# Seasonal and interannual variation in nutrient fluxes from tributary inputs, consumer recycling and algal growth in a eutrophic river impoundment

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## Abstract

We measured tributary inputs, algal nutrient demand and excretion rates of consumers (gizzard shad and zooplankton) at a eutrophic river impoundment. During two summers with contrasting flow regimes, tributary inputs accounted for 38% (1998) and 3% (1999) of algal N demand and 95% (1998) and 17% (1999) of algal P demand. Gizzard shad contributions averaged 14% and 20% of algal demand for N whereas P contributions were 31% and 58% (1998, 1999; respectively). Zooplankton recycling accounted for a comparable fraction of algal P demand (47%) but a larger fraction of N demand (43%) because their excretia were N rich (N:P = 13:1) compared to fish (7:1). Nutrient release by one of the consumers (gizzard shad) was compared with tributary loading over a nine-year period to assess inter-annual variation in their relative importance. Historical records of inflow chemistry, discharge and gizzard shad biomass showed that variation in tributary inputs was the primary determinant of seasonal and inter-annual variation in nutrient loading. Consumer-derived nutrients were important in late-summer and during years when tributary inputs were low. We propose a conceptual model in which primary production is regulated by external nutrient loading and consumer recycling acts to stabilize and sustain production during periods of diminished external inputs.

## Introduction

Phytoplankton production in aquatic ecosystems is regulated in part by the supply of nutrients from external sources ('new' production) and from internal cycling of nutrients stored in various biotic and abiotic compartments (Dugdale and Goering 1967; Caraco et al. 1992; Smith et al. 1999). Concerns regarding anthropogenic eutrophication stimulated the development of numerical models predicting lake chlorophyll concentrations as a function of external nutrient inputs (Dillon and Rigler 1974) and continue to drive research focusing on export of N and P from catchments (e.g., Soranno et al. 1996; Siver et al.

1999). The importance of physical processes in regulating internal nutrient supply through sediment release and hypolimnetic entrainment has long been recognized (Hutchinson 1957). Recent work has emphasized the role of zooplankton and certain fish species in recycling N and P and their potential importance in sustaining algal production (Vanni 1996; Drenner et al. 1998; Schaus et al. 2002).

Rates of consumer-mediated recycling reflect the abundance and species composition of consumer groups whereas rates of external nutrient loading are dependent upon the lake's hydrogeomorphic position and intensity of land-use within its catchment. These factors may not be independent because elevated ex-

ternal nutrient loading may stimulate internal nutrient regeneration through greater standing stocks of consumers and enrichment of suspended and sedimented food resources. Among lakes where tributary inputs and nutrient recycling by fish or zooplankton have been measured concurrently, no consistent pattern has emerged with respect to their relative importance. For example, data from Acton Lake (Ohio) show that tributary inputs of P were small in comparison to gizzard shad excretions (Schaus et al. 1997). However, data from Lakes Bautzen (Germany), Gyersjoen (Norway), and Pyhajarvi (Sweden) suggest that tributaries contribute more P than fish (Mehner et al. 1998; Brabrand et al. 1990; Helminen and Sarvala 1997; respectively). Comparisons between fish and zooplankton have generally shown that P contributions from fish are less than those of zooplankton (Brabrand et al. 1990; Kraft 1992; Schindler et al. 1993). However, a few studies have shown zooplankton contributions of P equal (Boers et al. 1991) or less than those of fish (Schindler et al. 1993).

A shortcoming of these previous studies is that they often rely on a single year of data to make inferences about the relative importance of external sources and consumer recycling. Fish and zooplankton biomass are known to vary widely from year to year (Carpenter 1988; Jeppesen et al. 1998) although the implications for nutrient recycling are unknown. Similarly, interannual climatic variability leads to large variation in the timing and magnitude of nutrient inputs from catchment sources (Jossette et al. 1999) and these have been shown to have direct effects on the severity of phytoplankton nutrient limitation (Sterner 1994; Bukaveckas and Crain 2002). A second shortcoming of prior studies is that they have focused on P whereas N has often been neglected (but see Schaus et al. 1997). An understanding of the factors regulating N availability may be particularly important in rivers and their impoundments which tend to have low N:P ratios (Soballe and Kimmel 1987) and are often N limited (Grover et al. 1999; Bukaveckas et al. 2002).

Consumers such as zooplankton and fish excrete a variable fraction of the nutrients they ingest which are directly available for algal uptake or made available following bacterial remineralization. Excretion rates are dependent upon the nutritive content of food resources and species-specific factors that govern feeding and assimilation rates (Peters and Rigler 1973; Urabe 1993; Schindler and Eby 1997). The feeding activities of fish have the potential to affect water column nutrient availability through a variety of mechanisms (Lamarra 1975; Mather et al. 1995; Vanni et al. 1997). Planktivorous fish recycle nutrients contained in various forms of suspended particulate matter that may include zooplankton, phytoplankton, bacteria or detritus, depending on the feeding mode and selectivity of the consumer. Benthivorous fish resuspend sedimented materials and, through ingestion and excretion, return sediment-bound nutrients to the water column (Vanni 1996; Schaus and Vanni 2000). Gizzard shad are facultative detritivores that switch from filter-feeding on suspended particulate matter to ingesting surficial sediments in response to changes in resource availability (Mundahl 1991; Buynak and Mitchell 1993). Because they often dominate the icthyomass of warm water rivers and impoundments (Garvey et al. 1998; Clayton and Maceina 2002), gizzard shad may play an important role in nutrient recycling. However, as these systems are typically characterized by high external nutrient loading, the relative importance of recycling by fish and other consumers may be diminished. We argue that the importance of external inputs vs. consumer recycling should be judged relative to nutrient demands associated with primary production. In this context, consumer recycling may be important even in eutrophic systems by sustaining primary production through periods of diminished external loading.

In this study, we quantify nutrient fluxes from tributary and consumer sources to assess seasonal and interannual variation in their importance relative to algal demand in a eutrophic reservoir (Taylorsville Lake). We measured nutrient regeneration by two groups of consumers (macrozooplankton, gizzard shad) that had been shown to be important in other systems (Schaus and Vanni 2000; Schindler et al. 1993). Gizzard shad (*Dorososma cepedianum*) typically comprise over 50% of fish biomass in Taylorsville Lake (DFWR, 1989-1997). Tibutary inputs and consumer regeneration were quantified monthly during May-October of 1998 and 1999 and compared to phytoplankton nutrient demands inferred from measured primary production and Redfield ratios. Historical data on tributary inputs and fish biomass allowed an assessment of interannual variation during the preceding nine years (1989-1997). We consider both N and P in our assessment and show that tributary inputs dominate nutrient sources but that consumer-driven recycling is important seasonally and in years of low to moderate flow.

## Materials and methods

Taylorsville Reservoir is located in north-central Kentucky approximately 40 km southeast of Louisville, Kentucky. The lake was created in 1983 as an impoundment of the Salt River which is also the primary inflow. The primary inflow accounts for 49% of the water, 63% of the phosphorus, and 77% of the nitrogen entering the lake (USACE, 1992). The lake's catchment is 914 km$^2$ in area with 76% of land devoted to agriculture (pasture and cropland), 20% to silviculture, and 4% to residential areas. The lake has a surface area of 12 km$^2$ (3050 acres), mean depth of 8.5 m, maximum depth of 24 m (near the dam) and an annual mean hydraulic residence time of 84 days. The lake is monomictic exhibiting a broad metalimnetic region (5-15 m) with poorly defined thermocline from May through October. A strong and stable oxycline (at 5 m) is apparent by June and persists until fall turnover.

Consumer excretion experiments and primary production measurements were performed at two stations, one located in the riverine portion of the reservoir (near primary inflow) and a second in the lacustrine zone (near dam). As our interests focused on nutrients supporting algal production, our assessment of nutrient fluxes was restricted to the warmwater phase (May – October) when algal production is highest. Experiments to measure gizzard shad N and P excretion were conducted in June, August, and October of 1998 and May of 1999 at both the upstream and downstream sites, and in August and September of 1999 at the downstream site only. Zooplankton excretion experiments were conducted in October of 1998 and July, August and September of 1999 at the downstream site. Gizzard shad experiments were analyzed using a two-factor analysis of variance to determine whether site and date were significant predictors of biomass-specific excretion rates. Zooplankton data were analyzed using a one-factor ANOVA to assess significant differences in biomass-specific excretion rates between dates.

Gizzard shad excretion experiments followed the methods of Schaus et al. (1997) whereby short-term incubations were used to estimate nutrient release rates. Gizzard shad were collected by electroshocking with an alternating current (60 pulses per second). Ten individuals were randomly selected from 20-30 collected at each site. Individual fish were placed in 3 L containers and four enclosures without fish served as controls. Water samples were taken at time zero (immediately after the fish were added) and at the termination of the experiment (60 min) and analyzed for $NO_3$, $NH_4$ and $PO_4$. Our protocol differed in that we incubated fish in lake water passed through a 63 $\mu$m mesh (to exclude large zooplankton) whereas Schaus et al. (1997) used filtered lake water (0.7 $\mu$m). We cannot discount the possibility that nutrient uptake by algae might favor conservative estimates of gizzard shad excretion although we did not observe measurable reductions in N or P within control enclosures. Biomass-specific nutrient excretion rates were calculated following determination of dry weight for each fish used in the experiment. Gizzard shad contributions to epilimnetic nutrient fluxes were derived from the product of biomass-specific excretion rates and whole-lake estimates of gizzard shad biomass. The Kentucky Department of Fish and Wildlife Resources determined lake gizzard shad abundance annually during 1989-1997 from cove rotenone samples taken in July or August (DFWR, 1989-1997). As no biomass data were available for 1998 and 1999, we estimated nutrient release by gizzard shad using average biomass during 1989-1997. We inferred historical loading rates from 1989 to 1997 based on the average excretion rate during 1998 − 1999 (all experiments) and measured biomass.

Our methods for determining nutrient release by zooplankton generally followed other studies (e.g., Urabe 1993; Attayde and Hansson 1999) in which zooplankton were incubated within enclosures and excretion rates were estimated from measured changes in ambient nutrient concentrations. As we were interested in whole-community excretion rates we did not sort individual zooplankton into species-specific groups. For each experiment, ten 3-l containers were filled with pre-filtered (63 $\mu$m) lake water and stocked with zooplankton collected from vertical epilimnetic tows (63 $\mu$m mesh). Four enclosures without zooplankton served as controls. Water samples were taken from each container at time zero (immediately following zooplankton addition) and at the termination of the experiment (60 min) and analyzed for $NO_3$, $NH_4$ and $PO_4$. Biomass-specific excretion rates were derived by dividing the quantity of N and P excreted by the dry weight of the zooplankton. Measurements for individual taxa (ash free dry mass method or CHN analysis) were used to estimate community biomass. Lake zooplankton biomass was quantified from duplicate, daytime, epilimnetic tows collected monthly. Zooplankton were preserved with a sugar-formalin solution and subsequently identified

and enumerated using an Olympus SZX12 stereomicroscope. Zooplankton contributions to epilimnetic nutrient fluxes were derived from the product of measured excretion rates and biomass estimates.

In situ rates of primary production were measured monthly to estimate algal demand for N and P. Water from 1, 2 and 3 m was placed in 60 ml bottles (2 light and 1 dark for each depth). Bottles were spiked with 1 $\mu$Ci of $NaH^{14}CO_3$ and incubated for 2 hours at the collection depth. Samples were placed on ice and kept in the dark ($<$ 2 h) until filtered (0.45 $\mu$m Whatman GF/F). Filters were placed into vials containing 5 ml scintillation fluid and analyzed (Packard Tri-Carb 1900 TR) with quench correction from an external standard. Calculations of carbon assimilated were based on Steemann Nielsen (1951). Dissolved inorganic carbon (DIC) and chlorophyll-a concentrations were determined in conjunction with primary production measurements. DIC samples were analyzed on a Shimadzu (model TOC-5050A) analyzer using the combustion/nondispersive infrared gas analyses method. Chlorophyll was measured on a Turner fluorometer following acetone extraction (Sterman 1988). Light profiles were taken using a LI-COR 1000 data logger for simultaneous measurement of surface (flat plane quantum sensor) and subsurface (cosine-corrected quantum sensor; 0.5 m intervals) irradiance. Biomass-specific primary production (per unit chlorophyll) was related to irradiance using the tangential equation of Jassby and Platt (1976). The photosynthesis-irradiance model coupled with measured light attenuation in the lake was used to estimate primary production within successive layers of the euphotic zone (typically 3-4 m). The 2 hour production rate was converted to daily production using the relationship between total daily insolation and that during the incubation period (Wetzel and Likens 1991). Lake stage and morphometry data were used to estimate the volume of the photic zone and calculate the total mass of carbon fixed. Redfield's ratio (1958) was used to estimate N and P demand based on carbon assimilated. Algal nutrient demands were expressed as daily volumetric rates for the upper mixed layer.

Nutrient inputs from the primary inflow were characterized based on monthly samples and continuous discharge measurements obtained at a United States Geological Survey gauging station located 6 km upstream from the reservoir. Nutrient analyses followed standard methods (EPA 1979). Nutrient analyses were performed on filtered samples (0.45 $\mu$m) by a Technicon Auto-analyzer using cadmium reduction ($NO_3$;

Method 353.2), phenate ($NH_4$; Method 350.1) and ascorbic acid ($PO_4$; Method 365.1) methods. Total phosphorus (TP) was analyzed from unfiltered samples following persulfate digestion. Lake water and samples collected during consumer excretion experiments were analyzed by the same methods as described for tributary samples. Particulate matter was collected on a pre-combusted 0.45 $\mu$m glass fiber filter and analyzed for N (Perkin-Elmer 2400 CHN analyzer) and P (following persulfate digestion). Tributary data are described in detail in previous publications (USACE 1992, 1998). For this analysis, we used inflow data for the two years during which we measured primary production and consumer excretion rates (1998-1999) and for the preceding nine years when gizzard shad abundance data were available (1989-1997). We did not find that tributary nutrient concentrations were correlated with discharge. Nutrient fluxes were calculated from the product of monthly discharge and concentration and divided by the numbers of days in each month to derive an average daily input for May to October of each year. The volumetric loading rate was obtained by dividing the daily input by the volume of the epilimnion. The temperature of inflowing water corresponded to lake temperatures at depths of 2-5 m suggesting that surficial inflows were retained within the upper mixed layer. In the absence of a well-defined thermocline, we assumed a constant depth for the epilimnion (5 m) based on the depth of the oxycline.

## Results

Average epilimnetic chlorophyll concentrations in Taylorsville Lake ranged from 6-36 $\mu$g $L^{-1}$ during May-October of 1998 and 1999 (Figure 1). Highest chlorophyll and primary production were observed in June, 1998 (36 $\mu$g $l^{-1}$, 43 $\mu$mol C $l^{-1}$ $d^{-1}$; respectively). Primary production was generally lower in 1999 ($<$ 10 $\mu$mol C $l^{-1}$ $d^{-1}$) and exhibited little monthly variation (peak = 16 $\mu$mol C $l^{-1}$ $d^{-1}$ in July). In both years, $NH_4$ was the dominant form of dissolved inorganic N with concentrations typically 2-3 $\mu$mol $l^{-1}$ except near the end of the stratified period (October). A single peak in $NO_3$ was observed in May, 1998 (7.1 $\mu$mol $l^{-1}$) but concentrations were otherwise less than 1 $\mu$mol $l^{-1}$. $PO_4$ concentrations showed no apparent seasonal trend and were similar between years (mean = 0.20 $\mu$mol $l^{-1}$). Epilimnetic
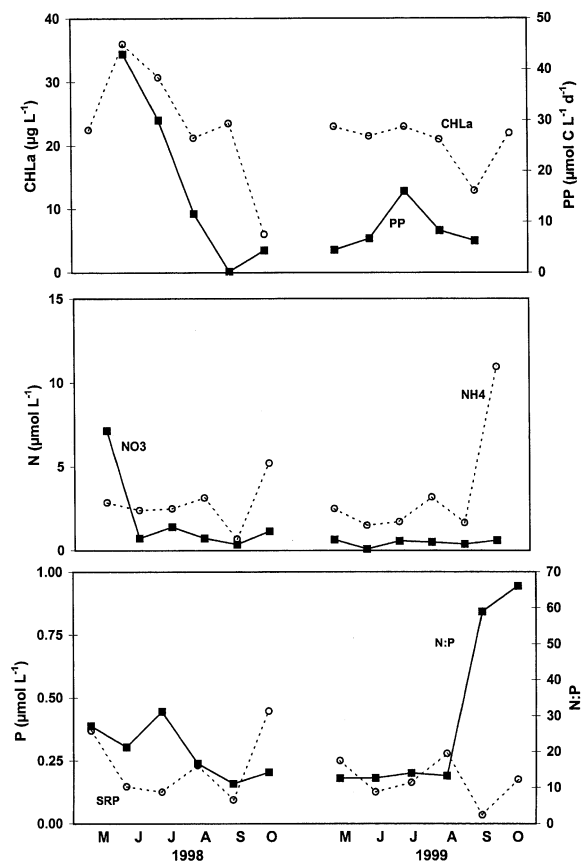
*Figure 1.* Epilimnetic chlorophyll and primary production (top panel), NO₃ and NH₄ (middle panel) and PO₄ and N:P (bottom panel) in Taylorsville Lake during May-October of 1998 and 1999.



*Figure 2.* Biomass-specific excretion rates of dissolved inorganic nitrogen (top panel) and $PO_4$ (bottom panel) by gizzard shad from Taylorsville Lake. Values shown are averages for 10 individuals per site and date (confidence intervals $\pm$ standard error). Filled and open circles represent downstream and upstream sites, respectively.

N:P ratios ranged from 10 to 65. Values above the Redfield ratio occurred early in the growing season (May-June) in 1998 and at the end of the growing season (September-October) in 1999.

Gizzard shad P excretion rates averaged 1.06 $\pm$ 0.31 (standard deviation) nmol mg$^{-1}$ (dry wt) h$^{-1}$ and exhibited little spatial or temporal variability (for site, P = 0.525; for date, P = 0.115). Excretion rates for P were similar across months and between years with the exception of the August 1998 experiment (upstream site) when rates were almost two-fold higher compared to all other months (Figure 2). Phosphorus excretion rates of gizzard shad collected at upstream and downstream sites were significantly different on only one of four dates when they were measured concurrently. Nitrogen excretion rates were more variable and significant differences were frequently observed among dates and between sites (for site, P = 0.004; for date, P = 0.001). Excretion rates for N av-

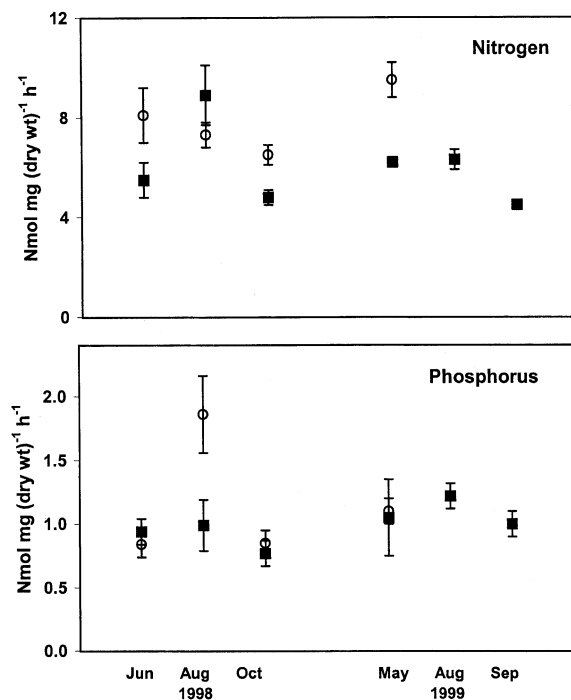eraged 6.8 ( $\pm$ 1.7) nmol mg$^{-1}$ h$^{-1}$ and were significantly higher at the upstream site on three of four dates (Figure 2). At the downstream site, highest N excretion rates were measured in August of both years although seasonal variation in 1999 was small. Ratios of N:P in fish excretia ranged from 4.5 to 9.6 (mean = 7.1).

Zooplankton biomass averaged 1020 mg m$^{-2}$ (as dry wt) in 1998 and 1680 mg m$^{-2}$ in 1999 with peak abundance occurring in June and September (1999) or October (1998). Biomass was high (1300-2000 mg m$^{-2}$) on each of the four dates when excretion rates were measured (Figure 3). Phosphorus excretion rates for zooplankton averaged 8.01 ( $\pm$ 1.30) nmol mg$^{-1}$ (dry wt) h$^{-1}$ and were not significantly different across dates (Figure 3). N excretion rates averaged 111 ( $\pm$ 45) nmol mg$^{-1}$ h$^{-1}$ and were more variable. Highest N excretion rates were measured in October, 1998 and lowest rates in July, 1999. In October, 1998 the community was dominated by *Daphnia* and calanoid copepods (12% and 84% of community biomass; respectively; Figure 3). Calanoid copepods
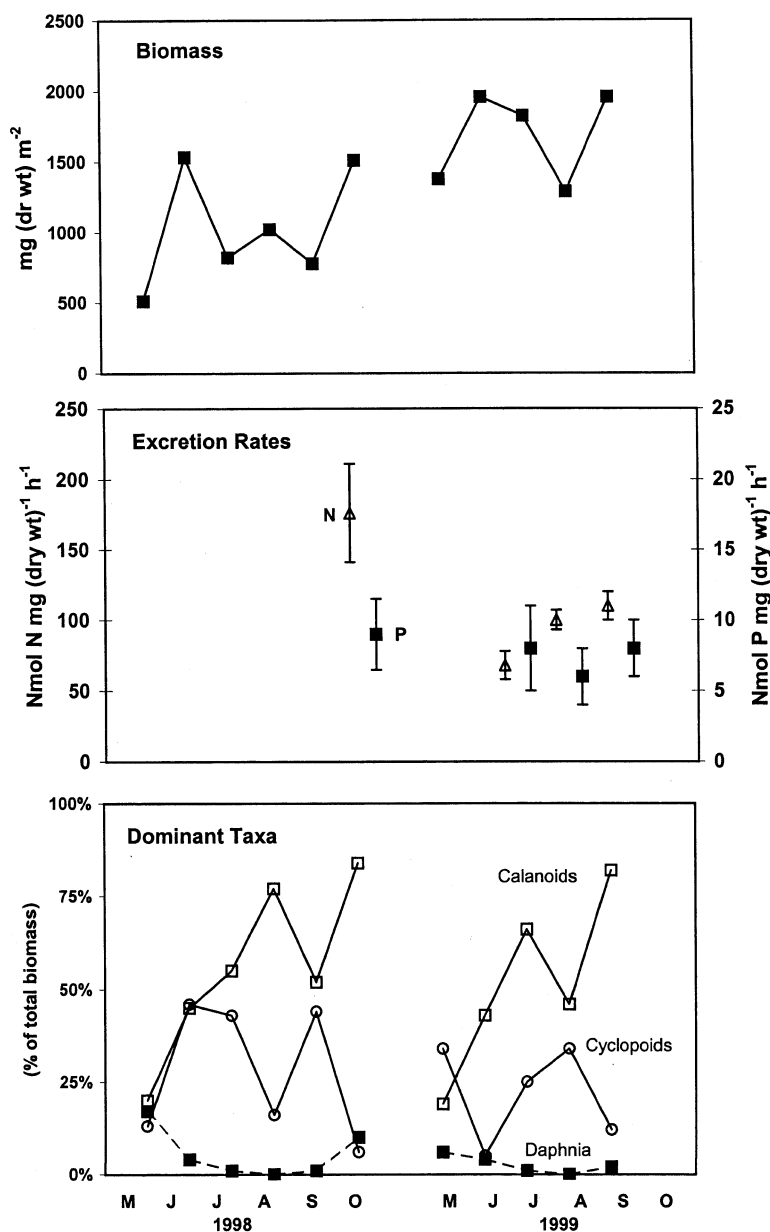
*Figure 3.* Zooplankton biomass (top panel), biomass-specific excretion rates of dissolved inorganic nitrogen and $PO_4$ (middle panel) and dominant taxa (as a proportion of total biomass) in Taylorsville Lake. Excretion rates are average values for ten experimental units per date (confidence intervals are $\pm$ standard error). N and P excretion rates were measured on the same dates but are offset for clarity.

were also dominant ($>50\%$ of biomass) during the July-September 1999 experiments. N:P of zooplankton excretia were higher than for gizzard shad ranging from 8.1 to 18.9 (mean = 13.1).

Total discharge for the 6-month period from May to October varied 8-fold (0.018–0.141 $km^3$) during 1989-1999 (Figure 4). Low flow years in 1991, 1993, 1994 and 1999 were interceded by four successive

high flow years during 1995-1998. The average concentration of DIN in the Salt River was 77 $\mu$mol $l^{-1}$ with no consistent long-term trend (Figure 4). $NO_3$ dominated the dissolved fraction (86%) with $NH_4$ accounting for a smaller proportion (14%) of inputs. Concentrations were typically higher during May-July (mean = 103 $\mu$mol $l^{-1}$) compared to August-October (mean = 46 $\mu$mol $l^{-1}$). The average concentra-
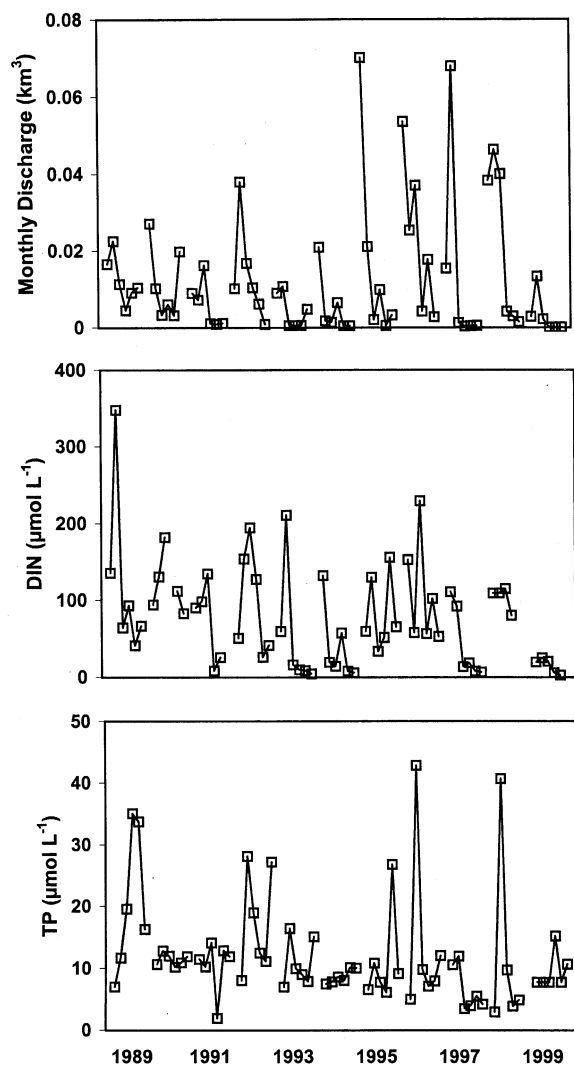
*Figure 4.* Monthly discharge and concentrations of dissolved inorganic nitrogen and total phosphorus for the primary inflow to Taylorsville Lake (Salt River) from 1989 to 1999. Discharge data are from a US Geological Survey gauging station located 6 km upstream from the lake. Chemistry data are from USACE (1992, 1998).
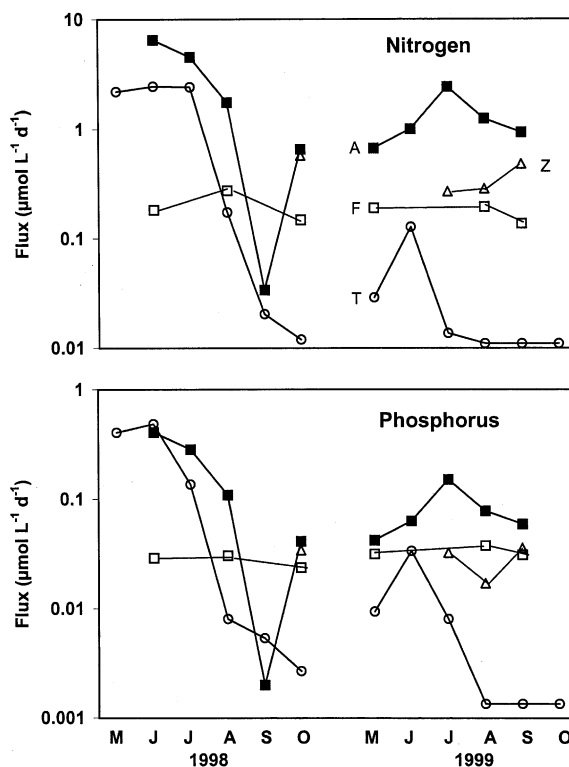


*Figure 5.* Epilimnetic nutrient fluxes in Taylorsville Lake associated with algal growth requirements ('A'; solid squares), tributary inputs ('T'; open circles) and recycling by gizzard shad ('F'; open squares) and zooplankton ('Z'; triangles). Fish inputs are inferred from measured excretion rates and average biomass estimates obtained from the Department of Fisheries and Wildlife Research (DFWR, 1989-1997).

tion of TP in the Salt River across all months and years was 12.3 $\mu$mol $l^{-1}$ and ranged from 2 $\mu$mol $l^{-1}$ to 44 $\mu$mol $l^{-1}$ (Figure 4). TP concentrations showed no consistent seasonal or inter-annual trends for the 11-year period of record. In most years, monthly values of less than 15 $\mu$mol $l^{-1}$ were interspersed with occasional measurements in the range of 30-45 $\mu$mol $l^{-1}$, except in 1989 and 1992 when three of six measurements in each year exceeded 30 $\mu$mol $l^{-1}$. For subsequent analyses, we derived estimates of tributary $PO_4$ concentrations from measurements of TP to facilitate comparisons with fluxes from consumer recycling and algal demand. We assumed that $PO_4$ was a constant fraction of TP (79%) based on a linear relationship within the subset of tributary data when both fractions were analyzed (N = 30 monthly samples; slope = 0.79 $\pm$ 0.03; $R^2$ = 0.96; p < 0.001).

Tributary inputs exhibited pronounced seasonal variation during 1998 and were followed closely by variation in algal demand (Figure 5). Peak algal demand occurred in June (N = 6.5 $\mu$mol $l^{-1}$ $d^{-1}$; P = 0.41 $\mu$mol $l^{-1}$ $d^{-1}$) and was followed by a steady decline until October. Highest tributary loadings occurred during May-July 1998 when inputs of N were 2 $\mu$mol $l^{-1}$ $d^{-1}$ and P inputs ranged from 0.14 $-$ 0.48 $\mu$mol $l^{-1}$ $d^{-1}$. Corresponding estimates of nutrient release from gizzard shad (June, 1998) were small by comparison (N = 0.18 $\mu$mol $l^{-1}$ $d^{-1}$; P = 0.029 $\mu$mol $l^{-1}$ $d^{-1}$). By August, tributary inputs declined tenfold

and remained low (N $<$ 0.2 $\mu$mol $l^{-1}$ $d^{-1}$; P $<$ 0.01 $\mu$mol $l^{-1}$ $d^{-1}$) through September and October. At this time, tributary sources of N and P were smaller than contributions from gizzard shad and zooplankton. Phosphorus recycling by zooplankton measured in October 1998 (0.034 $\mu$mol $l^{-1}$ $d^{-1}$) was comparable to gizzard shad contributions measured in August (0.030 $\mu$mol $l^{-1}$ $d^{-1}$) and October (0.024 $\mu$mol $l^{-1}$ $d^{-1}$). During the same period, N recycling by zooplankton (0.57 $\mu$mol $l^{-1}$ $d^{-1}$) was 2-3 fold higher than release from gizzard shad (0.15-0.28 $\mu$mol $l^{-1}$ $d^{-1}$).

Seasonal patterns in tributary inputs and algal nutrient demand differed between the two years (Figure 5). Tributary inputs during 1999 were low throughout May to October ($<$ 0.03 $\mu$mol N $l^{-1}$ $d^{-1}$; $<$ 0.009 $\mu$mol P $l^{-1}$ $d^{-1}$). with peak inputs (June: N = 0.13 $\mu$mol $l^{-1}$ $d^{-1}$; P = 0.034 $\mu$mol $l^{-1}$ $d^{-1}$) well below those observed during the previous year. Similarly, the peak in algal demand was smaller (N = 2.4 $\mu$mol $l^{-1}$ $d^{-1}$; P = 0.15 $\mu$mol $l^{-1}$ $d^{-1}$) and occurred later in the growing season (July). Algal demand did not exceed 1.2 $\mu$mol N $l^{-1}$ $d^{-1}$ and 0.08 $\mu$mol P $l^{-1}$ $d^{-1}$ in other months. Consumer regeneration was large in comparison to tributary inputs during most months. Zooplankton recycling of P averaged 0.028 ($\pm$ 0.010 SD) $\mu$mol $l^{-1}$ $d^{-1}$ and was equivalent to release from gizzard shad (0.033 $\pm$ 0.004 $\mu$mol $l^{-1}$ $d^{-1}$). For N, zooplankton contributions (0.34 $\pm$ 0.12 $\mu$mol $l^{-1}$ $d^{-1}$) were larger than those of gizzard shad (0.17 $\pm$ 0.03 $\mu$mol $l^{-1}$ $d^{-1}$). Differences between zooplankton and gizzard shad volumetric loading rates were small (ca. 2-fold) compared to differences in their biomass-specific excretion rates (8-fold for P, 16-fold for N). This disparity reflects the greater biomass of gizzard shad (32-96 kg $ha^{-1}$) over zooplankton (5-20 kg $ha^{-1}$) in Taylorsville Lake.

Tributary inputs represented a large fraction of algal demand for P ($>$ 50%) and N ($>$ 30%) during peak production in June-July of 1998 despite high growth requirements (Figure 6). Overall, tributary inputs accounted for 38% (1998) and 3% (1999) of algal N demand and 75% (1998) and 14% (1999) of algal P demand. Gizzard shad contributions relative to algal demand averaged 14% and 20% for N whereas P inputs were 31% and 58% (1998, 1999; respectively). Gizzard shad contributions accounted for a larger fraction of algal N and P demand than did tributary inputs during five of six months when corresponding data were available (excluding June, 1998). Zooplankton recycling averaged 43% (N) and
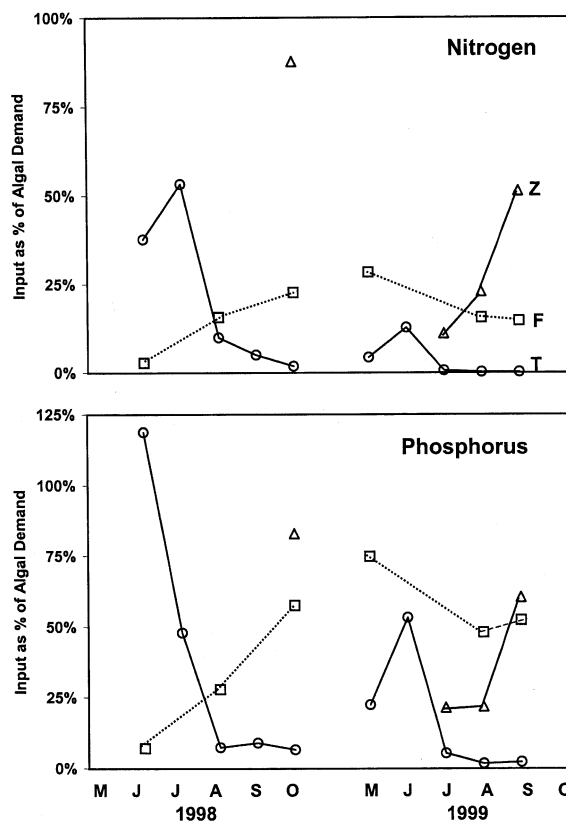


*Figure 6.* Epilimnetic P and N fluxes as a proportion of daily algal growth requirements. Symbols represent fluxes associated with tributary inputs ('T'; open circles) and recycling by zooplankton ('Z'; triangles) and gizzard shad ('F'; open squares).

47% (P) of algal demand during four months for which concurrent data were available. High zooplankton biomass in October, 1998 and September, 1999 coincided with periods of relatively low algal production and therefore zooplankton excretions accounted for a large fraction (50-80%) of algal demand. The sum of N fluxes from tributary and consumer sources corresponded to 39-112% of algal growth requirements during months when all fluxes were measured concurrently. The sum of P fluxes was larger (72-147%) and exceeded algal demand in October, 1998 and September, 1999. As these data were for mid- and late- summer months, tributary inputs were small in comparison to consumer contributions and algal demand. Daily algal demand as a proportion of ambient (lake) concentrations exceeded 100% (turnover $<$ 1 d) during periods of peak algal production in June-July 1998 and July 1999. In other months, daily algal demand was 5-50% of lake concentrations. Relative to lake concentrations, average
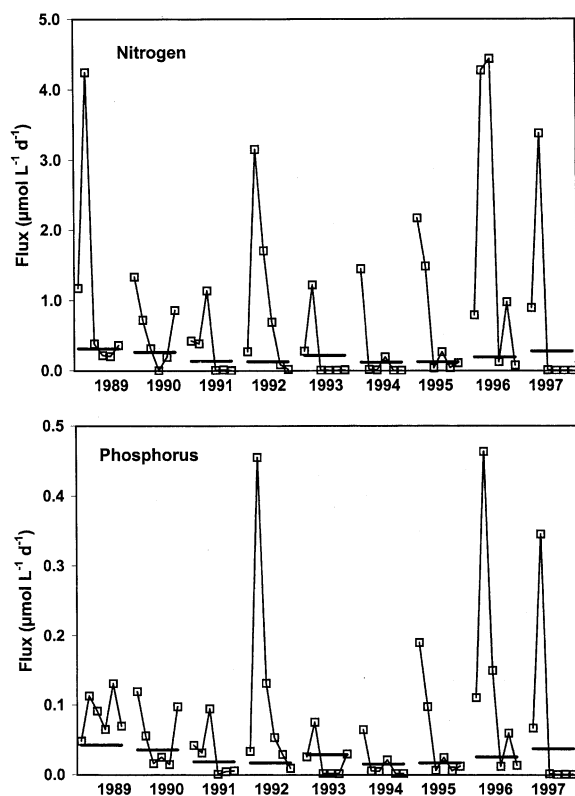
*Figure 7.* Seasonal and interannual variation in tributary inputs of N and P to Taylorsville Lake (open squares). Values are average daily epilimnetic loading rates for May to October of each year. Gizzard shad nutrient loading rates (horizontal line) were based upon reported biomass estimates for 1989-1997 and measured excretion rates during 1998-1999.

demand for P in 1998 (112%) and 1999 (72%) was higher than demand for N (77%, 54%; respectively).

We derived average daily tributary loading rates for each month (May-October) during the 9-year period for which estimates of gizzard shad abundance were available (Figure 7). N loading rates averaged 0.760 $\mu$mol l$^{-1}$ d$^{-1}$ whereas P inputs averaged 0.066 $\mu$mol l$^{-1}$ d$^{-1}$. Relative loading rates of N to P were typically at or below the Redfield ratio (mean = 13). Highest P inputs ($>$ 0.10 $\mu$mol l$^{-1}$ d$^{-1}$) occurred in years with elevated discharge (1996) or, when moderate discharge coincided with elevated P concentrations (1992). Interannual variation in N loading generally followed trends for P. Seasonal patterns were characterized by elevated discharge in May and June when DIN was also highest and resulted in substantially higher N fluxes early in the growing season ($>$ 1.0 $\mu$mol l$^{-1}$ d$^{-1}$). In comparison to tributary loadings, gizzard shad contributions were typically lower. P release varied between 0.015 $-$ 0.043 $\mu$mol l$^{-1}$ d$^{-1}$ (mean= 0.026 $\mu$mol l$^{-1}$ d$^{-1}$) and corresponded to 40% of the long-term average tributary input. N release ranged between 0.12 $-$ 0.31 $\mu$mol l$^{-1}$ d$^{-1}$ (mean= 0.20 $\mu$mol l$^{-1}$ d$^{-1}$) and represented 26% of the average tributary loading. Tributary inputs exceeded gizzard shad contributions by more than twofold in 22 of 54 months and these typically occurred early in the growing season (May or June). Gizzard shad contributions often equaled or exceeded tributary inputs during late summer of most years. Overall, the relative importance of fish contributions to nutrient supply was determined by fluctuations in tributary loadings since variation in tributary inputs was large ($>$ 100-fold) compared to the 3-fold variation in gizzard shad biomass (32–96 kg dry weight ha$^{-1}$).

## Discussion

We quantified nutrient fluxes from tributary inputs and consumer-mediated recycling to compare these with algal demand for N and P in a mid-latitude reservoir. The sum of nutrient fluxes from tributary, gizzard shad and zooplankton sources exceeded average algal P demand whereas N fluxes accounted for only 78% of algal demand. The lower rate of supply for N reflects the fact that N:P ratios of inflow water and consumer excretia were less than the Redfield ratio. Zooplankton contributions assumed greater importance with respect to N because their excretia were N rich (N:P = 13:1) relative to those of gizzard shad (7:1). Low rates of N supply relative to P favors N limitation and concurrent phytoplankton assays showed stronger responses to N addition than for P (Shostell 2001). Consumer excretia were in the form of NH$_4$ whereas tributary inputs were largely (86%) NO$_3$. As metabolic costs of NH$_4$ uptake are less than for NO$_3$, consumer recycling may account for a disproportionately large fraction of algal uptake even when NO$_3$ loading rates from tributaries are higher. A number of studies have documented higher uptake rates for NH$_4$ over NO$_3$ among marine and estuarine phytoplankton (Thompson et al. 1989; Levasseaur et al. 1993; Hamilton et al. 1999) and recent work has suggested that recycling of NH$_4$ sustains algal growth in some systems (Horner-Rosser and Thompson 2001; Presing et al. 2001). Dilution assays using Taylorsville Lake phytoplankton (4 experiments) showed equivalent growth rates with either NO$_3$ or NH$_4$
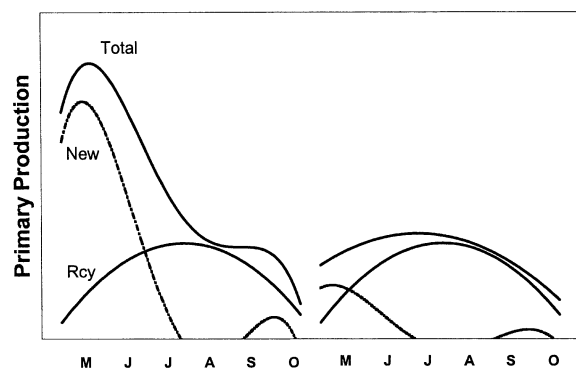
*Figure 8.* Hypothetical patterns of New, Recycled (Rcy) and Total Primary Production arising from seasonal variation in tributary nutrient loading and consumer-mediated nutrient recycling during years with high (left) and low (right) watershed inputs.

amendments (Shostell 2001) and therefore do not suggest higher growth efficiencies for recycled N.

The relative importance of tributary and consumer sources shifted seasonally and from year to year depending on inflow rates. In 1998, elevated discharge during May-June coincided with peak $NO_3$ concentration, algal biomass and production. The absence of tributary inputs during the same period in the following year was associated with lower $NO_3$, chlorophyll and primary production. These data suggest that tributary inputs contribute the bulk of nutrients supporting the production maximum and are an important determinant of yearly variation in annual primary production. Diminishment of inflows in August 1998 coincided with an increase in the severity of nutrient limitation measured during bioassay experiments (Shostell 2001). At this time and throughout 1999, consumer recycling assumed greater importance. Long-term data show that tributary sources exceeded contributions from gizzard shad by more than two-fold during the early summer of most years and that interannual variation in nutrient supply was largely determined by catchment runoff. Gizzard shad sources of N and P attained equal or greater importance during late summer when tributary inputs were low.

The effects of seasonal and interannual variation in tributary inputs and consumer recycling on primary production are depicted in a conceptual model (Figure 8). We argue that the magnitude and timing of the primary production maximum is principally determined by new production associated with nutrient inputs from the catchment. Production supported by consumer recycling is depicted as a unimodal func-

tion arising from higher biomass and temperature-dependent feeding rates during mid-summer. In years when tributary inputs are low, we predict smaller and delayed primary production maxima driven by consumer nutrient regeneration. In this way, consumer recycling acts to stabilize interannual variation in primary production despite large variation in catchment inputs. In Taylorsville Lake, primary production varied by only 2-fold between 1998 and 1999 despite a greater than 10-fold difference in tributary nutrient inputs. This conceptual model may be applicable to other advective systems (rivers, estuaries) that experience variation in nutrient loading arising from interannual and seasonal changes in flow regime. Paerl et al. (2001) reported that large rainfall events associated with hurricanes resulted in increased nitrogen loading and sustained algal blooms in a lagoonal estuary. External nutrient supply has been shown to regulate interannual variation in primary production in a variety of estuarine (Gallegos et al. 1992; Paerl et al. 1998) and riverine (Bukaveckas and Crain 2002) waters. These systems share a common feature in that their hydrogeomorphic position enhances their susceptibility to external loadings, particularly in catchments where anthropogenic influences dominate (Harris 2001). Despite their apparent reliance on external nutrient sources, our results and those from estuarine studies (Jassby et al. 2002; Eyre and McKee 2002) suggest an important role for internal processes including those mediated by consumers.

Comparisons of nutrient fluxes from diverse sources is complicated by uncertainty about error and bias in estimation of flux parameters. In the following section, we consider potential sources of error associated with nutrient flux estimates for tributary and consumer sources. Continuous measurement of discharge coupled with chemical sampling at discrete intervals yields tributary flux estimates that may be accurate to within 10% depending on the type of gauging equipment used and the intensity of the sampling program (Winter 1985). Nutrient inputs from ungauged sources (groundwater, small tributaries) will lead to underestimation of watershed loadings in systems where these sources constitute a significant fraction of total inputs. Our estimates of tributary loadings for Taylorsville Lake are likely to be conservative because prior studies of this reservoir have shown that the primary inflow accounts for 63% (P) and 77% (N) of catchment inputs (USACE 1992). As discharge and chemistry data for smaller tributaries were incomplete, we ignored these in our analyses but

such a correction would further emphasize the importance of catchment inputs over consumer recycling in this system.

Uncertainty in estimates of nutrient fluxes from consumers reflects error in determination of biomass-specific rates of excretion and whole-lake estimates of consumer abundance. The latter are likely the greater source of variation since abundance varied by threefold whereas excretion rates were typically within 50% among dates and sites. Abundance estimates are a greater source of potential error in part because measurements obtained at one (fish) or a few (zooplankton) points in space/time were extrapolated by a large factor to derive whole-lake estimates. Yan (1986) analyzed error arising from variable sampling intensity and found that estimates of zooplankton abundance derived from a single station sampled at monthly intervals were within 20% of estimates based on weekly sampling at multiple stations. However, that study was conducted in a small (44 ha) lake and likely underestimates spatial variability in reservoirs where longitudinal gradients associated with riverine and lacustrine zones are well documented.

Our estimates of excretion rates for a mixed zooplankton assemblage were similar to previously published values (Urabe 1993) despite differences in methodology. Our experiments were of shorter duration (1 h vs. 12-24 h), had higher zooplankton densities (14-21 mg $l^{-1}$ vs. < 2 mg $l^{-1}$) and were conducted at ambient nutrient concentrations. Urabe (1993) spiked chambers with N and P to ensure that algal nutrient uptake during the incubation would be detected from decreasing concentrations in control enclosures. Nutrient concentrations within our enclosures were above reported half-saturation concentrations (Cotner and Wetzel 1992; Grover et al. 1999) and therefore we assumed that algae in control enclosures could measurably decrease ambient nutrient levels. We did not detect measurable changes in nutrient concentrations within control enclosures suggesting that increases in our experimental enclosures approximate gross rather than net excretion. Despite the potentially conservative nature of our methods, our average values for zooplankton excretion of N (111 nmol $mg^{-1}$ $h^{-1}$) and P (8.0 nmol $mg^{-1}$ $h^{-1}$) were higher than those reported by Urabe (1993) for a mixed zooplankton community (N = 46 nmol $mg^{-1}$ $h^{-1}$; P = 4.7 nmol $mg^{-1}$ $h^{-1}$). Higher excretion rates in our study may be due to higher concentrations of particulate N (mean = 35 $\mu$mol $l^{-1}$) and P (mean = 4.5 $\mu$mol $l^{-1}$) in Taylorsville Lake compared to Urabe's experiments (mean = 9.6 $\mu$mol PN $l^{-1}$, 0.6 $\mu$mol PP $l^{-1}$). Normalizing biomass-specific excretion rates to ambient seston concentrations yields an estimate of the fraction of particulate N and P that is recycled per unit mass of zooplankton and time. We found that the proportion of P (0.18%) recycled by zooplankton in Taylorsville Lake was smaller than that observed during Urabe's experiments (0.78%) whereas estimates of N recycling were similar (0.32% and 0.48%; respectively). Differences in relative excretion rates between the two systems may be reflective of copepod-dominated (Taylorsville) vs. cladoceran-dominated (Urabe 1993) communities. In our study, highest rates of N excretion occurred when *Daphnia* were most abundant (October 1998). Although large-bodied zooplankton have higher feeding rates and per capita P excretion (Vadstein et al. 1995), we did not observe a corresponding increase in P excretion at this time.

Phosphorus excretion by gizzard shad in Taylorsville Lake ranged from 0.22 to 0.64 $\mu$mol $g^{-1}$ $h^{-1}$ and was comparable to estimates reported by Schaus et al. (1997) for Acton Lake (0.07-0.69 $\mu$mol $g^{-1}$ $h^{-1}$). Gizzard shad N excretion rates for Taylorsville Lake (1.28-2.71 $\mu$mol $g^{-1}$ $h^{-1}$) were within the lower range of values for Acton Lake (1.85-7.35 $\mu$mol $g^{-1}$ $h^{-1}$). Our estimates of nutrient release were similar even though our experiments were conducted using unfiltered lake water. We found that seasonal and spatial variation among rates of N and P excretion measured in Taylorsville Lake was smaller than the 3-fold interannual variation in biomass. These data suggest that interannual variation in fish nutrient cycling should largely reflect variation in their abundance and supports our approach for deriving historical estimates based on average excretion rates and long-term monitoring of biomass. Low and invariant rates of P excretion were observed for both types of consumers and may be attributed to low P intake relative to metabolic needs (Olsen and Ostgaard 1985; Vadstein et al. 1995). The P content of fish tissues is typically 1.5-2.5% (Davis and Boyd 1978; Tanner et al. 1999; Sterner and George 2000) and the presence of hydroxyapatite in skeletal structure also contributes to P demand. For zooplankton, P values of 0.6-2.1 % have been reported (Anderson and Hessen 1991; Elser et al. 1996). By comparison, the P content of suspended particulate matter in Taylorsville Lake was only 0.2-0.5%. Although we did not quantify P in benthic sediments, these materials typically have lower nutrient content (as %) due to remineralization

during sedimentation and post-depositional processing (Burns and Ross 1971). The apparent P deficiency of food resources may favor high efficiency in assimilation and retention with correspondingly low rates of excretion. It is interesting to note that on the one date when gizzard shad P excretion rates were significantly higher (August 1998; upstream station), P concentrations in suspended particulate matter were also higher (11 $\mu$mol l$^{-1}$) than observed in other months (2-7 $\mu$mol l$^{-1}$). Without data quantifying clearance rates we cannot discern whether these consumers are experiencing P limitation in their diet, although this has been suggested in other studies (Sterner 1990; Vanni 1996; Gulati and Demott 1997).

We compared our estimates of fish contributions to nutrient cycling with data from a nearby, well-studied reservoir (Acton Lake, Ohio) that is also dominated by gizzard shad (Vanni 1996; Schaus et al. 1997). To facilitate comparison, we converted our epilimnetic loading rates relative to whole-lake volume. Despite similar excretion rates, volumetric loadings to Taylorsville Lake (0.115 $\mu$mol N l$^{-1}$ d$^{-1}$ and 0.016 $\mu$mol P l$^{-1}$ d$^{-1}$) were less than one third of those reported for Acton Lake (0.560 $\mu$mol N l$^{-1}$ d$^{-1}$ and 0.044 $\mu$mol P l$^{-1}$ d$^{-1}$). Gizzard shad biomass in Taylorsville Lake averaged only half of that reported for Acton Lake and inferred loading rates never exceeded values for Acton Lake despite a 3-fold variation in biomass between 1989 and 1997. The value of our long-term data was apparent when comparing gizzard shad contributions with tributary inputs. Data presented by Schaus et al. (1997) were collected in 1994 when tributary inputs to the lake were low and comparable to nutrient release from gizzard shad. Our data for Taylorsville Lake show a similar result for 1994 but suggest that these conditions are rare since tributary inputs often exceeded gizzard shad contributions by more than two-fold. Our average daily loading rates for gizzard shad were based on mid-day measurements of excretion and July-August estimates of fish abundance. Schaus et al. (1997) found that excretion by gizzard shad is maximal during mid-day due to higher feeding rates and suggested that nutrient release should be highest in mid-summer when fish abundance is greater. Therefore our estimates may approximate maximal rates more closely than growing-season averages.

Estimation of algal nutrient demand from primary production measurements and the Redfield ratio is problematic in part because photosynthesis may become uncoupled from biomass dynamics when nutri-

ents are limiting. In a concurrent study, we modeled phytoplankton production during downstream transport within a regulated river (Sellers and Bukaveckas 2003). We found that photosynthesis-irradiance models could accurately depict production during much of the growing season except in late summer when nutrient limitation resulted in overestimation of biomass accrual. A second potential problem in relating algal nutrient demand to tributary and consumer-mediated nutrient supply is the different time scales over which these processes are depicted. Annualized or monthly estimates of tributary loadings may be large in comparison to algal demands but these inputs are often associated with a few discrete storm events that generate large fluxes (Bukaveckas et al. 1993). Nutrient inputs may be utilized by phytoplankton within hours or days and subsequent depletion may increase the importance of smaller but continuous supply from consumer recycling.

Our assessment of nutrient fluxes for Taylorsville Lake considered only a subset of the internal processes regulating nutrient supply and demand. We focused on macrozooplankton and gizzard shad regeneration to assess the magnitude of these inputs relative to tributary loading and phytoplankton demand. We recognize that nutrient fluxes across the thermocline and sediment-water interface are also important components of epilimnetic nutrient budgets. Hypolimnetic entrainment may be an important source of nutrients in Taylorsville Lake during late summer as weakening thermal gradients coincided with increasing epilimnetic NH$_4$ concentrations. Sediment release of P can be important in shallow lakes and cycling is mediated in part by changes in iron oxidation state in seasonally anoxic hypolimnia (Wetzel 2001). Our findings and those of prior studies suggest that gizzard shad may facilitate transfer of sediment-bound P to the water column through detritivory and excretion. Carbon fluxes via the microbial loop and grazing by microzooplankton are large in some riverine systems (Servais et al. 2000) and we cannot discount the possibility that associated N and P pathways may also be an important component of consumer regeneration. For nitrogen, a complete accounting of sources and fate requires quantification of gain and loss through atmospheric exchange. Eyre and McKee (2002) showed that N fixation and denitrification were the largest components of the input and output budgets for a subtropical coastal embayment. N fixation may also be important in Taylorsville Lake given the prevalence of N limitation in

phytoplankton assays (Shostell 2001) and low N:P ratios of external inputs and consumer regeneration. A mass balance for the period from August 2000 to October 2001 revealed that N loss via the outflow of Taylorsville Lake was small (44%) in comparison to tributary inputs (McGaha 2003) suggesting that N fixation is low relative to denitrification and storage. While a comprehensive assessment of all pathways of nutrient supply and demand was beyond the scope of this study, our findings suggest that external nutrient loading to Taylorsville Lake was large in comparison to nutrient regeneration by gizzard shad and macro-zooplankton. Moreover, variation in nutrient loading during a 10-year period was large (100-fold) in comparison to variation in gizzard shad N and P regeneration suggesting that seasonal and interannual differences in supply were largely determined by runoff. Nutrients recycled by consumers were important in stabilizing and sustaining primary production during late summer and in years of below-average inflow.

## Acknowledgements

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