1997

Calibration of a Water-Quality Model for Herrington Lake Using Empirically Derived Measurements of Phytoplankton Growth and Nutrient Assimilation

Digital Object Identifier: https://doi.org/10.13023/kwrri.rr.202

Paul A. Bukaveckas

Angela S. Crain

Research Report No. 202

Calibration of a Water-Quality Model for Herrington Lake Using Empirically Derived Measurements of Phytoplankton Growth and Nutrient Assimilation

by

Paul A. Bukaveckas
Principal Investigator

Angela S. Crain
Graduate Assistants

Project Number:95-06
Agreement No.: 14-08-0001-G2021
Period of Project: July 1995 to August 1997

University of Kentucky
Kentucky Water Resources Research Institute
Lexington, KY 40506-0107

The work on which this report is based was supported in part by the Department of the Interior, Washington, D.C. as authorized by the Water Resources Research Act P.L. 101-397

1997

Research Report No. 202

Calibration of a Water-Quality Model for Herrington Lake Using Empirically Derived Measuremnts of Phytoplankton Growth and Nutrient Assimilation

By

Paul A. Bukaveckas
Principal Investigator

Angela S. Crain
Graduate Assistant

Kentucky Water Resources Research Institute
University of Kentucky
Lexington, KY

Disclaimer: The activities on which this report is based were financed in part by the Department of the Interior, U.S. Geological Survey, through the Kentucky Water Resources Research Institute. The contents of this publication do not necessarily reflect the views and policies of the Department of the Interior, nor does mention of trade names or commercial products constitute their endorsement by the United States Government.

ABSTRACT

Importance of light limitation, nutrient availability, and hydrology in controlling the abundance and composition of the phytoplankton community of Herrington Lake (KY) was investigated over a two-year period. Selected environmental parameters were measured every two weeks (April-October) at five sampling stations located along the longitudinal gradient of the reservoir. In addition, short-term (48hr) nutrient enrichment experiments were conducted to assess the spatial and temporal variations in nutrient limitation. Phytoplankton growth responses to the combined addition of nitrogen (NO_3) and phosphorus (PO_4) were greater than those resulting from the addition of either nutrient alone. These results indicate that phytoplankton production was closely co-limited by the availability of both N and P. The magnitude of the phytoplankton responses to nutrient additions was greatest at downstream stations and in late summer suggesting that those populations experience more severe nutrient limitation. Significant interannual variations in nutrient limitation and primary production were observed during this study period (1995-1996). In 1995, nutrient limitation was more severe than in 1996. Above average rainfall and discharge in 1996 coincided with increased productivity (mg $C/m^3/hr$) and minimal nutrient limitation. Phytoplankton community composition showed similar patterns of seasonal succession in both years.

Focus Categories: NU, HYDROL, ECL

Keywords: Herrington Lake, hydrology, nutrient limitation, phytoplankton production, nutrient addition experiments

ACKNOWLEDGMENTS

Research was supported by grants from the U.S. EPA Clean Lakes Program, and the Kentucky Water Resources Institute through the U.S. Department of the Interior. Additional support was provided by a grant from the Kentucky Institute for Environment and Sustainable Development. We are grateful to Rich Shultz and Steve Rier for their analysis of nutrient samples. Special thanks to Rob M^{c}Candless and Don Metzmeier for their field assistance, Darryl Colebank and David Loy for their laboratory assistance, and Eric Jourdain for his statistical assistance.

TABLE OF CONTENTS

TABLES

ILLUSTRATIONS

INTRODUCTION

Herrington Lake is a large, eutrophic reservoir located on the Dix River in north-central Kentucky. As is true of many waterbodies in the southeastern United States, the reservoir suffers from excessive nutrient loading resulting in the deterioration of water-quality conditions and producing problematic algal blooms (Dave Liest, personal commun.). Nutrient inputs derive from agricultural non-point sources, municipal point sources, and shoreline development. The relative importance of these sources is unknown limiting the effectiveness of lake and watershed management decisions. Many resource management agencies concerned with developing nutrient control strategies rely strongly on dynamic water-quality models. Water-quality monitoring programs typically provide hydrological and chemical data for model development and calibration but often neglect site-specific information on nutrient-algal dynamics. In these situations, literature estimates for various biological rate coefficients are incorporated into the model. These may not accurately depict the ecological processes and thus compromise the validity of the model predictions. A quantitative understanding of the interactions between algae and nutrients is important for the purposes of water-quality modeling. Algae play an important role in regulating nutrient uptake, water transparency, and hypolimnetic oxygen levels which consequently influence the nutrient status of lakes and reservoirs. Excessive nutrient loading can produce large standing crops of algae resulting in decreased water transparency. The algae subsequently settle out and decompose within the hypolimnion contributing directly to oxygen depletion. Evaluation of site-specific nutrient-algal relations should aid in the improvement of water-quality models thereby, promoting the effectiveness of lake and watershed management decisions.

Algal dynamics in reservoirs, as in lakes, are largely controlled by light and nutrient availability. However, most reservoirs experience shorter residence times, higher concentrations of suspended solids, and hypolimnetic releases of water which influence nutrient inputs into the epilimnion resulting in different spatial and seasonal variation in reservoir phytoplankton production (Soballe & Kimmel, 1987). In addition, the complex morphology of large reservoir basins can result in greater spatial variation

(Knowlton & Jones, 1995). Understanding the relationships between nutrient availability, hydrology, and morphology is essential to understanding phytoplankton production in reservoirs (Kennedy & Walker, Kimmel et al. 1990). Light and nutrient availability are often emphasized as the two primary factors controlling phytoplankton productivity in reservoirs. A generalized reservoir model proposed by Kennedy and Walker (1990) suggests that nutrient availability decreases and light availability increases from upstream (riverine) to downstream (lacustrine) regions of the reservoir. According to the model, phytoplankton are presumed to be light-limited upstream and nutrient-limited downstream. Although light and nutrients are two important factors controlling productivity , the combination of hydrology and basin morphology are also important in the control of phytoplankton production. An advective flow regime in combination with a long, narrow basin morphology results in the establishment of a gradient (headwater to dam) in nutrient concentrations that ultimately impact phytoplankton production. In addition, advective forces, such as residence time, can influence phytoplankton production (Gloss et al. 1980; Soballe & Kimmel 1987). Assuming flow rates exceed the phytoplankton production rate, the accumulation of biomass and phytoplankton productivity can be limited by advective losses (Dickman 1969). However, Carmack et al. 1979 reported that advective losses can be important to reservoirs with intermediate residence times if the phytoplankton production rate is not exceeded by advective losses. With increased flow, nutrient availability increases resulting in enhanced phytoplankton production.

In recent years, small-scale, in situ, nutrient enrichment experiments have become a powerful tool for investigating spatial and temporal variations in phytoplankton to nutrient limitation. Several investigators have applied this approach to quantify temporal variation in the severity of nutrient limitation (Vanni & Temte 1990; Elser 1992). Other studies have examined longitudinal patterns of nutrient limitation in large lakes and reservoirs (Elser & Kimmel 1985; Aldridge et al. 1995). In this study, we measured phytoplankton growth responses (chlorophyll) during in-lake nutrient enrichment experiments to test the hypothesis that phytoplankton downstream would experience greater nutrient

limitation, particularly late in the growing season. We formulated this hypothesis in the context of the generalized reservoir productivity model described by Kennedy & Walker, 1990.

The goals of this research were to examine the spatial and seasonal variations of nutrient availability supporting phytoplankton production and to identify specific macronutrients (N and/or P) limiting phytoplankton growth. Specific objectives included: (1) quantifying seasonal and spatial variation in primary productivity (2) conducting in-lake enclosure experiments to assess patterns of nutrient limitation, and (3) taxonomic analyses of phytoplankton community composition in lake and enclosure samples.

MATERIALS AND METHODS

Study area

Herrington Lake is eutrophic reservoir located in north-central Kentucky (fig. 1). It has a surface area of 1190 ha, a length of 60 km, and mean and maximum depths of 24 m and 76 m, respectively. The reservoir's watershed (113,700 ha) is comprised of various land-use types including 71% agricultural, 26% silvicultural and 3% urban areas (Kentucky Division of Water, 1984a). The topography of the watershed is hilly in the south (headwaters), leading to gentle rolling hills in the north. The basin of Herrington Lake is a deep-narrow valley with the average retention time of 9.2 months. The major inflows include the Dix River and Clarks Run with contributions from other minor streams. The major outflow from Herrington Lake is the Dix River below the Dix River Dam.

Five sampling stations were selected to characterize in the upstream (riverine), middle (transition), and downstream (lacustrine) sections of the reservoir. Stations 1, 2, 3, and 5 were within the mainstem of the reservoir, whereas station 4 was located in a branch of the reservoir formed by the Cane Run Creek. Chlorophyll, light attenuation (PAR), temperature, and phytoplankton community composition were monitored at 1-2 week intervals from April to October 1995 and 1996 (fig. 1).

Temperature and light

Temperature and irradiance profiles were obtained for all 5 stations. Temperature was measured at 1-m intervals (surface to 44-m or to the bottom at shallower sites) using a YSI Model S-C-T thermistor. Light attenuation (PAR) profiles were measured using a Protomatic photometer equipped with upward and downward spherical sensors. Light profiles were recorded between 1000 and 1400 h. Depth profiles of upwelling and downwelling light were taken at 0.5 meter intervals from the surface to the lower boundary of the photic zone (1% of subsurface irradiance), and used to estimate coefficients of light attenuation (Kd). The attenuation coefficient for downwelling irradiance (Kd) was calculated from a linear regression of the natural logarithm of downwelling irradiance against depth (Kirk 1983). Secchi disc measurements were taken simultaneously with underwater photometer profiles. A detailed description of analytical procedures used for irradiance data is presented in Bukaveckas and Driscoll (1991).

Chlorophyll *a*

Water samples for chlorophyll analysis were taken at 3 equally spaced depths between the surface and the 1% light level using a 2.5 L Kemmerer water sampler. Samples were stored in 1L polyethylene bottles on ice, and processed within one to two hours of collection by filtration through 0.45 mm Gelman A/E glass fiber filters. The filters were subsequently frozen and processed within 2-7 days. Filters were macerated in 10.0 ml of 90% buffered acetone (buffering agent: $MgCO_3$) and allowed to extract for 12-16 hours at 4°C. Following centrifugation, the extracts were analyzed spectrophotometrically to determine chlorophyll *a* and pheophytin *a*. Extracts were analyzed using a Varian DMS 70 dual beam spectrophotometer equipped with long pathlength (4cm) cells and narrow (1nm) bandwidth. Optical densities were measured at 664 nm and 750 nm before acidification with 0.1N HCL and at 750 nm and 665 nm after acidification. Chlorophyll *a* concentrations were corrected for pheophytin *a* using the Lorenzen equations as modified by Speziale et al. (1984).

Phytoplankton production

Phytoplankton productivity was measured monthly using the isotope technique described by Vollenweider (1969). Samples were collected from 3 equally spaced depths approximating the epilimnetic region at all stations. Two light bottles and one dark bottle (60 ml BOD) from each of the three depths were inoculated with 1 μCi of [^{14}C]-NaHCO3 (310.80 MBq-mmol) and incubated for 2 h (1200-1400). After incubation, all samples were filtered through 0.45 mm Millipore membrane filters. The filtration pressure applied did not exceed 300 mmHg (Pregnall 1991). Filters were dissolved in 6.5 ml of Aqua-sol and radioactivity was determined using a Tri-Carb 1900 TR liquid scintillation analyzer. Quenching was corrected using an external unquenched ^{14}C standard with known activity.

Dissolved inorganic carbon (DIC) samples were collected in 60 ml acid-washed plastic syringes and stored on ice. Samples were analyzed within 1-2 days on an automated total carbon analyzer (Shimadzu Total Carbon Analyzer Model TOC-5050A) using the combustion/non-dispersive infrared gas analysis method (APHA 1992).

Photosynthesis-irradiance curves were modeled using the following equation:

$$P = P_{max} \tanh(\alpha I / P_{max})$$

where P is the biomass specific rate of production (primary productivity per unit chlorophyll) at irradiance I (Jassby & Platt, 1976). Alpha (α) is the slope of the light-saturation curve which measures the efficiency of fixing inorganic carbon at low light levels. P_{max} is the maximum photosynthetic rate at optimal illumination levels as described by the plateau of the line. We compared P-I models for data aggregated by site (all months) versus by month (all sites) and found that the monthly-aggregated data produced more accurate model predictions. These models were used to estimate productivity on sampling dates when only chlorophyll and light attenuation data were measured (N = 6). In addition, the models were used to derive growing season (July-October) estimates of productivity based on daily solar radiation data (T. Priddy, written commun.) and combined with lake bathymetric data (G.L. Jarrett,

unpub. data) to calculate whole-reservoir production. Productivity estimates were calculated using July-October data from 1995 and 1996. Early summer 1995 data was missing so therefore the period of July to October was chosen because of comparable sampling frequencies for both years.

Nutrient enrichment experiments

Nutrient enrichment experiments were conducted at 3 stations (S1, S3, S4) representing the upstream, middle, and downstream sections of the reservoir. Experiments were performed on six occasions (August, September, and October 1995 and May, July, and September 1996) using 10 liter polyethylene containers. Water was pumped from 1-m below the surface, transferred through a 150 μm zooplankton net and collected in a large polyethylene mixing container (128 L). The experimental design included 3 replicates each of a control (no nutrient addition), nitrogen addition, phosphorus addition, and the combination of nitrogen and phosphorus. Inorganic nitrogen was added as K_2NO_3 (200 μg/L in 1995 and 400 μg/L in 1996) and phosphorus was added as $NaPO_4$ (40 μg/L). The containers were incubated for 48 hours at a depth of 1-m. Chlorophyll and nutrient concentrations were measured at the beginning and end of each experiment to quantify phytoplankton growth responses and rates of nutrient assimilation. Phytoplankton growth responses to nutrients were quantified using the following formula:

$$\text{nutrient response} = \frac{(\text{Chlorophyll } a_{(\text{trmt})} - \text{Chlorophyll } a_{(\text{control})})}{\text{Chlorophyll } a_{(\text{control})}}$$

Where chlorophyll a_{trmt} is the mean chlorophyll concentration after 48 hours among 3 replicated receiving nutrient additions (+N, +P, +NP). Chlorophyll a_{control} is the mean chlorophyll concentration after 48 hours among replicates receiving no nutrients. Nitrate concentrations were determined using the automated cadmium reduction method (APHA 1992) and performed on an autoanalyzer (Skalar San Plus). Phosphorus (soluble reactive) concentrations were analyzed on unfiltered samples using the manual ascorbic acid method (APHA 1992).

Results from the nutrient enrichment experiments were analyzed using one-way analysis of variance (ANOVA) for all stations and dates. Classifications of nutrient limitation were based on summations of comparisons among the 3 treatment groups (+N, +P, +NP) with the controls (no nutrient addition) using p-values ($p < 0.05$). All statistical analyses were performed using SIGMASTAT (Ver. 2.0, 1992-1995).

Phytoplankton slide mounts and enumeration

Phytoplankton samples were collected from depths corresponding to those for chlorophyll analyses. A single composite sample was placed in a 125 ml amber glass bottle and preserved with 2.25 ml of M3 fixative (APHA 1992).

Phytoplankton sample processing included the preparation of permanent slide mounts mounted in EUPARAL (refractive index: 1:48). Samples were agitated and a subsample was filtered through 0.45 mm Millipore membrane filters. Gluteraldehyde was applied to the filters and allowed to dry on a slide warmer until filters turned clear (5-15 minutes).

Phytoplankton identifications were made using an Olympus BH-2 microscope at 500X and 1250X. Observations were made under Nomarski differential interference contrast. Phytoplankton taxa identifications were determined from Prescott (1978), Whittford & Schumacher (1984), Smith (1978), Desikachary (1959), and Dillard (1989).

Enumeration of phytoplankton species followed standard procedures (APHA 1992). Replicate slides was made from selected lake samples (stations 1, 3, and 5). Control and NP-addition samples from the nutrient enrichment experiments were also counted. Only live diatoms mounted in EUPARAL were tallied. Ten to sixty fields were counted in vertical strips covering the entire diameter of the filter to yield a total of 500-600 cells. The number of fields counted per slide was density dependent. Five fields were counted per slide for a total of ten fields. If, after 10 fields, the total number of cells counted was less than 500, then additional fields were counted to reach the total absolute cell count. Knowing the size

of area examined, the total area of the filter ($A=pr^2$), and the volume of water filtered, the number of organisms per milliliter was calculated (Wetzel & Likens 1991). Cell measurements were made on 20 randomly selected cells from species occurring in at least 80 % of the samples and volumes were approximated from simple geometric shapes. The volume of each measured cell was calculated to derive a mean cell volume. Mean cell volume was multiplied by cell population density to estimate biovolume. Biovolume was then converted to biomass assuming a specific gravity of 1. Carbon biomass was converted from volume biomass using taxonomic-specific factors to describe the amount of carbon content per wet mass of organisms (Olrik et al. 1996).

A multivariate procedure (canonical correspondence analysis) was used to explore the relationship between measured environmental variables and phytoplankton community composition based on relative biomass. All environmental variables (temperature, light, chlorophyll, dissolved oxygen, and specific conductance were log-transformed due their non-normal distributions with the exception of pH. Site scores were calculated from the linear combination of the six environmental variables that form the ordination axes (Ter Braak 1988). Station 5 (June 1996) was excluded from analysis because it was determined to be an outlier.

RESULTS

Hydrology

The 1995 growing season (July-October) was characterized by low rainfall and discharge (fig. 2). Monthly data for 1995 indicate that highest precipitation and discharge occurred in May and that late summer (July-October) was characterized by low precipitation (< 4 in/mo) and low discharge (<300 m^3/s). In contrast, late summer and early fall of 1996 was characterized by more variable precipitation inputs (1-8 in/mo) and higher discharge (250-900 m^3/s). Cumulative discharge for the period of July-October corresponded to 45% (1996) and 14% (1995) of lake volume (fig.2).

Light availability and temperature

Marked longitudinal gradients in water column transparency were evident in both 1995 and 1996 (fig. 3A). The highest light attenuation (lowest transparency) was measured at the upstream station in both years. Variations in light attenuation among the stations was attributed to differences in the scattering of light by suspended particulates (data not shown) and generally corresponded to periods of elevated discharge. Monthly averaged attenuation coefficients (Kd) ranged from 0.63 to 5.57 in 1995 and 0.71 to 4.71 in 1996 during April-October. The depth of the photic zone (1% light level) ranged from 0.5 to 3 m at the upstream station to 5 to 10 m at downstream stations during April-October. During the period April-October, the reservoir was thermally stratified at all stations. Mean monthly epilimnetic temperature regimes at station 5 ranged from 15 to 29°C and hypolimnetic temperatures ranged from 8 to 18°C (fig. 3B). The average epilimnetic water temperatures during in April-October 1995 and 1996 were 24 and 22°C , respectively.

Nutrient Chemistry

During late summer of 1995, epilimnetic soluble reactive phosphorus (SRP) concentrations decreased along the longitudinal gradient of the reservoir (table 1). The mean SRP concentration at station 1 (16.6 µg/L SRP) was two-fold higher than that at station 4 (8.1 µg/L). SRP concentrations in 1996 showed only a slight decrease between station 1 (50.2 µg/L) and station 4 (47.8 µg/L). Mean SRP concentrations were significantly different between the two sampling years 11.6 µg/L in 1995, 47.1 µg/L in 1996; p-value = 0.004.

Epilimnetic nitrate ($N\text{-}NO_3$) concentrations were consistently higher at the upstream station compared to the mid-lake and downstream stations (table 1). Mean $N\text{-}NO_3$ concentrations (1995) (89 µg/L) were significantly different from 1996 (366 µg/L) (p-value = 0.017).

Chlorophyll, primary productivity and phytoplankton biomass

Monthly averages of chlorophyll concentrations ranged from 2 μg/L to 33 μg/L (fig. 4). At the upstream station, highest chlorophyll concentrations were observed in late-summer (July-October). At the mid-lake and downstream stations, highest concentrations occurred in April-May. A transitional period was evident in June when chlorophyll was uniform throughout the reservoir. This pattern was similar in both years, and average chlorophyll concentrations were not significantly different (p-value = 0.386).

Mathematical models relating primary productivity per unit chlorophyll and light were used to interpret seasonal and spatial variation in photosynthesis within the reservoir. Separate photosynthesis-irradiance curves were derived for monthly-aggregated data to assess the model parameters sensitivity to changing seasonal conditions (fig. 5A-D). Data for all stations and depths were pooled to generate the monthly P-I curves. The models accounted for 79% to 92% of the variation in productivity. Estimates of light utilization efficiency (α) generally increased from June (0.05) to October (1.82). The maximum photosynthetic rate (P_{max}) ranged from 1.51 (July) to 3.84 (October).

Depth-integrated estimates of epilimnetic productivity were generally similar in June-July (57-67 mg C day-1) and decreased somewhat in late summer (37 mg C day-1) (fig. 6A). The decline in September productivity coincided with lower levels in chlorophyll during the same period. Epilimnetic productivity varied considerably among the stations. Productivity was notably higher at the farthest upstream station (73 mg C day-1) compared with stations 2, 3, and 5 downstream (fig. 6B). The embayment (station 4) showed the highest productivity (95 mg C day-1) within the reservoir.

The proportion of whole-reservoir productivity occurring within segments of the reservoir delineated by the 5 sampling stations corresponded closely with the proportion of lake volume represented by each segment (table 2). The mid-lake segment (S2-S3) represents the largest fraction of lake volume (43%) and accounted for a similar proportion of lake productivity. The upstream segment (S1-S2) represents 22% of lake volume and accounted for 27% (1996) and 36% (1995) of productivity.

The downstream segment (S3-S5) represents 32% of lake volume and accounted for 28% (1996) and 18% (1995) of productivity. These analyses suggest that in 1995 a disproportionate fraction of lake productivity (relative to volume) occurred in the upstream segment. Although, the embayment exhibited the highest productivity, this segment accounted for a small proportion of the lake's volume (2%) and a correspondingly small fraction of whole-lake productivity.

Phytoplankton biomass showed considerable variability during both years ranging from less than 100 to >1000 µg/L (fig. 7). No consistent difference were observed between upstream, mid-lake, and downstream stations in either year. Phytoplankton biomass was notably higher during June of 1995, and as a result, mean biomass was higher in 1995 than in 1996 (348 and 169 µg/L, respectively).

Phytoplankton community composition

A multivariate analyses, based on a unimodal model of species response, using the relative biomass of the 56 major phytoplankton species was performed to identify environmental variables that best explain species distributions. We used canonical correspondence analysis (CCA) to maximize the dispersion of species along the ordination axes. Axes 1 and 2 were chosen based on relatively high eigenvalues ($\lambda 1 = 0.55$, $\lambda 2 = 0.30$) and high species-environmental correlation (0.90 for axis 1, 0.79 for axis 2) which together accounted for 79% of the variance explained by the environmental variables. These results indicate a strong relationship between the distribution of species composition and the six environmental variables utilized in the ordination analysis. Environmental variables included temperature, dissolved oxygen, specific conductivity, pH, light attenuation, and chlorophyll.

The canonical correspondence analysis performed on the 1995 and 1996 phytoplankton communities indicated general differences between the two sampling years (fig. 8). Communities present in 1996 were represented by negative scores on axis-1 (11 of 11 samples), whereas the majority of 1995 samples (6 of 11) were represented by positive scores. However, overlap did exist (upper left quadrant of fig. 8), suggesting some degree of similarity for both years.

Seasonal variability in species composition was evaluated using CCA. Distinctive seasonal patterns in species composition were evident for both years (fig. 9A-B) by division into 3 discrete seasons: April-May, June-July, and August-October. During 1995, general successional patterns in species composition progressed from an early summer assemblage dominated by centric diatoms (*Cyclotella pseudostelligera*), and two cyanophytes (*Aphanocapsa delicatissima* and *Oscillitoria limnetica*) to a late summer assemblage dominated solely by cyanophytes (*Dactylococcopsis irregularis, Merismopedia tennuissima, and Chroococcus minutus*). Phytoplankton were not counted in late spring of 1995 due to high turbidity within the reservoir which precluded accurate identification in slide mounts. In April and May of 1996, the phytoplankton community was dominated by *Cyclotella pseudostelligera, Synedra tenera,* and *Aphanocapsa delicatissima*. The succession of phytoplankton into the summer periods progressed to cyanophytes and cryptophytes (almost exclusively *Oscillitoria limnetica* and *Rhodomonas minuta*).

Enclosure experiments

A total of 18 experiments (3 stations * 6 dates) were conducted during 1995 and 1996. Of the 18 experiments, 61% were classified as co-limited (+NP), 6% were classified as N-limited, and 33% limited by some factor other than N or P. In 1995, we observed that the magnitude of the response to the combined addition of +NP was consistently higher at the furthest downstream station (fig. 10 A-B). At the upstream site, phytoplankton growth responses following nutrient enrichment were weaker (<50% increase in chlorophyll) and were generally similar among the three treatments (+P,+N,+PN) (fig. 10A-B). It is unclear whether nutrient limitation is an important factor regulating phytoplankton growth in the upper part of the reservoir. The 1996 experiments did not exhibit consistent spatial patterns in nutrient limitation and phytoplankton growth responses to nutrient addition were generally weaker (<100% chlorophyll increase) than in 1995 (fig. 10C-D). Phytoplankton exhibited stronger responses to either phosphorus or nitrogen alone than to the combined addition inferring single nutrient limitation.

However, only one experiment showed statistical significance to being limited by a single nutrient (nitrogen).

Changes in phytoplankton community composition among the initial, control, and +NP treatment groups were analyze using correspondence analysis (CA) (fig. 11A-B). These data were subsequently compared with changes in phytoplankton growth responses (% chlorophyll). Four types of responses were expected: (1) minimal changes in both biomass and species composition; (2) shifts in species composition with minimal changes in biomass; (3) shifts in species composition accompanied by and increase in biomass, and (4) an increase in biomass without changes in species composition. Comparisons were made between the initials and controls at each station to assess enclosure effects on phytoplankton communities composition (fig. 11A). Of the 9 experiments of which both species and biomass data were available, 4 exhibited minimal change in biomass or species composition, 4 exhibited shifts in community composition with little change in chlorophyll, and 1 exhibited both an increase in biomass and changes in community composition. Species showing little response to confinement included: *Dactylococcopsis irregularis, Euglena gracilus, Cylindrospermopsis philippinensis,* and *Melosira spp.* The species composition (station 3) shifted from mainly cyanophytes to chlorophytes (*Treubaria setigerum* and *Tetrastrum minimum).* Station 4 also experienced a shift in species composition becoming dominated by a filamentous cyanophyte (*Anabaenopsis circularis)* and a chrysophyte (*Peridenium umbotanum).* In September, station 1 was dominated by a new species (*Cryptomonas erosa*).

Differences in phytoplankton assemblages between the control and +NP treatment showed a distinct spatial pattern in community composition (fig. 11B). This result corresponds to the severity of nutrient limitation experienced by the phytoplankton along the longitudinal gradient of the reservoir (fig. 10A). Phytoplankton communities at the upstream station showed little response to nutrient addition and were dominated by *Euglena gracilus* and *Cryptomonas erosa* during late summer. The dominant phytoplankton in the embayment remained the same following a positive response to nutrient

addition (*Sphaerocystis schroeteri, Tetrastrum minimum,* and large centric diatom species. During August and September, the dominant phytoplankton (*Cylindrospermopsis philippinensis* and *Chrysophyte spp.*) at station 3 showed little response to nutrient addition. However, there was a significant growth response by *Melosira varians* in mid-October.

DISCUSSION

Because of the advective influence of river impoundment, reservoirs are often spatially heterogeneous environments that possess longitudinal gradients in environmental factors that control phytoplankton productivity (Gloss et al. 1980; Marzolf 1984; Kimmel et al. 1990). In this study, significant interannual differences among the major environmental parameters, e.g., light, nutrients, chlorophyll, and carbon fixation were observed along the longitudinal gradient of the reservoir. The relationship between these environmental parameters helped to provide insight into the controlling factors of nutrient-algal dynamics. The spatial gradients observed among the environmental parameters was consistent with the generalized model described by Kennedy & Walker (1990). According to the model, phytoplankton are presumed to be light-limited in the upstream regions and nutrient-limited in downstream regions. In this study, light penetration was lowest at upstream stations and increased with distance downstream. Light penetration was low upstream due to increased suspended solids while nutrient concentrations decreased downstream (toward the dam) because of increased phytoplankton production being supported by greater light penetration. Nutrient concentration (SRP and NO_3) gradients were in agreement with the generalized reservoir model.

Hydrodynamics also played an important role in the control of nutrient-algal dynamics. In this study, discharge was a prominent controlling factor among both years. Discharge in the 1995 growing season (July-October) was below average due to low rainfall levels and preceding years of drought. This resulted in low productivity and severe nutrient limitation by phytoplankton. In comparison, above average rainfall levels and discharge in 1996 coincided with increased productivity and minimal nutrient

limitation. In addition, marked longitudinal gradients of chlorophyll, light attenuation, and nutrient concentrations developed from the combined influence of hydrodynamics and basin morphology.

Chlorophyll levels remained relatively high in both years despite the significant differences in discharge and precipitation. This suggests that increased discharge, by itself, does not ensure low phytoplankton production, However, this does not eliminate the role discharge plays in phytoplankton dynamics. Seasonal changes in phytoplankton abundance were categorized into 3 periods based on longitudinal gradients observed in the reservoir. During high flows in April and May, chlorophyll concentrations were highest downstream, presumably because of high turbidity and advective losses upstream precluded phytoplankton community development. A transitional period of decreasing flow was evident in June when chlorophyll was uniform throughout the reservoir. During summer base flow (July-October), chlorophyll concentrations were consistently higher at the upstream station, possibly because of nutrient limitation in downstream regions.

The results from the depth-integrated estimates of epilimnetic productivity in 1996 were consistent with the model described by Kennedy & Walker (1990) and Kimmel et al. (1990) which predicts spatial heterogeneity in phytoplankton production in relation to longitudinal gradients. Productivity was notably higher at the upstream station compared with stations 2, 3, and 5 downstream. In 1995, the close correspondence between the proportion of whole-reservoir productivity within the segments of the reservoir and with the proportion of lake volume suggests that a disproportionate fraction of lake productivity (relative to volume) occurred in the upstream segment. Station 4 (embayment) showed the highest productivity within the reservoir, but only accounted for a small proportion of the lakes volume (2%) and a correspondingly small fraction of whole-lake productivity.. The higher productivity at station 4 could possibly be the influence of extensive shoreline development.

The depth-integrated estimates of epilimnetic productivity in 1996 showed that phytoplankton in late spring (June) experienced increased light intensities (clear-water period) indicating that cell growth was limited on the phytoplankton's ability to fix carbon. However, phytoplankton in September

experienced lower light levels, but had relatively higher photosynthetic efficiencies than June phytoplankton. This could possibly be due to a relatively higher pigment content within the phytoplankton, thus improving the capacity to absorb light.

Results from the nutrient addition experiments showed distinct spatial and temporal patterns in the incidence of nutrient limitation by N and P combined (+NP). During 1995, co-limitation (+NP) was significant in 78% of all experiments. Although previous studies suggest that only one nutrient can limit phytoplankton production at any one time (Schindler 1977), more recent studies demonstrate co-limitation of algal production by N and P from a variety of lakes and reservoirs (Vanni & Temte 1990; Elser & Kimmel 1985). In theory, a species cannot be simultaneously limited by more than one nutrient. However, co-limitation probably arises because several taxa are close to being limited by the "nonlimiting" nutrient (Vanni & Temte 1990). Thus, if a species experiencing P limitation receives an addition of P (no nitrogen) and fails to increase biomass, then the species is most likely to experience N limitation (Suttle & Harrison 1988). When both nutrients are added, neither nutrient is limiting and phytoplankton exhibit a positive growth response.

The magnitude of the phytoplankton response was consistently higher at the downstream station which was consistent with our hypothesis of greater nutrient limitation downstream. It is unclear whether nutrient limitation is an important factor regulating phytoplankton production in upstream regions of the reservoir. Based on these observations, it is possible to hypothesize the downstream stations of the reservoir are the most sensitive to variations in external and internal nutrient loading. It should be noted that zooplankton removal from enclosures may increase the severity of nutrient limitation (Bukaveckas, oral commun.; Elser & Frees 1995.). Results of the 1996 experiments showed less apparent spatial patterns and exhibited weaker growth responses to nutrient additions. The effects of nutrient limitation on phytoplankton communities appeared to be most severe in late summer. The frequency of nutrient limitation in the reservoir during our study period coincided with significant changes in discharge.

The spatial patterns of nutrient limitation observed in the enclosure experiments help to explain the phytoplankton community stability. Comparisons among the initial, control, and +NP treatment groups indicated that enclosure confinement caused some alterations in the community structure while nutrient additions primarily caused significant biomass responses (increase in chlorophyll) with no shifts in species composition at each station. Diatom abundances were extremely low in the summer, after spring peaks. High cyanophyte and chlorophyte abundances were maintained throughout the summer, particularly the filamentous forms of cyanophytes in late summer.

Seasonal succession in temperate lakes and reservoirs often progresses from spring dominance in diatoms, to chlorophyte dominance in early summer, eventually yielding to cyanophyte dominance in late summer (Wetzel 1983). Tilman et al. (1986) suggest that this sequence is related to interactive effects involving water temperature and nutrient concentrations. This succession of phytoplankton assemblages was generally observed throughout both sampling seasons using CCA ordination. In addition, cryptophytes were also abundant throughout the reservoir especially in mid- to late-summer.

The effect of anthropogenic nutrient enrichment on primary productivity is a topical concern for many lakes and reservoirs. Therefore, many management strategies are developed using dynamic water-quality models. However, accurate depictions of ecological processes is often neglected. In this study, we examined nutrient-algal interactions and the influences hydrology and morphology have on primary production for the purposes of water-quality modeling. The results suggest that phytoplankton growth downstream is more severely limited by N and P availability and therefore, may be more sensitive to changes in nutrient loading. Studies that focus on phytoplankton community responses to short-term nutrient enrichment experiments cannot be expected to reproduce all aspects of the actual environment to nutrient loading. However, enrichment experiments are valuable tools in understanding the ecological processes relevant to nutrient management strategies.

REFERENCES

Aldridge, F.J., E.J. Philips, and C.L. Schelske. 1995. The use of nutrient enrichment bioassays to test for spatial and temporal distribution of limiting factors affecting phytoplankton dynamics in Lake Okeechobee, Florida. Arch. Hydrobiol. Beih. Ergebn. Limnol., 45: 177-190.

American Public Health Association. 1992. Standard Methods for the Examination of Water and Wastewater. 19th Ed. American Public Health Association, Washington, DC. 1,268 p.

Bukaveckas, P.A., and C.T. Driscoll. 1991. Effects of whole-lake base addition on the optical properties of three clearwater acidic lakes. Can. J. Fish. Aquat. Sci. 48: 1030-1040.

Carmack, E.C., C.B. Gray, C.H. Pharo, and R.J. Daley 1979. Importance of lake-river interaction on seasonal patterns in the general circulation of Kamloops Lake, British Columbia. Limnol. Oceanogr. 24:634-644.

Desikachary, T.V. 1959. Cyanophyta. Academic Press, New York. 686 p.

Dickman, M. 1969. Some effects of lake renewal on phytoplankton productivity and species composition. Limnol. Oceanogr. 14:660-666.

Dillard, G.E., 1989. Freshwater algae of the southeastern United States. Part I. Chlorophyceae. Day. Cramer.

Elser, J.J. 1992. Phytoplankton dynamics and the role of grazers in Castle Lake, California. Ecology. 73(3): 887-902.

Elser, J.J., and B.L. Kimmel. 1985. Nutrient availability for phytoplankton production in a multiple-impoundment series. Can. J. Fish. Aquat. Sci. 42: 1359-1370.

Elser, J.J., and D.L. Frees. 1995. Microconsumer grazing and sources of limiting nutrients for phytoplannkton growth: Applications and complications of a nutrient-deletion/dilution-gradient technique. Limnol. Oceangr. 40:1-16.

Gloss, S.P., L.M. Mayer, and D.E. Kidd. 1980. Advective control of nutrient dynamics in the epilimnion of a large reservoir. Limnol. Oceanogr. 25: 219-228.

Jassby, A.D., and T. Platt. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceangr. 21: 540-547.

Kennedy, R.H., and W.W. Walker. 1990. Reservoir nutrient dynamics. Pages 109-132 in K.W. Thornton et al. (eds.) Reservoir Limnology: ecological perspectives. Wiley and Sons, New York.

Kentucky Division of Water (KDOW). 1984a. Trophic state and restoration assessments of Kentucky lakes. Final report: Frankfort, Kentucky, Kentucky of Natural Resources and Environmental Protection Cabinet, Department for Environmental Protection, 476 p.

Kimmel, B.J., O.T. Lind, and L.J. Paulson. 1990. Reservoir primary production. Pages 133-194 in K.W. Thornton et al. (eds.). Reservoir Limnology: ecological perspectives. Wiley and Sons, New York.

Kirk, J.T.O. 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, New York, NY, 401 p.

Knowlton, M.F., and J.R. Jones. 1995. Temporal and spatial dynamics of suspended sediment, nutrients, and algal biomass in Mark Twain Lake, Missouri. Arch Hydrobiol. 135(2): 145-178.

Marzolf, R. 1984. Reservoirs in the Great Plains of North America, p. 291-302. *In* F.B. Taub [ed.] Lake and reservoir ecosystems. Elsevier Scientific Publishing Co., Amsterdam, The Netherlands.

Olrik, K., P. Blomqvist, P. Brettum, G. Cronberg,., and P. Eloranta. 1996. Methods for quantitative assessment of phytoplankton in freshwaters. Part 1: Sampling, processing, and application in freshwater environmental monitoring programmes. 86 p.

Pregnall, A.M. 1991. Photosynthesis/Translocation: Aquatic. pp. 53-75. In Carbon Isotope Techniques, (David C. Coleman and Brian Fry, ed.). Academic Press Inc., New York.

Prescott, G.W. 1978. How to know the freshwater algae. W.C. Brown Co., Dubuque, Iowa. 293 p.

Schindler, D.W. 1974. Eutrophication and recovery in experimental lakes: implications for lake management. Science. 184: 897-899.

Smith, G.M. 1950. The freshwater algae of the United States. 2nd ed. McGraw-Hill, New York. 719 p.

Soballe, D.M., and B.J. Kimmel. 1987. A large scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology. 68: 1943-1954.

Speziale, B.J., S.P. Schreiner, P.A. Giammatteo, and J.E. Schindler. 1984. Comparison of DMF, DMSO, and acetone for extraction of phytoplankton chlorophyll. Can. J. Fish. Aquatic Sci. 41:1519-1522.

Suttle, C.A., and P.J. Harrison. 1988. Ammonium and phosphate uptake rates, N:P supply ratios, and evidence for N and P limitation in some oligotrophic lakes. Limnol. Oceangr. 33: 186-202.

Ter Braak, C.J.G. 1987-1992. CANOCO - a FORTRAN program for Canonical Community Ordination. Microcomputer Power, Ithaca, New York, USA.

Tilman, D., R. Kiesling, R. Sterner, S.S. Kilham, and F.A. Johnson. 1986. Green, blue-green, and diatom algae: Taxomonic differences in competitive ability for phosphorus, silicon, and nitrogen. Arch. Hydrobiol. 106: 473-485.

Vanni, M.J., and J. Temte. 1990. Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake. Limnol. Oceanogr. 35(3): 697-709.

Wetzel, R.G. 1983. Limnology, 2nd Ed. Saunders College Publishers, 767 p.

Wetzel, R.G., and G.E. Likens. 1991. Limnological Analyses. 2nd ed. Springer-Verlag, New York. 391p.

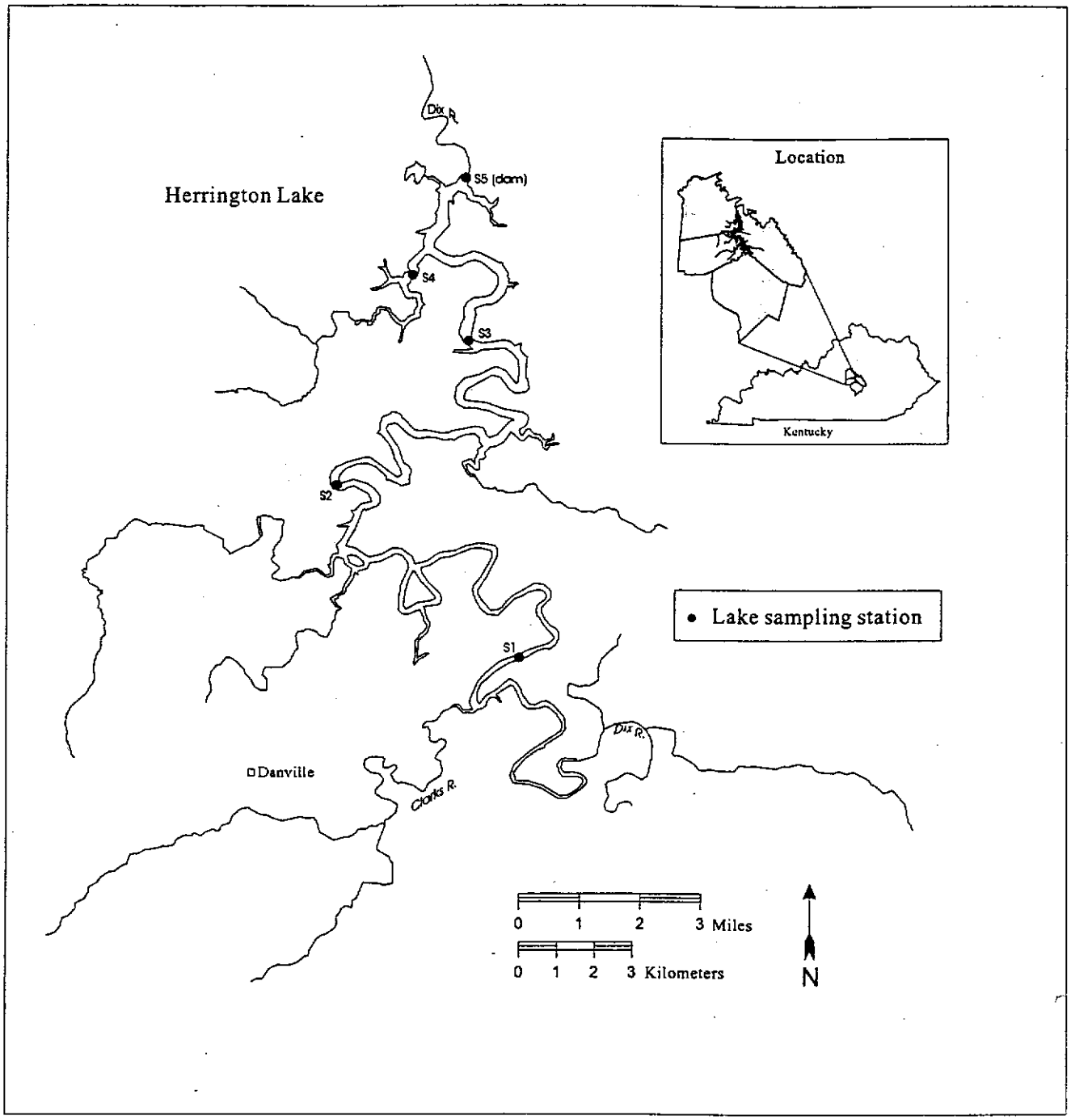
Whitford, L.A., and G. J. Schumacher. 1984. A manual of fresh-water algae. Sparks Press, Raleigh, North Carolina. 337 p.

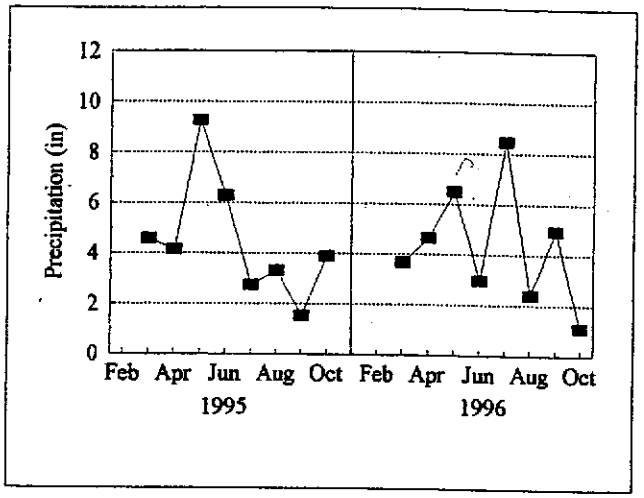
Table 1. Average soluble reactive phoshorus (SRP), and nitrate concentrations (ug/L) during August-October 1995 and July and September 1996. Samples were collected on dates corresponding to enclosure experiments.

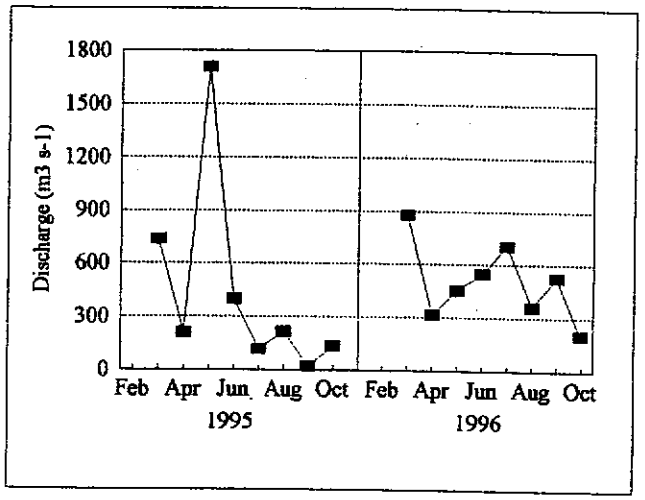
	1995		1996	
STATION	SRP ug/L	NO3 ug/L	SRP ug/L	NO3 ug/L
1	16.6	174	50.2	524
3	10.1	41	43.1	287
4	8.1	51	47.8	285
AVERAGE	11.6	89	47.0	366

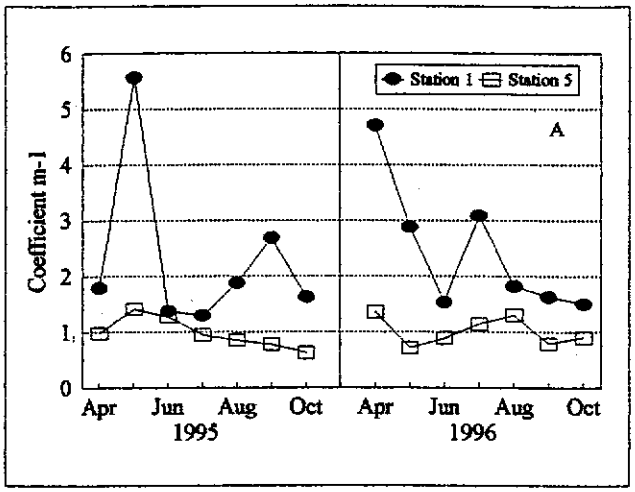
Table 2. Percent contribution of productivity (kg C growing season-1) in assigned reservoir segments for the 1995 and 1996 growing seasons. Productivity was calculated for growing seasons. Productivity was calculated for growing seasons of 95 and 98 days (1995 and 1996, respectively).

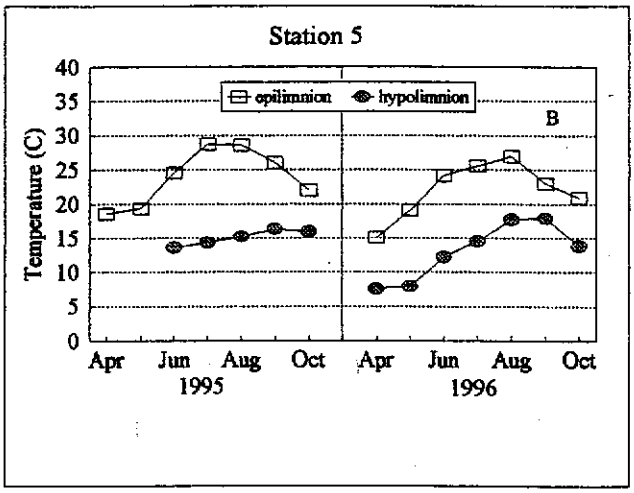
PRODUCTIVITY	STATION				
	S1-S2	S2-S3	S3-S5	S4-MC	S5-DAM
	% contribution	% contribution	% contribution	% contribution	% contribution
1995	35.6%	43.8%	18.1%	1.8%	0.6%
1996	27.2%	41.8%	27.9%	2.2%	0.9%
VOLUME (m3)	22.5%	43.3%	31.5%	1.7%	1.0%

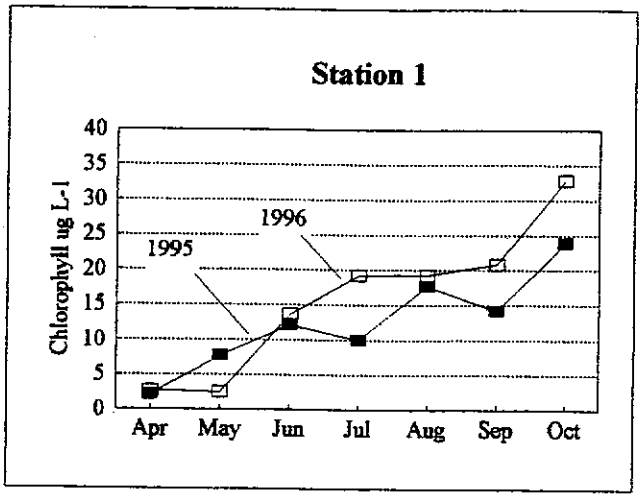

Herrington Lake
Dix R.
S5 (dam)
S4
S3
S2
S1
Danville
Clarks R.
Dix R.
Location
Kentucky
Lake sampling station
0 1 2 3 Miles
0 1 2 3 Kilometers
N

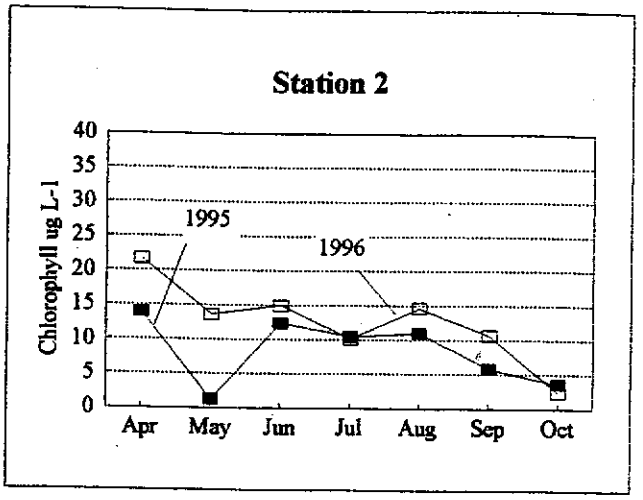

Precipitation (in)
12
10
8
6
4
2
0
Feb Apr Jun Aug Oct Feb Apr Jun Aug Oct
1995
1996

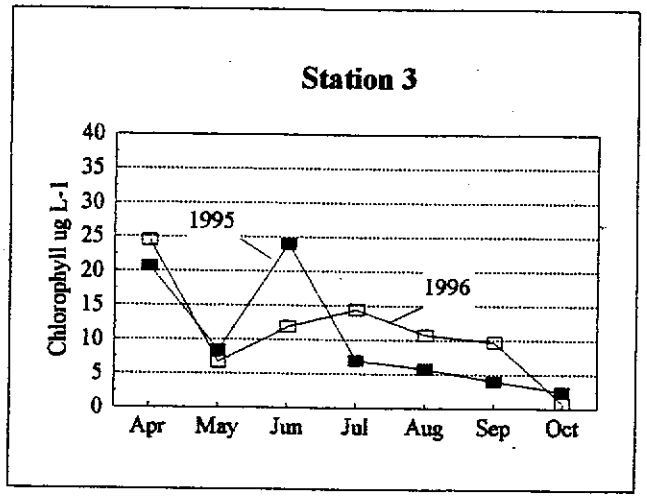

Discharge (m3 s-1)
1800
1500
1200
900
600
300
0
Feb Apr Jun Aug Oct Feb Apr Jun Aug Oct
1995
1996

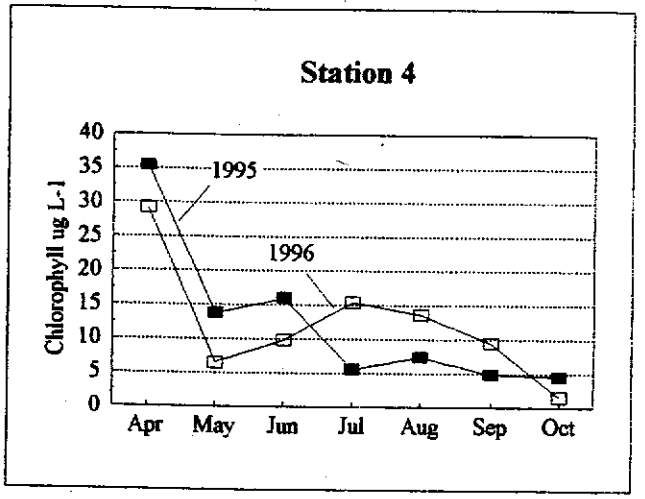

Station 1
Station 5
A
Coefficient m-1
6
5
4
3
2
1
0
Apr
Jun
Aug
Oct
1995
1996

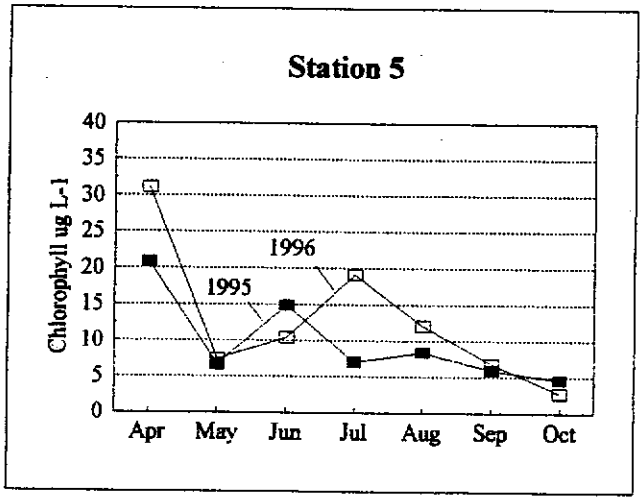

Station 5
epilimnion
hypolimnion
B
Temperature (C)
40
35
30
25
20
15
10
5
0
Apr
Jun
Aug
Oct
1995
1996

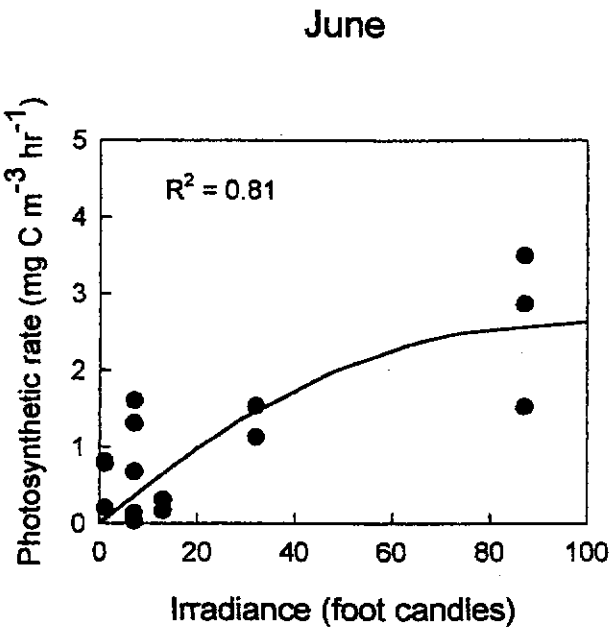

Station 1
Chlorophyll ug L-1
40
35
30
25
20
15
10
5
0
1995
1996
Apr
May
Jun
Jul
Aug
Sep
Oct

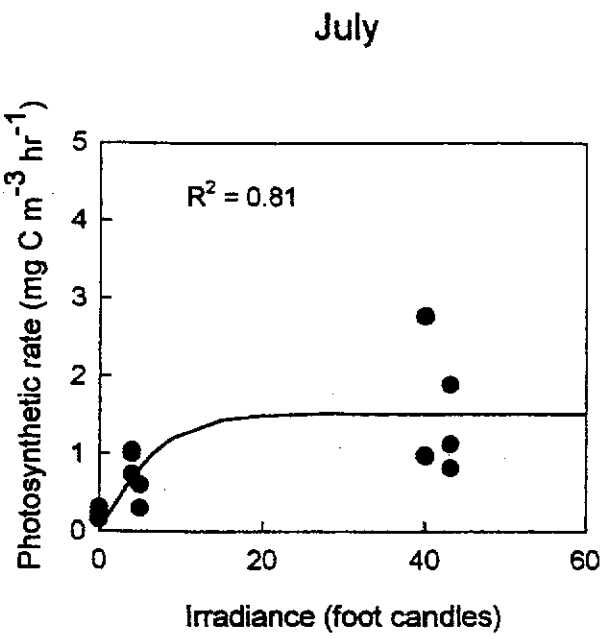

Station 2
Chlorophyll ug L-1
40
35
30
25
20
15
10
5
0
1995
1996
Apr
May
Jun
Jul
Aug
Sep
Oct

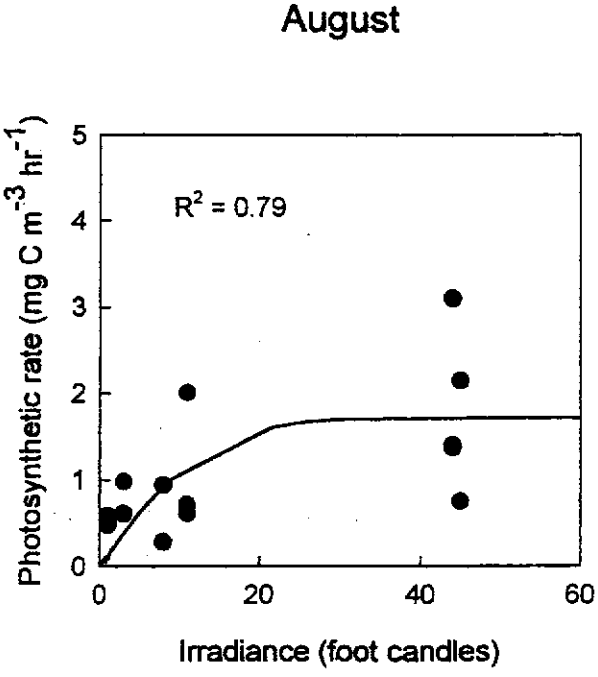

Station 3
Chlorophyll ug L-1
40
35
30
25
20
15
10
5
0
1995
1996
Apr
May
Jun
Jul
Aug
Sep
Oct

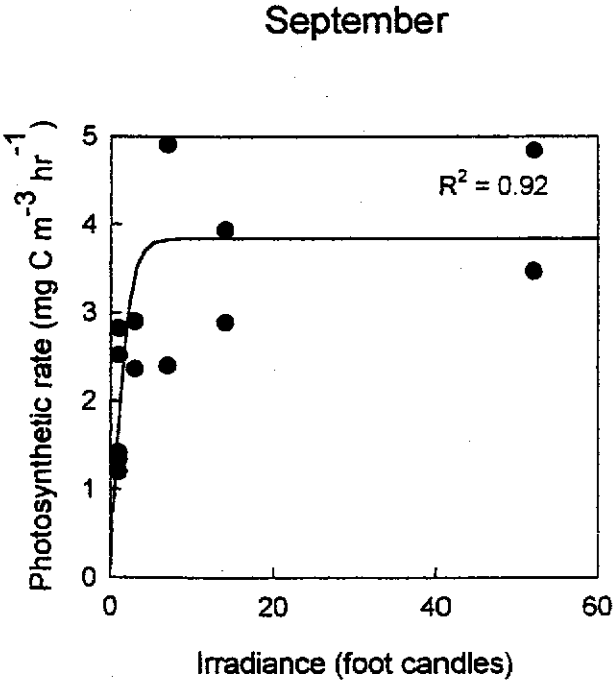

Station 4
Chlorophyll ug L-1
40
35
30
25
20
15
10
5
0
1995
1996
Apr
May
Jun
Jul
Aug
Sep
Oct

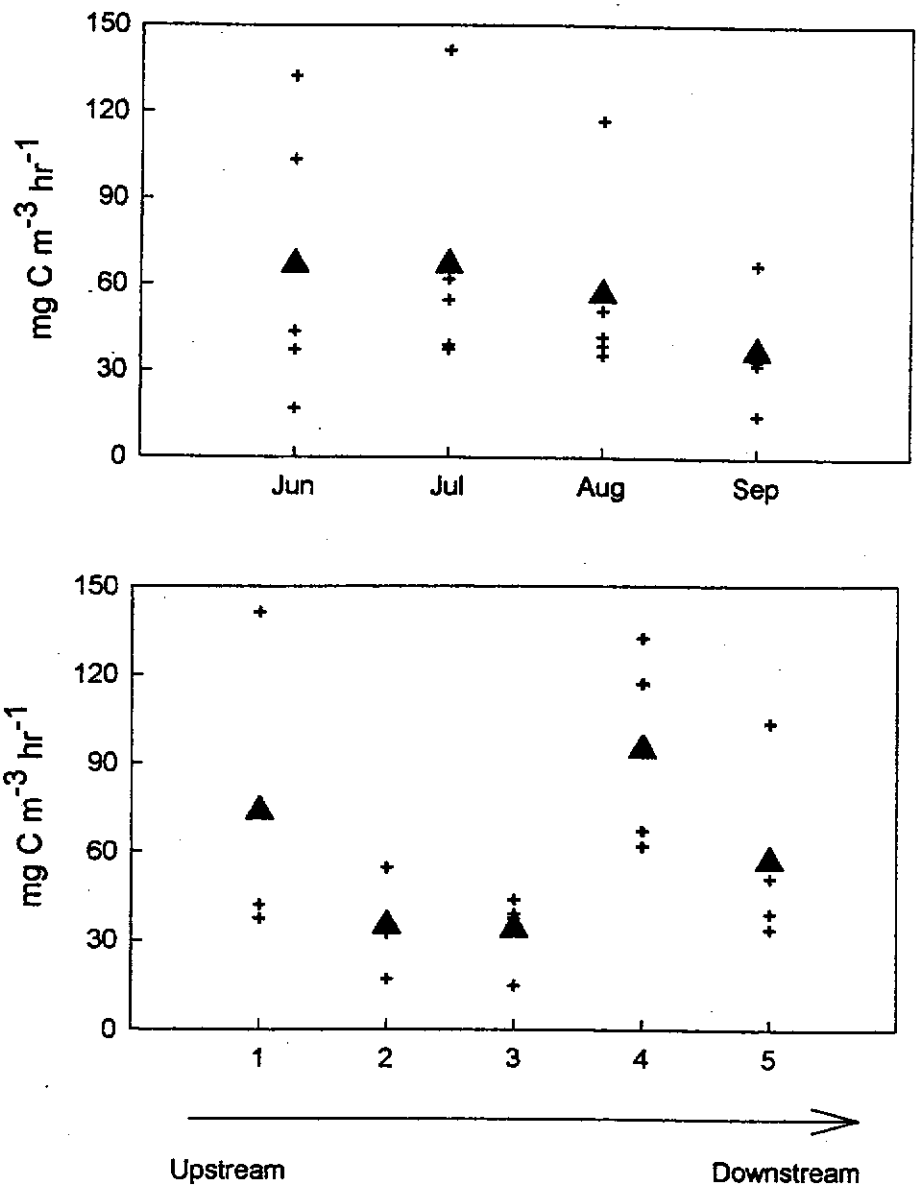

Station 5
Chlorophyll ug L-1
40
35
30
25
20
15
10
5
0
1996
1995
Apr
May
Jun
Jul
Aug
Sep
Oct

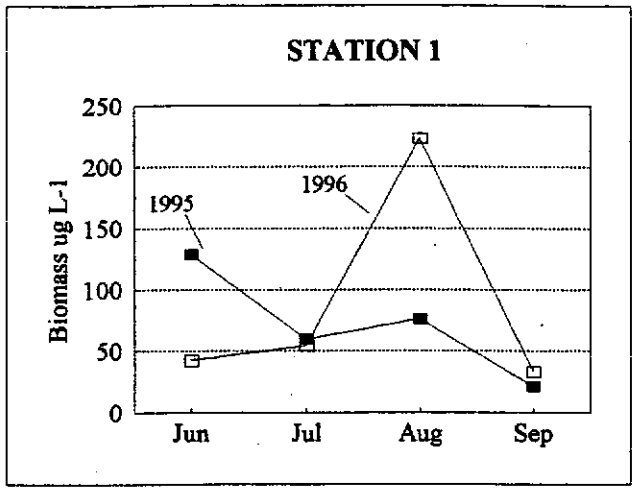

June
Photosynthetic rate (mg C m-3 hr-1)
R2 = 0.81
0
1
2
3
4
5
0
20
40
60
80
100
Irradiance (foot candles)

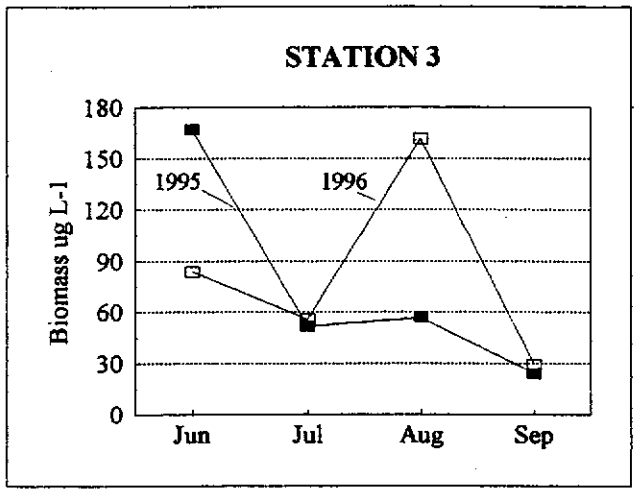

July
Photosynthetic rate (mg C m-3 hr-1)
R2 = 0.81
0
1
2
3
4
5
0
20
40
60
Irradiance (foot candles)

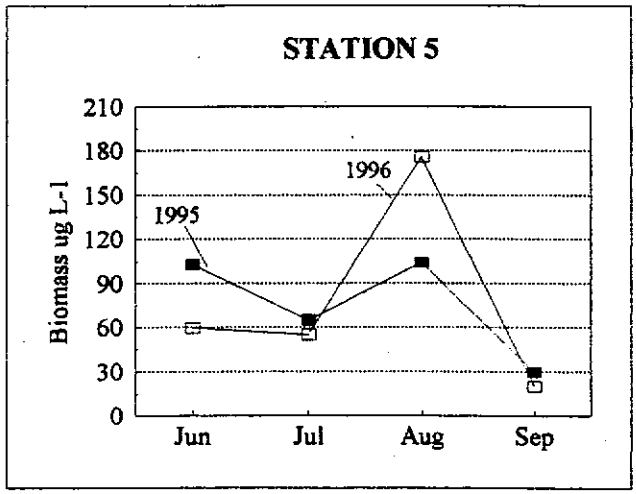

August
Photosynthetic rate (mg C m-3 hr-1)
R2 = 0.79
0
1
2
3
4
5
0
20
40
60
Irradiance (foot candles)

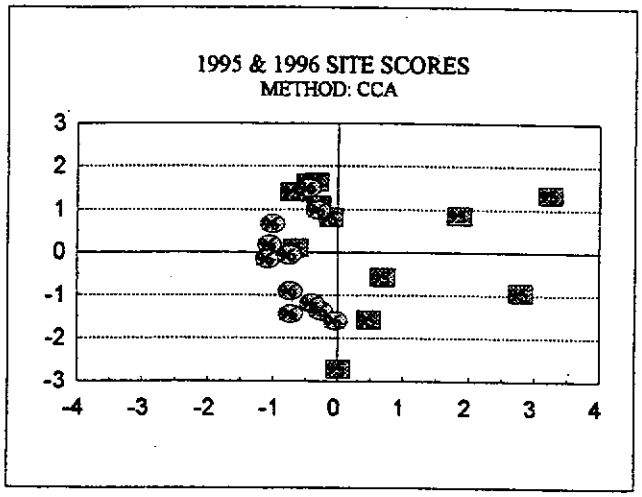

September
Photosynthetic rate (mg C m-3 hr-1)
R2 = 0.92
0
1
2
3
4
5
0
20
40
60
Irradiance (foot candles)

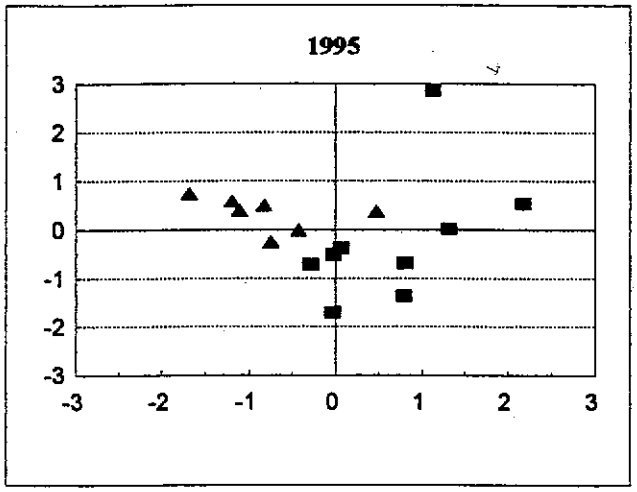

150
120
90
60
30
0
mg C m-3 hr-1
Jun
Jul
Aug
Sep
150
120
90
60
30
0
mg C m-3 hr-1
1
2
3
4
5
Upstream
Downstream

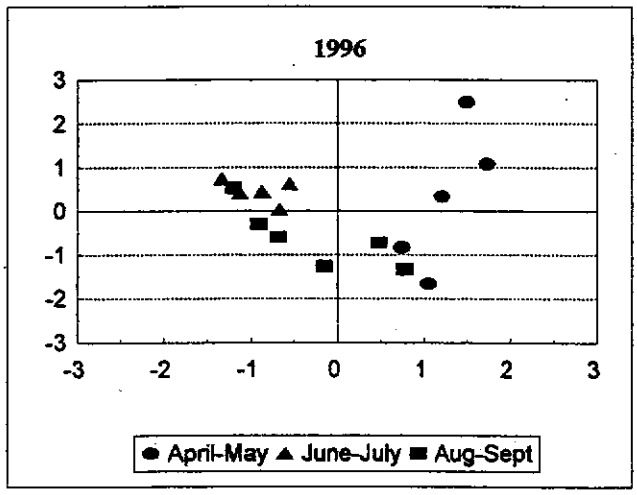

STATION 1
Biomass ug L-1
250
200
150
100
50
0
1995
1996
Jun
Jul
Aug
Sep

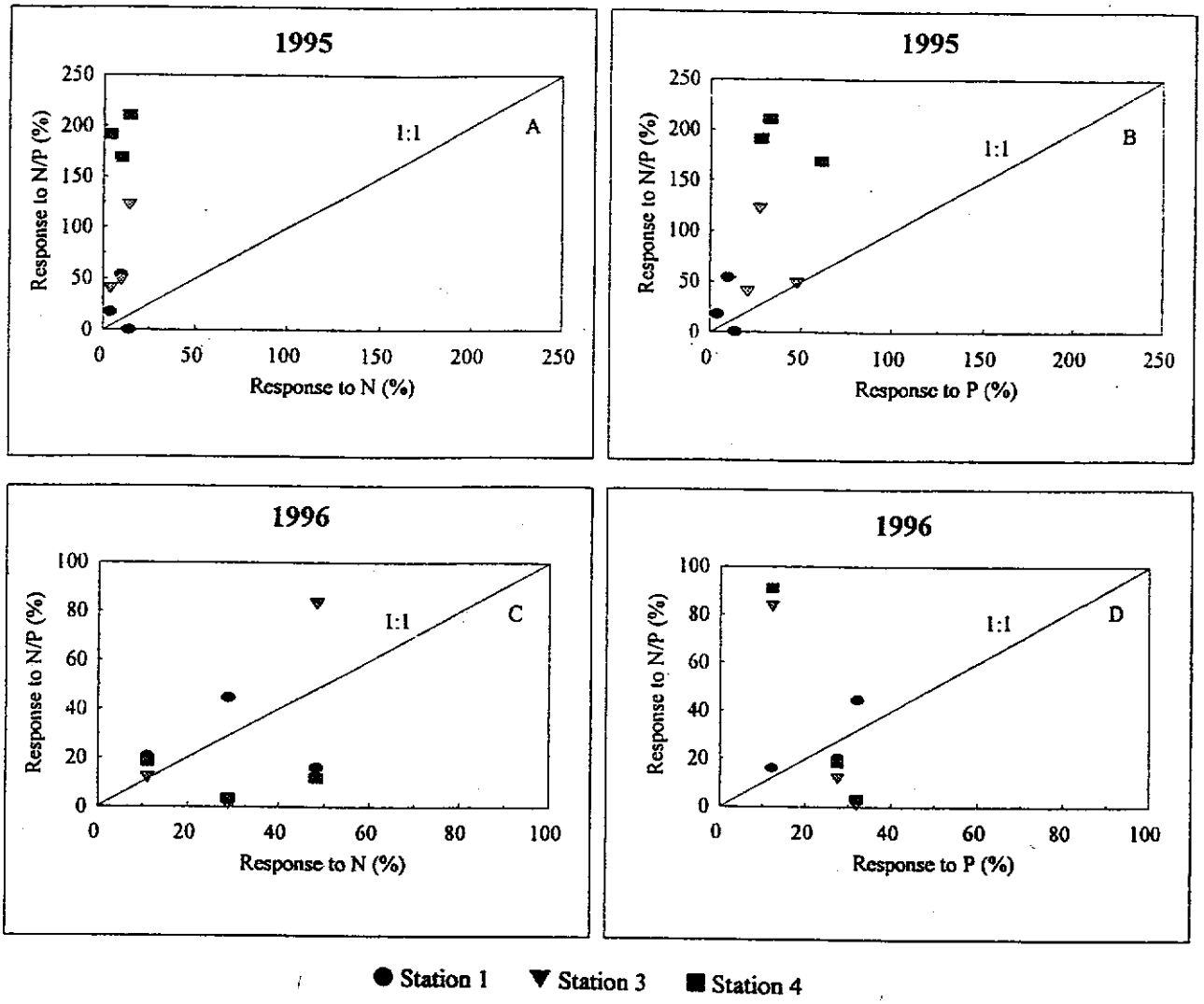

STATION 3
Biomass ug L-1
180
150
120
90
60
30
0
1995
1996
Jun
Jul
Aug
Sep

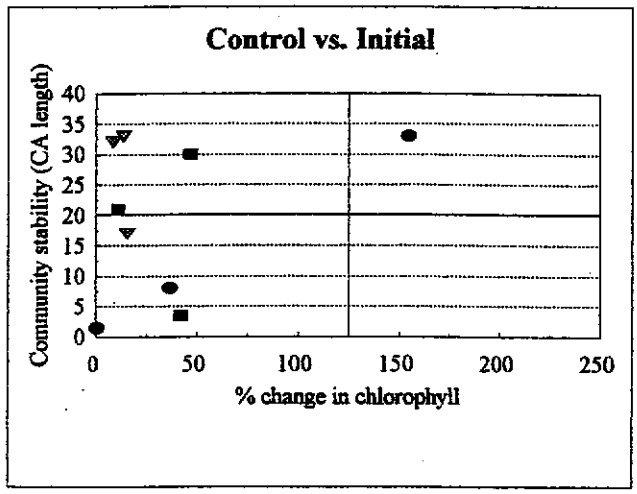

STATION 5
Biomass ug L-1
210
180
150
120
90
60
30
0
1995
1996
Jun
Jul
Aug
Sep

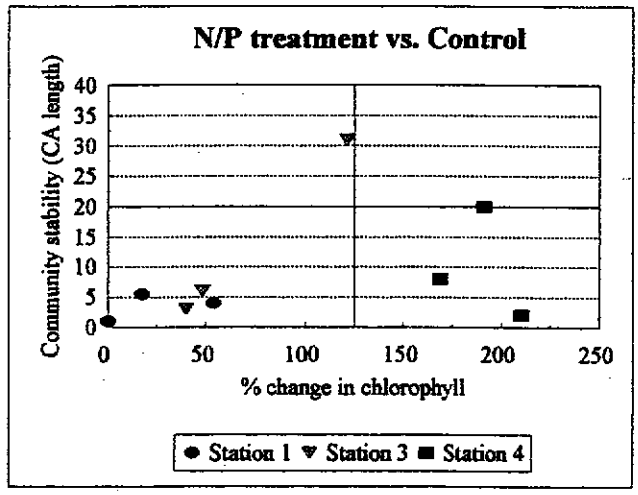

1995 & 1996 SITE SCORES
METHOD: CCA
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
4


1995
3
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3


1996
3
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3
April-May
June-July
Aug-Sept


1995
Response to N/P (%)
Response to N (%)
1:1
A
1995
Response to N/P (%)
Response to P (%)
1:1
B
1996
Response to N/P (%)
Response to N (%)
1:1
C
1996
Response to N/P (%)
Response to P (%)
1:1
D
Station 1
Station 3
Station 4


Control vs. Initial
Community stability (CA length)
40
35
30
25
20
15
10
5
0
0
50
100
150
200
250
% change in chlorophyll


N/P treatment vs. Control
Community stability (CA length)
40
35
30
25
20
15
10
5
0
0
50
100
150
200
250
% change in chlorophyll
Station 1
Station 3
Station 4

PERSONNEL WHO WORKED ON THE PROJECT

Project No. ________

Principal Investigator	Academic Area	Percent Time on Project	Year	Summer
Bukaveckas	Biology		1995	1 month

* *

Student Research Assistants	Academic Area	Undergraduates	M.S.	Ph.D.	Postdoc.	Support by Institute Yes	No
Angie Crain	Biology		XX			X	
David Loy	Biology	XX				X	
Don Metzmeier	Biology	XX				X	
Rob McCandless	Biology	XX				X	
Darryl Colebank	Biology	XX				X	
Hudson Lindenberger	Biol.	XX				X	

PUBLICATIONS AND PRESENTATIONS

Crain, A.S., 1998. Hydrologic constraints on phytoplankton production and nutrient assimilation in a eutrophic Kentucky reservoir. (in prep), "MS thesis", Biology Department, University of Louisville, Louisville, Kentucky, 36p.

Crain, A.S., P.A. Bukaveckas, and G.L. Jarrett. 1997. "Development and calibration of a water-quality model for Herrington Lake" *in* Waterworks Newsletter, Kentucky Water Resources Research Institute, University of Kentucky, v.3, no.1, 4p.

Abstract/poster; Hydrologic constraints on nutrient assimilation and phytoplankton production in a eutrophic Kentucky reservoir. 16^{h} Annual Midwest Ecology and Evolution Conference. April 4-6, 1997.

Abstract/presentation; Hydrologic constraints on nutrient assimilation and phytoplankton production in Herrington Lake, Kentucky. Kentucky Water Resources Annual Symposium, February 12, 1997.

Abstract/presentation; Hydrologic constraints on nutrient assimilation and phytoplankton production in a eutrophic Kentucky reservoir; 16th International Symposium of the North American Lake Management Society, November 13-16, 1996.

Abstract/presentation;. Nutrient availability for phytoplankton production in a eutrophic Kentucky lake. 15th Annual Midwest Ecology and Evolution Conference. April 12-14, 1996.