increase sediment loading, thus decreasing the photic zone and primary production between sampling years. The overall mean date levels were generally similar between Years 1 and 2; however, the magnitude of the spring peaks was much greater in Year 2, resulting in an overall significant increase in epilimnion TP concentration. Median TP values slightly increased between sampling years, suggesting that the increase in episodic loading and suspended sediments more drastically affected mean TP concentrations than median as was reported by Reckhow (*40*). Dissolved P (as SRP) was essentially inversely related to the primary production in the annual cycle as was observed by Gloss and coworkers (*35*). SRP was greatest during the high flow winter and early spring seasons but as the seasons progressed into summer (algal growing season) available P was removed by the settling of suspended sediments (*34*).

Annual site mean TP displayed pronounced, decreasing, longitudinal gradients from the headwaters to the lacustrine zone of Beaver Lake. The results were similar to those observed by Walker (*29*) but in our study the magnitude of TP levels increased in the transitional and lacustrine zones. Seasonal breakdown of the longitudinal gradients revealed similar decreasing gradients of varying magnitude in virtually all the seasons. Other research (*31, 35*) has shown evidence of marked longitudinal gradients throughout reservoirs in the summer and that no gradient with similar levels throughout the reservoir was evident in winter. In our study, the fall episodic events started a flush of high TP concentrations throughout the upper reaches of Beaver Lake. Spates increase the importance of advective velocity and decrease that of dispersion (*41*). TP gradients are regulated by sedimentation and sediment-water interactions. This sedimentation results in a loss of P throughout the reservoir from the primary sources to the lacustrine zone (*27,* 34). Significant P losses occur coincident with sedimentation of nonbiotic particulate matter (*30*). Elser and Kimmel (*39*) indicated that P deficiency in phytoplankton increased down- reservoir. It may be that longitudinal gradients in TP and other physico-chemical parameters produce longitudinal biological and physiological gradients (*41*).

The proportion of TP as SRP appeared to increase with distance throughout Beaver Lake, whereas relative concentrations decreased from the riverine to the lacustrine zone. Temporal variation in the amount and proportion of TP as SRP existed seasonally and annually. The greatest magnitude of SRP occurred during spring runoff and the lowest during summer and/or fall. During low flow year (Year 1), there was a greater removal of bioavailable P than in high flow year (Year 2). This is consistent with the appreciable removal of molybdate reactive P reported by Turner and coworkers (*34*) throughout an impoundment under high and low inflow conditions. During high flow years more P is bioavailable, but increased suspended sediment loading inhibits potential primary production. The relative amount of dissolved, inorganic P in the water is controlled by the equilibrium P concentration (EPC) of the suspended sediments (*42*). The rate of release of P when ambient levels are below the EPC is controlled by the desorption kinetics of the sediments (*43*).

Nitrogen gradients in reservoirs have received little attention, possibly because of the lack of marked gradients and the preferential removal of P by the settling of suspended sediments (*30*). The upper reaches of Beaver Lake did display a decreasing down-reservoir gradient in Year 1, but in Year 2 the gradient was not evident. Seasonal breakdown of Year 1 TKN gradients produced slightly decreasing gradients in the spring and summer. It appears that the annual site means displayed the most pronounced gradient throughout Beaver Lake. Neither of the dissolved inorganic N species (NO_3^--N and NH_4^+-N) produced any gradients annually or seasonally during this study period. Temporal distribution of N produced winter and spring peaks in TN and NO_3^--N, which appears to be influenced by the increased precipitation and movement of NO_3^--N during runoff events. During this period NO_3^--N comprised approximately half of the TN in the reservoir.

Parameter-Chlorophyll Relationships: Previous research has demonstrated strong relationships between P and Chl*a* in lakes (*1, 2, 6-8*). This relationship has been examined within and among lakes of different latitudes. Reservoirs are noted for the light limitation caused by suspended nonalgal particulates and for the weaker chlorophyll - P relationship (*12, 14, 26-28*). The upper reaches of Beaver Lake fit this pattern. Walker (*28*) found a limited relationship between chlorophyll and P in Beaver Lake, and in our study TP concentrations could explain very little of the variation in Chl*a*, whereas PP provided a slightly better relationship. Smith (*5*) also found that PP produced a stronger relationship to primary productivity when other factors such as light are limiting. In our study the best relationship with N or P was actually TKN. Aquatic ecosystems under N limitation have traditionally displayed a stronger relationship with N than P (*44, 45*), but the weaker chlorophyll-P relationship is most likely due to the association between suspended sediments and TP (*25*).

Although Beaver Lake does not display strong individual sample correlations between nutrients and chlorophyll levels, using mean site or mean date values reduces some of the sample variation and augments our results. Date and site means of Chl*a* and PP or TKN increased correlation coefficients but the lower number of samples reduced the significance of the relationships. When we limiting the investigations to Year 1, the data yielded a surprisingly strong, positive log-linear trend ($r = 0.85$) between mean site chlorophyll production and TKN, whereas PP displayed a slightly weaker relationship ($r = 0.70$). The mean date relationships between Chl*a* and TKN or PP displayed lower correlation coefficients than mean site relationships ($r = 0.63$ and $r = 0.55$, respectively) in Year 1. The mean date data produced a decreasing trend ($r =-0.15$) in Year 2 between primary productivity and PP. This trend is possibly explained by an increase in TP related to the increase in suspended sediments. Examination of the mean site data produced similar log-linear trends for PP with varying intercepts between Years 1 and 2. Although TKN was more scattered in Year 2, the data appeared to fall along the same log-linear trend as indicated by regression analysis of both years in combination ($r = 0.73$, $P < 0.001$, Chl*a* = 2.21TKN - 5.63). The separation of PP relationships between years suggests that the relationship between P and phytoplankton production was hindered by the proportion of P as inorganic particulate P when light was limiting phytoplankton production. The combination of PP and TKN in year 1 may be the best log-linear relationship between primary productivity and nutrients ($r = 0.94$, $P < 0.001$, Chl*a* = 0.29PP + 1.87TKN - 5.03).

Summary: The difference between the trophic state indicated by Secchi depth, Chl*a* and TP in Beaver Lake demonstrates the necessity of measuring more than one index of eutrophication in a reservoir as previous research has noted (*9, 10, 26, 29*). Thorten and coworkers (*31*) identified variation in trophic status classification depending upon the location of the single sampling site. But, overall, reservoirs tend to shift from the eutrophic condition in the headwaters to more pristine conditions in the lacustrine zone (*12*) as did Beaver Lake. Reservoirs, compared to lakes, typically receive more external nutrient loading. Settling sediments in the reservoir can remove nutrients, particularly P, from the epilimnion, reducing the immediate impact on the down-reservoir areas (*27,30*). However, Schindler (*8*) suggested that lakes and reservoirs that have received high nutrient loads for a considerable length of time slowly recover once nutrient inputs are decreased due to the future release of nutrients from saturated sediments. Thus, the effects of high nutrient loading in reservoirs may not become evident until the internal nutrient cycling from sediments affects the entire lacustrine zone. While the lacustrine zone of Beaver Lake does not currently appear to be eutrophic, anthropogenic eutrophication may not become evident until internal processes dominate nutrient cycling in the lower portion of the reservoir.

ACKNOWLEDGMENTS

We would like to thank B. Shreve, D. Pote, J. Nichols, L. Self-Davis, M. van Benschoten, H. Peterson, B. Scopa, B. Green, S. Fisher and M. Adams for their help in the field and laboratory. We would also like to thank W. Fisher, T. Sauer and three anonymous reviewers for their helpful suggestions and editing. Funding for this project was provided by the U.S.E.PA. competitive grants program. Mention of a trade name does not imply endorsement by any institution or agency contributing to this research.

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Received: March 31, 1999; Accepted: August 24,1999