

Phytoplankton primary production and photosynthetic parameters in reservoirs along a gradient of watershed land use

Lesley B. Knoll¹

Department of Zoology, Miami University, Oxford, Ohio 45056; Department of Botany, Miami University, Oxford, Ohio 45056

Michael J. Vanni

Department of Zoology, Miami University, Oxford, Ohio 45056

William H. Renwick

Department of Geography, Miami University, Oxford, Ohio 45056

Abstract

We investigated how watershed land use (a gradient of agricultural vs. forested land) relates to phytoplankton primary production (PPr) and photosynthetic parameters in 12 reservoirs in Ohio and examined spatial variation in these parameters. Shallow sites near stream inflows had higher light attenuation, total phosphorus (TP), chlorophyll, nonvolatile suspended solids (NVSS), light-saturated photosynthesis (P_m^B), and volumetric PPr than deeper sites near dam outflows, but areal PPr and the initial slope of the photosynthesis–irradiance curve (α^B) were not significantly different between sites. Mean mixed layer irradiance and the severity of light limitation did not differ between sites because shallower depths compensated for higher light attenuation at inflow sites. Watershed land use (percent agriculture) was only weakly (but significantly) related to mean annual PPr, TP, and chlorophyll, but there was a well-defined upper limit to the effect of land use on all three of these parameters. Multiple regression showed that inclusion of additional watershed factors (the ratio of watershed land area to reservoir volume and the ratio of cropland area to number of livestock) greatly increased the variance explained compared to land use alone. TP and chlorophyll were highly correlated with each other and with PPr. Comparison of our TP–chlorophyll, TP–PPr, and chlorophyll–PPr regressions with those of other studies suggests that reservoirs have lower PPr per unit TP than natural lakes, probably because of lower light intensity and higher concentrations of nonalgal P in reservoirs.

Watershed land use affects the amount of nutrients exported into lakes and reservoirs via stream inflows. Watersheds dominated by agricultural or urban lands typically export nutrients at higher rates than undisturbed watersheds (Vitousek et al. 1979; Beaulac and Reckhow 1982; Puckett 1995). However, considerable variation exists in the relationship between land use and watershed nutrient export (Mueller et al. 1995; Puckett 1995), as well as in the relationship between nutrient loading rate and eutrophication indicators such as nutrient concentrations, algal biomass, and algal productivity (Carpenter et al. 1998; Correll 1998; Smith 1998). Export of sediments from watersheds is also a function of land use. In particular, agricultural watersheds export considerable quantities of sediment as well as nutri-

ents. Loading of sediments can reduce algal productivity by decreasing light intensity (Hoyer and Jones 1983; Kimmel et al. 1990; Knowlton and Jones 1995).

Quantitative relationships between watershed land use and indicators of lake eutrophication are exceedingly scarce (e.g., Field et al. 1996; Siver et al. 1999; Arbuckle and Downing 2001; Prepas et al. 2001). This is surprising, considering that land use patterns are changing rapidly in many parts of the world (Sala et al. 2000) and that lakes integrate watershed processes. To our knowledge, no multiple-lake studies have explicitly quantified the relationship between land use and phytoplankton primary productivity. In addition, we know of no studies explicitly relating land use to any eutrophication indicators in reservoirs. In this paper, we explore how agricultural land use in watersheds is related to phytoplankton primary productivity, photosynthetic parameters, and associated eutrophication indicators in reservoirs.

Reservoirs can be especially influenced by inputs of nutrients and sediments because they have relatively large watersheds compared to natural lakes (Kimmel et al. 1990; Wetzel 1990). In addition, many reservoirs in the U.S. Midwest reside in agricultural watersheds and likely experience high rates of sediment and nutrient inputs (Kimmel et al. 1990; Knowlton and Jones 1995; Knowlton and Jones 2000). Because of the influence of stream inflows, reservoirs often exhibit pronounced longitudinal gradients in light and nutrients, which can result in gradients in the physiological pro-

¹ To whom correspondence should be addressed. Present address: Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824 (knollle1@msu.edu).

Acknowledgments

We thank K. Arend, H. Boone, A. Bowling, B. Bunnell, A. Christian, J. Headworth, E. Johannes, J. Pyzoha, and L. Theis for assistance in the field and lab; E. Fee for advice on estimating primary production; S. Harper for help with primary production computer programs; and A. Bowling, C. Glaholt, S. Harper, M. Horgan, K. Sigler, and two anonymous reviewers for comments on an earlier draft of the manuscript. Funding was provided by NSF grant DEB 9726877 to M.J.V. and W.H.R. and a Miami University Undergraduate Research Grant to L.B.K.

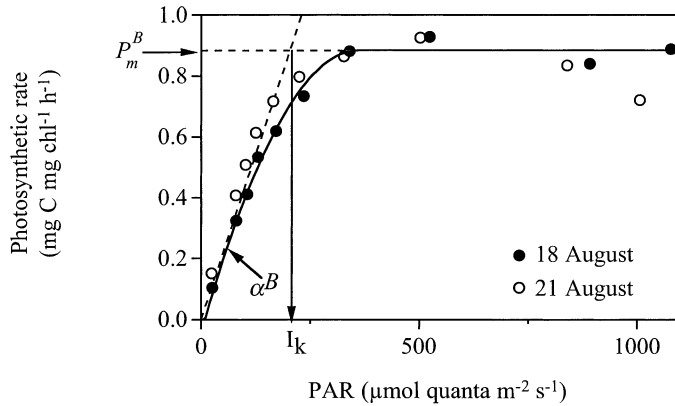


Fig. 1. Representation of photosynthetic parameters and data from a test of holding time on photosynthetic rate using Acton Lake phytoplankton.

cesses underlying photosynthesis and, hence, primary production rates (Kimmel et al. 1990). α^B , the slope of the light-limited part of the photosynthesis–irradiance (P-I) curve, and P_m^B , the light-saturated photosynthesis rate (Fig. 1) are parameters often used to characterize phytoplankton photosynthetic physiology (Fee et al. 1992). α^B and P_m^B can vary with lake trophic status (Fee et al. 1987) and along gradients of light and nutrients. However, we know of no studies that have explicitly investigated the relationships between land use and these photosynthetic parameters.

Here, we examine how agricultural land use in watersheds affects primary productivity and photosynthetic parameters among and within 12 reservoirs and relate these variables to light and nutrient concentrations. We sampled sites near stream inflows, where nutrient and sediment inputs are hypothesized to be relatively high, and near the dam where these inputs are hypothesized to have fewer effects. We hypothesize that as watersheds become increasingly dominated by agriculture, primary production, α^B , and P_m^B will increase because of increased nutrient inputs. Furthermore, we hy-

pothesize that both photosynthetic parameters will be higher at inflow sites than at dam sites; P_m^B because nutrient availability is higher at inflow sites and α^B because phytoplankton at inflow sites should be better adapted to low light conditions.

Methods

Study sites—We quantified primary productivity, photosynthetic parameters (α^B and P_m^B), and potential predictor variables (watershed parameters, nutrients, light intensity, and the concentration of nonvolatile suspended solids) in 12 Ohio reservoirs between April and October 1998–2000. These reservoirs span a wide gradient of watershed land use, total phosphorus (TP), and chlorophyll (Table 1). In 1998, we sampled all 12 reservoirs (except Piedmont) at least twice, whereas in 1999 and 2000, we sampled six reservoirs (Table 1). With a few exceptions (Table 1), we sampled each reservoir at a site near stream inflows and a site near the outflow (dam). “Inflow” sites were usually shallow and well-mixed, and the euphotic zone usually encompassed the entire water column. “Outflow” sites were located at the deepest area of a lake, near the dam, and usually were thermally and chemically stratified.

Land use—Land use data were obtained from the Ohio Department of Natural Resources Geographic Information Management Systems database (www.dnr.state.oh.us/gims). Land use data were generated in 1994 from thematic mapper imagery with a pixel size of 30 × 30 m.

Sampling—Integrated water samples taken from the euphotic zone (depths where photosynthetically available radiation [PAR] ≥ 1% of surface intensity) using a piece of weighted tygon tubing were used for primary production (PPr) and chemical analyses. We also collected water for chlorophyll analyses at 1-m intervals using a Van-Dorn sampler. PAR was measured at 0.5- or 1.0-m intervals with a

Table 1. Characteristics of study lakes and their watersheds and the number of times lakes were sampled for primary production, photosynthetic parameters, and potential predictor variables. Total P and chlorophyll values represent simple means of all dates sampled during the 3 yr.

Lake	Surface area (ha)	Mean depth (m)	Total P ($\mu\text{g L}^{-1}$)	Chlorophyll ($\mu\text{g L}^{-1}$)	Watershed area (km ²)	Watershed land use (% of watershed area)			No. of dates sampled (1998, 1999, 2000)
						Agriculture	Forest	Other	
Acton (A)	232	3.9	129.9	56.3	257	88.8	9.3	2.0	7,8,10
Alum Creek (M)	935	7.8	27.6	11.5	321	72.4	21.8	5.9	2,2,1
Berlin (E)	1560	4.5	25.9	4.9	640	53.5	38.9	7.6	2,*0,0
Burr Oak (B)	266	4.5	43.0	10.8	86	13.6	80.9	5.6	3,*5,7
Caesar Creek (C)	719	11.0	48.9	10.0	608	84.3	12.5	3.3	4,0,0
Delaware (D)	453	3.5	91.7	31.8	1060	84.2	13.5	2.2	3,2,1
Knox (K)	195	2.1	77.6	25.6	80	67.3	28.0	4.6	2,*0,0
La Due (L)	566	3.7	50.4	15.9	93	35.2	47.1	17.7	2,2,1
Piedmont (I)	982	4.5	49.8	12.2	222	36.7	56.2	7.1	1,0,0
Pleasant Hill (P)	312	4.8	85.5	32.9	512	50.8	44.8	4.4	2,3,7
Stonelick (S)	58	2.1	153.1	14.2	60	78.4	19.4	2.2	4,0,0
Tappan (T)	964	3.3	59.1	20.8	184	28.6	63.7	7.7	2,0,0

* On all dates in Berlin, one date in Burr oak, and one date in Knox, only the outflow site was sampled.

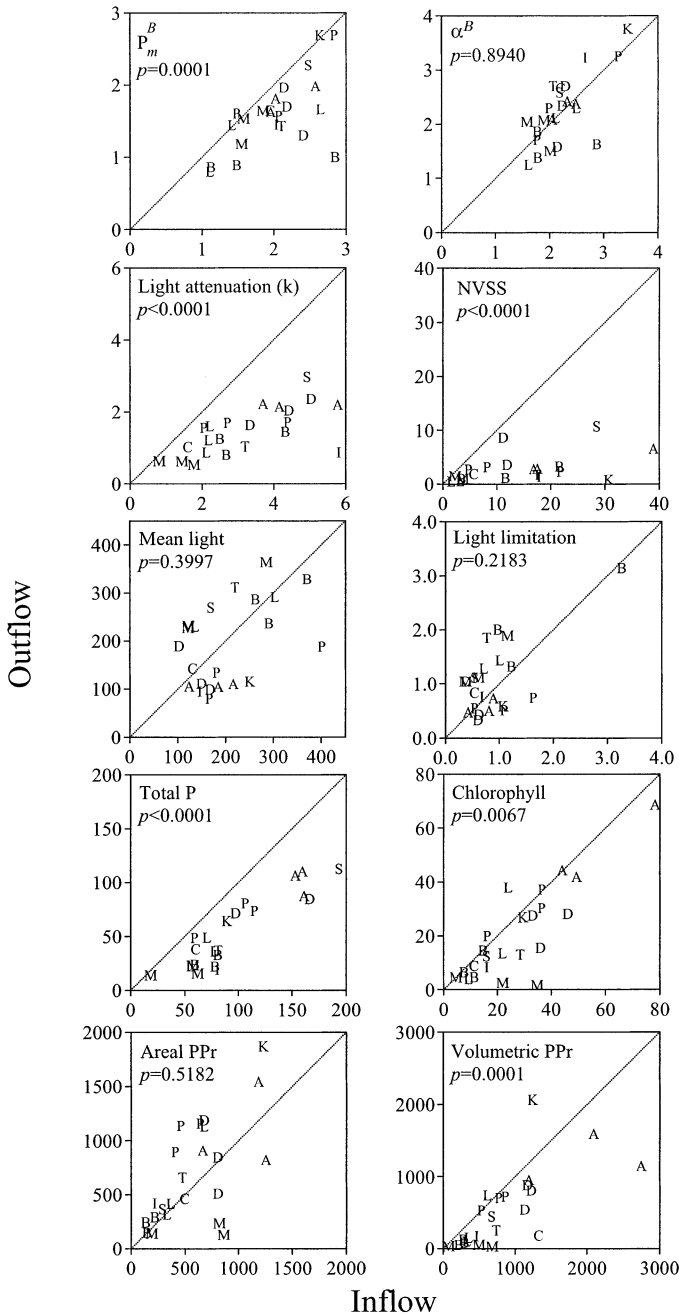


Fig. 2. Spatial variation in primary production, photosynthetic parameters, and associated variables. Each point represents a mean of all observations for a particular year. Dashed lines indicate 1:1 relationships. Lake codes are given in Table 1. Units: P_m^B , mg C (mg Chl) $^{-1}$ h $^{-1}$; α^B , mg C (mg Chl) $^{-1}$ (mol PAR) $^{-1}$ m $^{-2}$; light attenuation, m $^{-1}$; NVSS, mg L $^{-1}$; mean light in mixed layer, μ mol photons m $^{-2}$ s $^{-1}$; light limitation, I_{mix}/I_k ; total P, μ g P L $^{-1}$; chlorophyll, μ g chlorophyll L $^{-1}$; areal PPr, mg C m $^{-2}$ d $^{-1}$; volumetric PPr, mg C m $^{-3}$ d $^{-1}$, averaged over the euphotic zone.

LiCor model Li-189 quantum photometer radiometer equipped with a spherical underwater sensor and used to determine the light attenuation coefficient (k) following the relationship $k = \ln(I_0/I_z)/z$, where I_0 and I_z are PAR at the lake surface and at depth z . Mean PAR in the mixed layer

(I_{mix} ; μ mol photons m $^{-2}$ s $^{-1}$), using simulated cloud-free solar data, was determined with the computer program DTO-TAL (Fee 1990). We inferred that phytoplankton were light limited when $I_{\text{mix}}/I_k < 1$, where $I_k = P_m^B/\alpha^B$ (Fig. 1). Dissolved oxygen and temperature, used to determine mixed layer depths, were measured at 0.5- or 1.0-m intervals using a YSI Model 58 meter.

Primary production—All of our PPr data represent simulated cloud-free rates (Fee et al. 1987, 1992). Integrated samples for PPr analyses were stored in 2-liter amber nalgene bottles (to block light; Fee et al. 1989, 1992) at euphotic zone temperatures until PPr estimates were made. In the laboratory, samples were transferred to a 1-liter dark glass bottle, and NaH 14 CO $_3$ (2.5–10 μ Ci) was added. After thorough mixing, water was allocated to 12 66-ml pyrex glass bottles and exposed to a range of light intensities for 1–3 h in a clear Plexiglas box illuminated with a 1,000 W Sylvania Metalarc metal halide bulb at temperatures within 2°C of euphotic zone temperatures (Fee et al. 1989, 1992). To estimate 14 C available to phytoplankton, four 0.5-ml samples from the dark glass bottle and four samples from incubated bottles were transferred to scintillation vials containing 9.5 ml Scintiverse BD fluor. After incubation, water from each bottle was filtered through a Gelman A/E glass fiber filter to collect phytoplankton. Filters were placed in scintillation vials in a drying oven at 60°C overnight, and 10 ml fluor was added to each vial. Radioactivity was assayed with a Beckman LS-1800 scintillation counter and corrected for quenching with a cpm-H number relationship (e.g., Cole et al. 1992). Except for the first few experiments in 1998, we used 10 light intensities and two dark bottles to generate a P-I curve for each estimate of primary production (i.e., for each reservoir site on each date). 14 C uptake rates in dark bottles were subtracted from those in light bottles to correct for nonphotosynthetic uptake. On average, 14 C uptake rate in dark bottles was 6.4% that of light-saturated uptake rates (SE = 1.1%).

We attempted to measure PPr as quickly as possible after sample collection. However, lengthy travel times to many lakes precluded PPr measurements on the same day on which samples were collected. Twenty-seven percent of PPr measurements were made on the same day of sample collection, whereas 54, 16, and 3% were made 1, 2, or 3 d after collection. We verified that holding samples in the 2-liter dark nalgene bottles for up to 3 d does not affect PPr using water from Acton Lake (which had the highest mean phytoplankton biomass; Table 1) collected on 18 August 1998. We measured PPr (as well as chlorophyll and DIC) on that day and again on 21 August 1998. In the intervening 3 d, water was held in the dark bottle at euphotic zone temperature. We found that the P-I curves were nearly identical whether PPr was quantified on the day of collection or 3 d later (Fig. 1). Therefore, we are confident that our estimates of photosynthesis were not biased by the holding period.

The photosynthetic parameters α^B and P_m^B were estimated from P-I curves and chlorophyll concentrations using the computer program PPARMS (Fee 1990). Simulated cloud-free PPr was calculated for a single date and seasonally using the computer programs DPHOTO and YPHOTO, respec-

tively (Fee 1990). Inflow and outflow sites were run separately. For depths common to both inflow and outflow sites, depth-specific photosynthetic rates were averaged for the two sites and then multiplied by the lake-wide volume of that depth stratum to give productivity in each stratum. Strata were summed to give whole-lake productivity. In order to obtain areal productivity ($\text{mg C m}^{-2} \text{d}^{-1}$), whole-lake productivity was divided by the surface area of the lake. Whole-lake volumetric productivity within the euphotic zone (e.g., Smith 1979) was obtained by dividing areal productivity by the euphotic zone depth.

Analytical procedures—Chemical analyses included chlorophyll, dissolved inorganic carbon (DIC), TP, and nonvolatile suspended solids (NVSS). Chlorophyll was quantified on integrated samples (to estimate chlorophyll-specific photosynthetic rates from our incubations) and on depth-specific samples (used to generate water column productivity). Other analyses were conducted only on integrated samples. For chlorophyll, samples were filtered onto a Gelman A/E glass fiber filter, frozen, extracted with acetone, and quantified using a Turner model TD-700 fluorometer calibrated with commercial standards dissolved in acetone. DIC available for photosynthesis was quantified using gran alkalinity titrations. NVSS concentrations were quantified because light attenuation in reservoirs is often due to suspended inorganic particles (Kimmel et al. 1990; Knowlton and Jones 2000). To quantify NVSS concentrations, we filtered water through pre-ashed, preweighed Gelman A/E filters. Filters were then dried and reweighed to obtain total suspended solids, then ashed and reweighed to obtain NVSS (Knowlton and Jones 2000). Samples collected for TP analyses were placed in translucent nalgene bottles, then frozen (1998) or acidified (1999 and 2000) until analysis. TP was determined with the molybdenum blue technique following potassium persulfate digestion. In 1998, TP analyses were done manually, whereas in 1999 and 2000, analyses were conducted with a Lachat FIA+ QuikChem 8000 series autoanalyzer.

Statistical analyses—Because lakes were sampled at variable frequencies, we standardized data as simple means for each variable for each year to facilitate statistical analyses. This procedure helps equalize the contribution of each lake and reduces problems of pseudoreplication (Hurlbert 1984) associated with having several samples from the same lake within a single growing season.

To evaluate differences between inflow and outflow sites in primary production, photosynthetic parameters, and potential predictor variables, we conducted paired *t*-tests on annual means from the two sites. We conducted these analyses on log-transformed data to stabilize variances, but we show untransformed data in graphics to facilitate presentation of spatial trends.

To evaluate the extent to which PPr and photosynthetic parameters can be predicted by watershed land use (percent agricultural land), TP, and chlorophyll, we performed simple linear regression analyses of these predictor variables with PPr, α^B , and P_m^B as dependent variables, using annual means as observations. We performed regressions using lakewide data as well as site-specific data. However, lakewide regres-

sions involving α^B and P_m^B were treated differently from those involving other dependent variables. For regressions in which chlorophyll and TP were dependent variables, lakewide values were obtained on each date as the simple mean of inflow and outflow data. Annual means of these lakewide values were then used in lakewide regressions. This seemed reasonable given that TP and chlorophyll are mass quantities for which lakewide averages have inherent meaning. For α^B and P_m^B , however, the mean of two spatially distinct values has little meaning. Therefore, we used both inflow and outflow data together for lakewide regressions. For lakewide and site-specific regressions, we used the arcsine-square root transformation on percent land use and the logarithmic transformation on other variables, but we show untransformed data in graphics to facilitate visual depiction of relationships.

Theoretical principles suggest that some ecological relationships can display “triangular” or “wedge-shaped” distributions rather than linear or log-linear patterns. In this case, the scatter of points in a bivariate plot is distributed in the shape of a triangle lying beneath an upper bound (Blackburn et al. 1992; Goldberg and Scheiner 1993; Kaiser et al. 1994). For example, it has been argued that the relationship between a potential limiting nutrient and algal biomass (e.g., TP and chlorophyll) should be triangular because the limiting factor sets the upper bound of algal biomass, but other factors keep biomass at lower levels (Kaiser et al. 1994). Inspection of our plots of land use against TP, chlorophyll, and PPr strongly suggested triangular distributions in all three cases, so we conducted additional analyses to quantify the nature of these relationships following procedures outlined by Blackburn et al. (1992). To do so, we divided the predictor variable (percent agricultural land, after arcsine-square root transformation) into intervals of 10% and obtained the maximum value of the (log-transformed) dependent variable for each interval. These maxima were then regressed against percent agricultural land. This procedure resulted in six intervals, which falls within the range suggested by Blackburn et al. (1992).

We also employed stepwise multiple regression using additional watershed features to predict TP, chlorophyll, and PPr. Thus, in addition to percent agricultural land, we used the ratio of watershed land area to lake volume (a presumed index of relative watershed influence) and the ratio of cropland area to the number of livestock animals in the watershed. The latter ratio is an index of farming practice that is positively correlated with lake N:P ratios in Midwestern landscapes, presumably because fertilizers have a high N:P, whereas animal wastes have a low N:P (Arbuckle and Downing 2001). Data on cropland area and livestock were not available on a watershed-specific basis, so we used countywide data for 1998 and 1999 from the U.S. Department of Agriculture National Agricultural Statistics Service (<http://www.usda.gov/nass/>). For each county, we added the total land area (acres) planted with the five most common crops (corn, soybean, wheat, oats, and hay) and for livestock we added the total number of cattle, hogs, and sheep (poultry data were not available). The quotient of these two sums yielded a cropland:livestock ratio for each county. Some watersheds spanned parts of more than one county, in which case, we used a simple mean of the county-specific ratios to

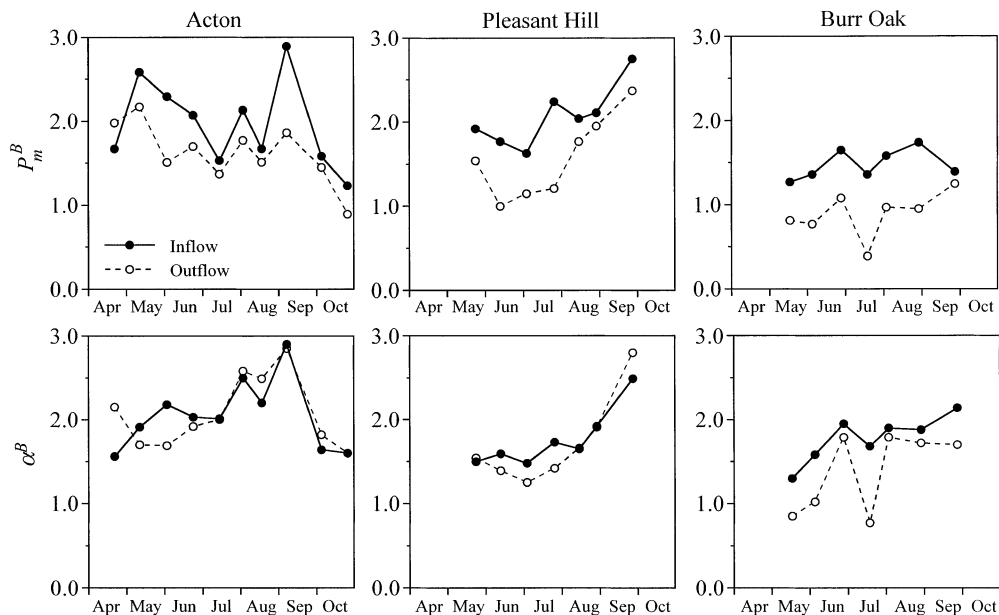


Fig. 3. Seasonal variation in photosynthetic parameters at inflow and outflow sites in Acton, Burr Oak, and Pleasant Hill Lakes in 2000.

obtain an overall ratio for that reservoir. The watershed area:lake volume and cropland:livestock ratios were log-transformed prior to regressions.

Results

Spatial trends—Light-saturated, chlorophyll-specific photosynthesis (P_m^B) was higher at inflow sites than at outflow sites, as hypothesized (Fig. 2). Contrary to our hypothesis, α^B did not significantly differ between sites, even though NVSS concentration and light attenuation (k) were much higher at inflow sites than at outflow sites (Fig. 2). Most likely, α^B was not significantly different between sites because mean light in the mixed layer (I_{mix}) was not significantly different between sites (Fig. 2). Further evidence that the light climate was similar at inflow and outflow sites derives from the light limitation index (I_{mix}/I_k), which also was not significantly different between sites (Fig. 2). TP and phytoplankton biomass (chlorophyll a) were significantly higher at inflow sites than at outflow sites (Fig. 2). Volumetric primary production ($\text{mg C m}^3 \text{ d}^{-1}$) was higher at inflow sites than outflow sites, whereas areal primary production ($\text{mg C m}^{-2} \text{ d}^{-1}$) did not differ significantly between sites (Fig. 2), apparently because the greater depth of the mixed layer at the outflow sites compensated for lower volumetric production rates.

Seasonal trends—Acton, Pleasant Hill, and Burr Oak were the only reservoirs sampled intensively enough to examine seasonal variation in α^B and P_m^B . Although Acton was sampled regularly throughout the season in all three years, Pleasant Hill and Burr Oak were sampled regularly only in 2000, so here we compare seasonal trends in photosynthetic parameters only for 2000. α^B tended to increase to a maximum in late summer, especially at Pleasant Hill (Fig. 3).

P_m^B was also highest in late summer in Pleasant Hill, but showed weak, if any, seasonal trends in the other two lakes. Spatial trends in these three lakes generally followed the same as those observed for the entire set of 12 lakes. Thus, on 23 of 24 dates for these three lakes, P_m^B was higher (often much higher) at the inflow site than at the outflow site (Fig. 3). α^B was consistently higher at the inflow site than at the outflow site in Burr Oak and was usually higher at the inflow site in Pleasant Hill, but in Acton Lake, there was no consistent difference between sites in α^B (Fig. 3).

Relationships of primary productivity and photosynthetic parameters to land use, TP, and chlorophyll—Using simple linear regression on transformed data, we found a weak but significant positive correlation between watershed land use (percent agricultural land in watershed) and PPr (Fig. 4; Table 2). When sites were considered separately, the correlation between land use and PPr was higher for inflow sites than when lakewide data were used, but the correlation with outflow site PPr was low and not significant (Table 2). Relationships between land use and photosynthetic parameters were generally weak (Table 2). In contrast to PPr, considering sites separately for photosynthetic parameters improved the relationship for outflow sites but not for inflow sites (Table 2). The land use–TP and land use–chlorophyll relationships were also relatively weak but significant (Fig. 4; Table 2). When considering sites separately, the relationship between land use and chlorophyll was stronger for inflow sites, but the relationship between land use and TP was stronger for the outflow sites (Table 2). Land use was negatively correlated with the light limitation index (I_{mix}/I_k); that is, as percent agriculture increased, phytoplankton became more light limited. Variance explained was greater for the land use–light limitation index than for any other regression involving land use as a predictor (Table 2). TP and chloro-

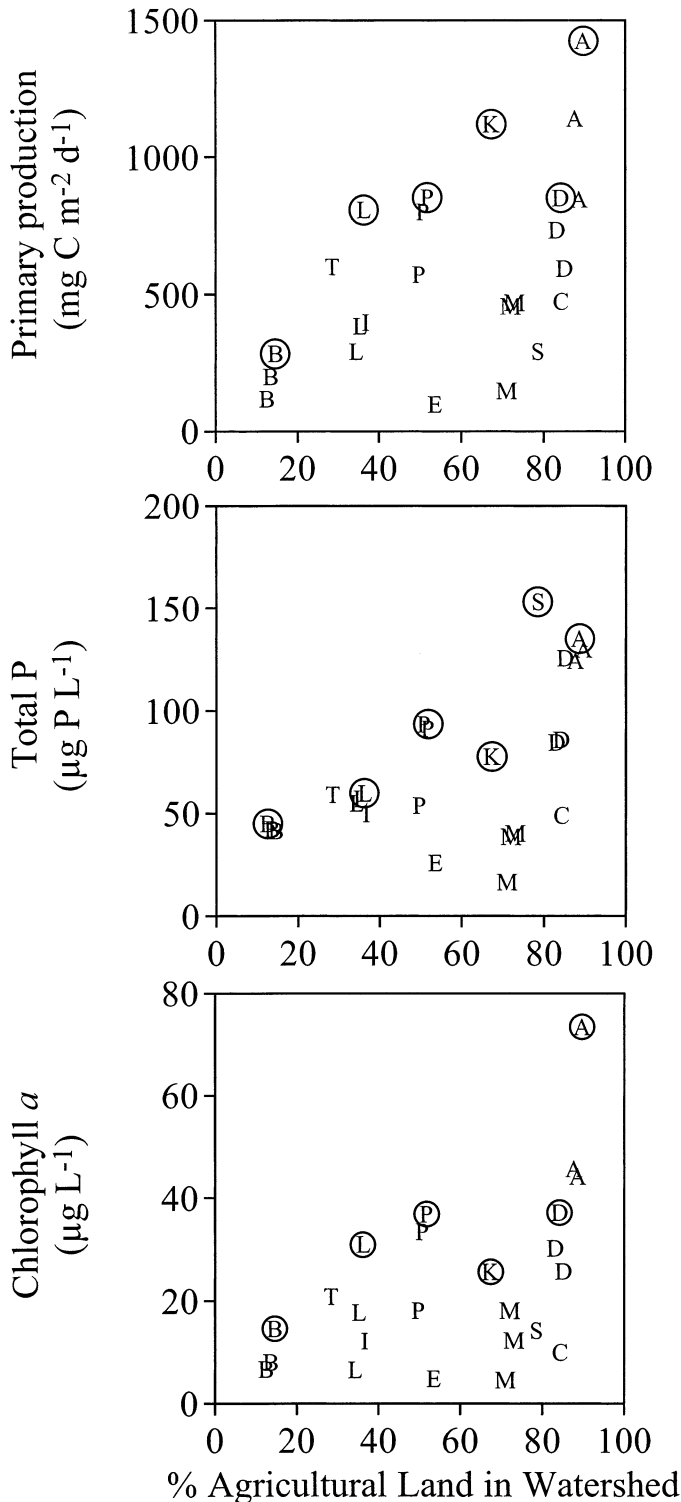


Fig. 4. Relationships between watershed land use (% agricultural land) and primary production, chlorophyll, and TP. Each point represents a mean of all observations in a particular year. Lake codes given in Table 1. Within a lake, land use (% agricultural land) values were offset by 1% from one another on the x-axis to facilitate data display if multiple years are presented. For lakes with multiple years, 1998, 1999, and 2000 are oriented from left to right. Circled points are those used in regressions using interval maxima.

phyll were poor predictors of α^B and somewhat better predictors of P_m^B ; analyses of data on a site-specific basis did not substantially improve relationships (Table 2).

Our data suggested that relationships between land use (percent agricultural land) and dependent variables (PPr, TP, and chlorophyll) might be triangular (Fig. 4), and more formal analyses supported this observation. Specifically, when land use data were divided into intervals and regressed against interval maxima, much higher correlations were observed than with simple linear regressions (Fig. 4). Thus, r^2 was 0.718, 0.852, and 0.676 for regressions of percent agricultural land versus interval-maximum PPr, TP, and chlorophyll, respectively.

Stepwise multiple regression using all 24 lake-years showed that inclusion of the watershed area:lake volume ratio, the cropland:livestock ratio, and percent agriculture increased the amount of variance explained compared to simple regression with only percent agricultural land (Table 3). For both areal PPr and chlorophyll, all three predictor variables entered into the models. For PPr, percent agricultural land entered first and explained the most variation, followed by the cropland: animal and watershed area:lake volume ratios, respectively; the order of entry was reversed for chlorophyll. For TP, only the watershed area:lake volume ratio entered into the stepwise regression model, and this explained 56% of the variation in TP. Note that for all three dependent variables, the variance explained using multiple regression on all data was less than that explained by simple regression on interval maxima.

TP and chlorophyll were highly correlated with each other, whether lakewide or site-specific data were used (Fig. 5; Table 2). TP and chlorophyll were more highly correlated at outflow sites than at inflow sites, whereas the lakewide correlation was intermediate in strength (Table 2). Both TP and chlorophyll were effective predictors of lakewide primary production, but the relationship was stronger with chlorophyll than with TP (Fig. 5).

Discussion

Spatial trends—As hypothesized, light-saturated, chlorophyll-specific photosynthesis (P_m^B) was higher at inflow sites than outflow sites, presumably because phosphorus supply is higher, as evidenced by spatial differences in TP (Fig. 2). Contrary to our hypothesis, α^B did not differ between inflow and outflow sites, corresponding to a lack of a spatial effect on mean light in the mixed layer. Thus, although light attenuation was much greater at inflow sites than outflow sites, the shallower depth of the mixed layer at inflow sites resulted in mean light intensities that were on average equal to those at outflow sites. Under these conditions, phytoplankton adaptation to low light should be similar at inflow and outflow sites. The severity of light limitation (I_{mix}/I_k) also was not significantly different between sites, which is also the expected result of the similar mean light climate at inflow and outflow sites. Studies in the tidal freshwater portion of the Hudson River (Cole et al. 1992) and in a New York reservoir (Melcher et al. 1997) found no significant spatial variation in α^B and P_m^B , even though spatial gradients were

Table 2. Statistics for regression relationships. "Land use" refers to the proportion of watershed land area comprised of agriculture. Land use proportion data were arcsine-square root transformed, and all other variables were log-transformed before regression analyses were conducted. Equations are for transformed data. For each regression, the independent variable is listed first. Units before transformations are the same as those in Fig. 1.

Regression	Lakewide			Inflow only			Outflow only		
	Equation	r ²	p	Equation	r ²	p	Equation	r ²	p
Land use vs. areal PPr	y=0.010x+2.193	0.257	0.0114	y=0.012x+2.076	0.495	0.0002	y=0.007x+2.341	0.106	0.1210
Land use vs. P _m ^B	y=0.004x+0.044	0.167	0.0044	y=0.002x+0.180	0.098	0.1466	y=0.005x-0.087	0.310	0.0047
Land use vs. α ^B	y=0.001x+0.265	0.037	0.1976	y=0.000x+0.318	0.007	0.7130	y=0.002x+0.212	0.072	0.2035
Land use vs. TP	y=0.007x+1.470	0.207	0.0253	y=0.004x+1.706	0.111	0.1289	y=0.009x+1.176	0.280	0.0078
Land use vs. chlorophyll	y=0.009x+0.801	0.212	0.0235	y=0.009x+0.905	0.255	0.0140	y=0.008x+0.728	0.090	0.1537
Land use vs. I _{mix} /I _k	y=-0.009x+0.362	0.374	<0.0001	y=-0.008x+0.282	0.350	0.0037	y=-0.010x+0.443	0.414	0.0012
TP vs. P _m ^B	y=0.274x-0.260	0.293	0.0001	y=0.160x-0.020	0.088	0.1797	y=0.266x-0.267	0.257	0.0114
TP vs. α ^B	y=0.094x+0.163	0.058	0.1054	y=0.051x+0.241	0.016	0.5735	y=0.138x+0.096	0.087	0.1614
Chlorophyll vs. P _m ^B	y=0.147x+0.047	0.145	0.0082	y=0.028x+0.253	0.005	0.7511	y=0.145x+0.006	0.172	0.0439
Chlorophyll vs. α ^B	y=0.066x+0.250	0.050	0.1325	y=-0.011x+0.354	0.001	0.8657	y=0.100x+0.211	0.101	0.1310
TP vs. chlorophyll	y=1.085x-0.698	0.638	<0.0001	y=0.942x-0.480	0.517	0.0002	y=1.258x-0.942	0.709	<0.0001

found for some parameters (e.g., chlorophyll, light, or nutrients).

Volumetric primary productivity was significantly higher at inflow sites than outflow sites, but no significant difference was found for areal productivity because greater mixed layer depth at outflow sites compensated for lower volumetric production rates. Several other parameters were consistently higher at inflow sites than at outflow sites, including light attenuation, NVSS, TP, and chlorophyll (Fig. 2). This spatial trend agrees with prior studies on reservoirs, which demonstrated well-defined horizontal gradients in light and nutrients (Kimmel et al. 1990). Thus, although the gradients we observed in physical and chemical variables thought to limit phytoplankton production are consistent with conceptual models for reservoirs, we found no spatial effect on areal PPr.

Seasonal trends—α^B increased from spring to summer in all three of our intensively studied reservoirs, whereas P_m^B increased from spring to summer in Pleasant Hill but not in the other two lakes (Fig. 3). Several studies have shown that α^B and P_m^B exhibit maximal values during mid- or late summer and lower values in winter and spring (Lastein and Gargas 1978; Williams 1978; Cole et al. 1992; Pierson et al. 1992). However, Fahnenstiel et al. (1989) and Makarewicz (1991) observed such seasonality in some years but not others, and Melcher et al. (1997) found no seasonality in these parameters in a reservoir. In addition, there appears to be considerable year-to-year variability in both photosynthetic parameters in lakes in which such variation has been assessed (e.g., Fahnenstiel et al. 1989; Makarewicz 1991; Fee et al. 1992).

Primary productivity in reservoirs and natural lakes—The relatively high concentration of NVSS in reservoirs could result in lower primary production than would be predicted based on phosphorus-PPr relationships developed for natural lakes, via two mechanisms (Walker 1984; Knowlton and Jones 2000). First, NVSS attenuates light, as mentioned above. Second, NVSS could also represent a significant source of nonalgal P. Thus, we could expect phytoplankton biomass and primary production to be lower in reservoirs than in natural lakes for a given TP concentration (Walker 1984). Indeed, using untransformed data, the slope of our TP-PPr regression (Fig. 5) was 3.80 (4.94 omitting Stonelick), whereas Smith (1979) reported a slope of 10.4 for a TP-PPr regression derived primarily from natural lakes. In addition, for the chlorophyll-PPr regression on untransformed data, our slope was 11.03 compared to a slope of 22.9 reported by Smith (1979) for primarily natural lakes. Few data exist on the dependence of PPr on TP or chlorophyll in other reservoirs. However, Jones and Knowlton (1993) present data on the relationship between chlorophyll and TP for 94 Missouri reservoirs. We compared our data to theirs (see table 2 in Jones and Knowlton 1993) using analysis of covariance (ANCOVA) on log-transformed data. We used the two data sets as categories, TP as a covariate, and chlorophyll as the dependent variable. The interaction term (data set × TP) was not significant (p = 0.6094), indicating that the slopes of the TP-chlorophyll relationships

Table 3. Results of stepwise multiple regressions relating land use and other watershed features to primary production, total P, and chlorophyll. Data were transformed prior to analyses using either the arcsine-square root (proportion agricultural land) or log (all other variables) transformation. Parameters are from regressions using transformed variables.

Step	Parameter	Estimate	SS	F	p	R ²
Dependent variable: areal primary production						
	Intercept	2.252				
1	Percent agricultural land	0.010	0.335	5.164	0.0342	0.257
2	Cropland: animals	-0.586	0.214	3.298	0.0844	0.372
3	Watershed area:lake volume	0.192	0.115	1.765	0.1990	0.423
Dependent variable: chlorophyll						
	Intercept	0.823				
1	Watershed area:lake volume	0.338	0.354	5.888	0.0248	0.374
2	Cropland: animals	-0.661	0.272	4.525	0.0460	0.423
3	Percent agricultural land	0.008	0.199	3.311	0.0838	0.505
Dependent variable: total P						
	Intercept	1.348				
1	Watershed area:lake volume	0.399	0.738	27.973	<0.0001	0.560

are not significantly different between data sets. Therefore, we deleted the interaction term and reran the ANCOVA. We found no significant difference between data sets (ours vs. that of Jones and Knowlton; $p = 0.1227$) and a significant effect of TP on chlorophyll ($p < 0.0001$). Variance explained was relatively high (adjusted $R^2 = 0.719$). Comparison of our results with these other studies strongly suggests a general trend of lower phytoplankton biomass and production for a given amount of phosphorus in reservoirs compared to natural lakes. Clearly, there is a need for studies that explicitly investigate differences between natural lakes and reservoirs with regard to the dependence of primary production on nutrients and algal biomass.

Relationships of primary productivity and photosynthetic parameters to land use, TP, and chlorophyll—Our analyses reveal triangular or “wedge-shaped” distributions for relationships between land use (percent of watershed area comprised of agricultural land) and PPr, chlorophyll, and TP. Simple regressions of these variables explained relatively little variance, whereas regressions using maximum values for dependent variables explained much more variance. These results strongly suggest that there is a well-defined upper bound to the effects of watershed land use on these eutrophication indicators but that other factors determine variation below this upper bound. Multiple regression using watershed area:lake volume and cropland:livestock ratios showed that these two predictor variables explained additional variance above that explained by land use. However, multiple regressions on actual data explained considerably less variation than simple regressions with maximum values. This suggests that additional, unmeasured factors must contribute to the regulation of PPr, TP, and chlorophyll.

TP and chlorophyll were highly correlated with each other, and both were highly correlated with PPr, yet all three variables were only weakly correlated with land use. This suggests that land use itself (in this case, percent of agricultural land) is not an effective predictor of nutrient loading, that PPr is strongly influenced by nutrient sources other than watershed inputs, or both. Regarding the former, there is con-

siderable variation in the relationship between land use and nutrient export rates (Mueller et al. 1995; Puckett 1995; Vanni et al. 2001). In addition, other landscape-level parameters, such as the spatial positioning of various land use practices (Soranno et al. 1996) and location and extent of riparian buffers (e.g., Osborne and Kovacic 1993), might play an important role in determining nutrient export from watersheds.

Regarding other nutrient sources, loading of nutrients from within lakes is also probably quite important in these reservoirs. Nutrient release from sediments via geochemical, microbial, and other processes are other sources of nutrients that are likely to be important and that could vary greatly from lake to lake. In Acton Lake, excretion of nutrients into the water column by sediment-feeding fish (gizzard shad, *Dorosoma cepedianum*) can be an important source of nutrients in summer, especially when gizzard shad biomass is high (Schaus et al. 1997, 2002; Vanni et al. 2001). Gizzard shad abundance increases greatly, and sometimes exponentially, with trophic status in reservoirs and natural lakes (Bachmann et al. 1996; DiCenzo et al. 1996; Michaletz 1997). However, gizzard shad biomass is also highly variable among lakes and among years (Bachmann et al. 1996; Schaus et al. 2002), and this could lead to variation in primary production. Furthermore, gizzard shad abundance is probably subsidized by both sediment inputs from agricultural watersheds and increased phytodetritus produced by sinking phytoplankton (Schaus et al. 2002; Vanni and Headworth in press). Both sources of detritus represent increased food for these sediment-feeding fish; deposition rates of both types of detritus increase with increasing agriculture in watersheds, and both could stimulate abundance of gizzard shad. Therefore, it is possible that PPr in our reservoirs is regulated jointly by gizzard shad and watershed nutrient inputs (Vanni and Headworth in press). We do not have gizzard shad biomass data from all 12 of our lakes, but biomass data from three intensively sampled reservoirs (Acton, Burr Oak, and Pleasant Hill) show that gizzard shad biomass increases greatly with increasing lake productivity in these three lakes (Vanni et al. unpubl. data). This suggests that

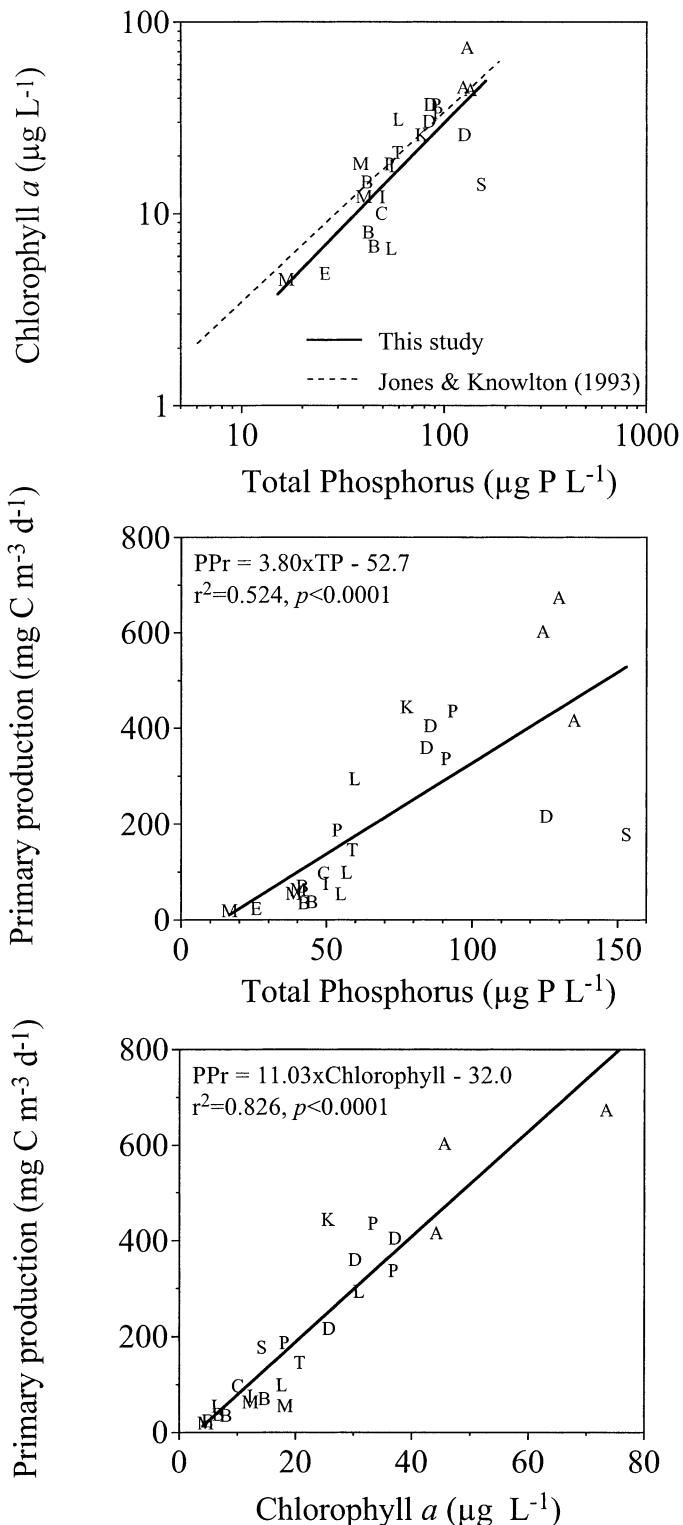


Fig. 5. Relationship of total P and chlorophyll from this study and from Jones and Knowlton's (1993) study of Missouri reservoirs, and the relationships between TP and PPr and between chlorophyll and PPr from this study. For data derived from this study, each point represents a mean of all observations in a particular year. Lake codes given in Table 1. The dashed regression line in the top panel was derived from Table 2 in Jones and Knowlton (1993).

nutrient flux through gizzard shad could support more primary production as trophic status increases.

Our data suggest that land use sets an upper limit to primary production but that production is also influenced by other factors, including but not limited to the watershed area:lake volume ratio and the cropland:livestock ratio. In addition, our study suggests that reservoirs exhibit lower primary productivity than natural lakes at a given nutrient concentration or phytoplankton biomass.

References

- ARBUCKLE, K. E., AND J. A. DOWNING. 2001. The influence of watershed land use on lake N:P in a predominantly agricultural landscape. *Limnol. Oceanogr.* **46**: 970–975.
- BACHMANN, R. W., B. L. JONES, D. D. FOX, M. HOYER, L. A. BULL, AND D. E. CANFIELD. 1996. Relations between trophic state indicators and fish in Florida (USA) lakes. *Can. J. Fish. Aquat. Sci.* **53**: 842–855.
- BEAULAC, M. N., AND K. H. RECKHOW. 1982. An examination of land use–nutrient export relationships. *Water Res. Bull.* **18**: 1013–1024.
- BLACKBURN, T. M., J. H. LAWTON, AND J. N. PERRY. 1992. A method of estimating slope of upper bounds of plots of body size and abundance in natural animal assemblages. *Oikos* **65**: 107–112.
- CARPENTER, S. R., N. F. CARACO, D. L. CORRELL, R. W. HOWARTH, A. N. SHARPLEY, AND V. H. SMITH. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* **8**: 559–568.
- COLE, J. J., N. F. CARACO, AND B. L. PEIERIS. 1992. Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? *Limnol. Oceanogr.* **37**: 1608–1617.
- CORRELL, D. L. 1998. The role of phosphorus in the eutrophication of receiving waters: A review. *J. Environ. Qual.* **27**: 261–266.
- DICENZO, V. J., M. J. MACEINA, AND M. R. STIMPET. 1996. Relations between reservoir trophic state and gizzard shad population characteristics in Alabama reservoirs. *North Am. J. Fish. Manag.* **16**: 888–895.
- FAHNENSTIEL, G. L., J. F. CHANDLER, H. J. CARRICK, AND D. SCAVIA. 1989. Photosynthetic characteristics of phytoplankton communities in Lakes Huron and Michigan: P-I parameters and end-products. *J. Gt. Lakes Res.* **15**: 394–407.
- FEE, E. J. 1990. Computer programs for calculating in situ phytoplankton photosynthesis. Canadian Technical Report of Fisheries and Aquatic Science 1740. Dept. Fish. Oceans.
- , R. E. HECKY, AND H. A. WELCH. 1987. Phytoplankton photosynthesis parameters in central Canadian lakes. *J. Plankton Res.* **9**: 305–316.
- , AND OTHERS. 1989. Lake variability and climate research in northwestern Ontario: Study design and 1985–1986 data from the Red Lake district. Canadian Technical Report of Fisheries and Aquatic Science 1662. Dept. Fish. Oceans.
- , J. A. SHEARER, E. R. DEBRUYN, AND E. U. SCHINDLER. 1992. Effects of lake size on phytoplankton photosynthesis. *Can. J. Fish. Aquat. Sci.* **49**: 2445–2459.
- FIELD, C. K., P. A. SIVER, AND A. M. LOTT. 1996. Estimating the effects of changing land use patterns on Connecticut lakes. *J. Environ. Qual.* **25**: 325–333.
- GOLDBERG, D. E., AND S. M. SCHEINER. 1993. ANOVA and ANCOVA: Field competition experiments, p. 69–93. *In* S. M. Scheiner and J. Gurevitch [eds.], *Design and analysis of ecological experiments*. Chapman and Hall.
- HOYER, M. V., AND J. R. JONES. 1983. Factors affecting the relation

- between phosphorus and chlorophyll-*a* in Midwestern reservoirs. *Can. J. Fish. Aquat. Sci.* **40**: 192–199.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**: 187–211.
- JONES, J. R., AND M. F. KNOWLTON. 1993. Limnology of Missouri reservoirs: An analysis of regional patterns. *Lake Reserv. Manag.* **8**: 17–30.
- KAISER, M. S., P. L. SPECKMAN, AND J. R. JONES. 1994. Statistical models for limiting nutrient relations in inland waters. *J. Am. Stat. Assoc.* **89**: 410–423.
- KIMMEL, B. L., O. T. LIND, AND L. J. PAULSON. 1990. Reservoir primary production, p. 133–193. *In* K. W. Thornton, B. L. Kimmel, and F. E. Payne [eds.], *Reservoir limnology: Ecological perspectives*. Wiley.
- KNOWLTON, M. F., AND J. R. JONES. 1995. Temporal and spatial dynamics of suspended sediment, nutrients, and algal biomass in Mark Twain Lake, Missouri. *Arch. Hydrobiol.* **135**: 145–178.
- , AND ———. 2000. Non-algal seston, light, nutrients and chlorophyll in Missouri reservoirs. *Lake Reserv. Manag.* **16**: 322–332.
- LASTEIN, E., AND E. GARGAS. 1978. Relationship between phytoplankton photosynthesis and light, temperature and nutrient in shallow lakes. *Verh. Int. Verein. Limnol.* **20**: 678–689.
- MAKAREWICZ, J. C. 1991. Photosynthetic parameters as indicators of ecosystem health. *J. Gt. Lakes Res.* **17**: 333–343.
- MELCHER, J., R. J. SORACCO, AND C. W. BOYLEN. 1997. Spatial delineation of biotic and abiotic gradients in a rural New York reservoir. *J. Am. Water Resour. Assoc.* **33**: 35–54.
- MICHALETZ, P. H. 1997. Factors affecting abundance, growth, and survival of age-0 gizzard shad. *Trans. Am. Fish. Soc.* **126**: 84–100.
- MUELLER, D. K., P. A. HAMILTON, D. R. HELSEL, K. J. HITT, AND B. C. RUDDY. 1995. Nutrients in ground water and surface water of the United States—an analysis of data through 1992. U.S. Geological Survey Water Resources Investigations Rep. 95-4031.
- OSBORNE, L. L., AND D. A. KOVACIC. 1993. Riparian vegetated buffer strips in water quality restoration and stream management. *Freshw. Biol.* **29**: 243–258.
- PIERSON, D. C., K. PETERSSON, AND V. ISTVANOVICS. 1992. Temporal changes in biomass specific photosynthesis during the summer: Regulation by environmental factors and the importance of phytoplankton succession. *Hydrobiologia* **243**: 119–135.
- PREPAS, E. E., AND OTHERS. 2001. Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: A comparison of wetland- and upland-dominated catchments. *Can. J. Fish. Aquat. Sci.* **58**: 1286–1299.
- PUCKETT, L. J. 1995. Identifying the major sources of nutrient water pollution. *Environ. Sci. Tech.* **29**: 408–414.
- SALA, O. E., AND OTHERS. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**: 1770–1774.
- SCHAUS, M. H., M. J. VANNI, T. E. WISSING, M. T. BREMIGAN, J. A. GARVEY, AND R. A. STEIN. 1997. Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnol. Oceanogr.* **42**: 1386–1397.
- , AND ———. 2002. Biomass-dependent shifts in omnivorous gizzard shad diets: Implications for growth, food webs and ecosystem effects. *Trans. Am. Fish. Soc.* **131**: 40–54.
- SIVER, P. A., A. M. LOTT, E. CASH, J. MOSS, AND L. J. MARSIANO. 1999. Century changes in Connecticut, USA, lakes as inferred from siliceous algal remains and their relationships to land-use change. *Limnol. Oceanogr.* **44**: 1928–1935.
- SMITH, V. H. 1979. Nutrient dependence of primary productivity in lakes. *Limnol. Oceanogr.* **24**: 1051–1064.
- . 1998. Cultural eutrophication of inland, estuarine, and coastal waters, p. 7–49. *In* M. L. Pace and P. M. Groffman [eds.], *Successes, limitations, and frontiers in ecosystem science*. Springer.
- SORANNO, P. A., S. L. HUBLER, S. R. CARPENTER, AND R. C. LATHROP. 1996. Phosphorus loads to surface waters: A simple model to account for spatial pattern of land use. *Ecol. Appl.* **6**: 865–878.
- VANNI, M. J., AND J. L. HEADWORTH. *In press*. Cross-habitat transport of nutrients by omnivorous fish along a productivity gradient: Integrating watersheds and reservoir food webs. *In* G. A. Polis, M. E. Power, and G. L. Huxel [eds.], *Food webs at the landscape level*. Univ. of Chicago Press.
- , W. H. RENWICK, J. L. HEADWORTH, J. D. AUCH, AND M. H. SCHAUS. 2001. Dissolved and particulate nutrient flux from three adjacent agricultural watersheds: A five-year study. *Biogeochemistry* **54**: 85–114.
- VITOUSEK, P. M., J. R. GOSZ, C. C. GRIER, J. M. MELILLO, W. A. REINERS, AND R. L. TODD. 1979. Nitrate loss from disturbed ecosystems. *Science* **204**: 469–474.
- WALKER, W. W., JR. 1984. Empirical prediction of chlorophyll in reservoirs, p. 292–297. *In* United States Environmental Protection Agency, lake and reservoir management. US EPA 440/5-84-001.
- WETZEL, R. G. 1990. Reservoir ecosystems: Conclusions and speculations, p. 227–238. *In* K. W. Thornton, B. L. Kimmel, and F. E. Payne [eds.], *Reservoir limnology: Ecological perspectives*. Wiley.
- WILLIAMS, N. J. 1978. Annual variation of photosynthetic parameters in Lake Tahoe. *Verh. Int. Verein. Limnol.* **20**: 419–425.

Received: 19 June 2002

Accepted: 16 September 2002

Amended: 22 October 2002