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NUTRIENT CYCLING BY FISH SUPPORTS RELATIVELY MORE PRIMARY PRODUCTION AS LAKE PRODUCTIVITY INCREASES

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Abstract. Animals can be important in nutrient cycling in particular ecosystems, but few studies have examined how this importance varies along environmental gradients. In this study we quantified the nutrient cycling role of an abundant detritivorous fish species, the gizzard shad (*Dorosoma cepedianum*), in reservoir ecosystems along a gradient of ecosystem productivity. Gizzard shad feed mostly on sediment detritus and excrete sediment-derived nutrients into the water column, thereby mediating a cross-habitat translocation of nutrients to phytoplankton. We quantified nitrogen and phosphorus cycling (excretion) rates of gizzard shad, as well as nutrient demand by phytoplankton, in seven lakes over a four-year period (16 lake-years). The lakes span a gradient of watershed land use (the relative amounts of land used for agriculture vs. forest) and productivity.

As the watersheds of these lakes became increasingly dominated by agricultural land, primary production rates, lake trophic state indicators (total phosphorus and chlorophyll concentrations), and nutrient flux through gizzard shad populations all increased. Nutrient cycling by gizzard shad supported a substantial proportion of primary production in these ecosystems, and this proportion increased as watershed agriculture (and ecosystem productivity) increased. In the four productive lakes with agricultural watersheds (>78% agricultural land), gizzard shad supported on average 51% of phytoplankton primary production (range 27–67%). In contrast, in the three relatively unproductive lakes in forested or mixed-land-use watersheds (>47% forest, <52% agricultural land), gizzard shad supported 18% of primary production (range 14–23%). Thus, along a gradient of forested to agricultural landscapes, both watershed nutrient inputs and nutrient translocation by gizzard shad increase, but our data indicate that the importance of nutrient translocation by gizzard shad increases more rapidly. Our results therefore support the hypothesis that watersheds and gizzard shad jointly regulate primary production in reservoir ecosystems.

Key words: agricultural land use vs. forest watersheds; Dorosoma cepedianum; *gizzard shad; lakes and reservoirs; nitrogen and phosphorus flux; nutrient limitation and cycling; primary productivity.*

INTRODUCTION

Animals can be important in nutrient cycling in a variety of ecosystems, including those in terrestrial (e.g., Belovsky and Slade 2000, Frank et al. 2000, Sirotnak and Huntly 2000, Lovett et al. 2002), marine (e.g., Kuenzler 1961, Bracken and Nielsen 2004), and freshwater (reviewed by Vanni 2002) biomes. Animals consume, release, and translocate nutrients at variable rates in different ecosystems, potentially affecting nutrient flux and primary producer communities to variable degrees. However, we know little about how animal-mediated nutrient cycling varies among ecosystems or along environmental gradients. Even for species known to have strong effects on nutrient dynamics in specific ecosystems, it is largely unknown how such effects vary spatially and temporally.

In aquatic ecosystems, animals as diverse as zooplankton, insects, mollusks, and fish can be important in nutrient cycling (Vanni 2002). However, no study has explicitly quantified the importance of nutrient cycling by a particular species along environmental gradients such as productivity or ecosystem size. The gizzard shad (*Dorosoma cepedianum*; see Plate 1) is an omnivorous fish that can be important in nutrient cycling, particularly in certain reservoir ecosystems in eastern North America (Vanni et al. 2005). Nonlarval gizzard shad (i.e., individuals less than ~3 months old) often consume

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relatively large amounts of detritus from sediments (Mundahl and Wissing 1987, Yako et al. 1996, Higgins et al. 2006). They then excrete some of the sediment-derived nutrients into the water column in dissolved inorganic forms available to primary producers. Thus gizzard shad translocate nutrients from sediments to water, providing a subsidy of "new" nutrients (sensu Dugdale and Goering 1967, Caraco et al. 1992) to phytoplankton that can utilize excreted nutrients (Vanni 1996, 2002). Gizzard shad are often abundant, so their populations can translocate nutrients at relatively high rates (Schaus et al. 1997, Shostell and Bukaveckas 2004, Vanni et al. 2005).

We know relatively little about how the importance of nutrient translocation varies with ecosystem productivity. Gizzard shad abundance increases greatly with increasing productivity (or lake trophic status) in both natural lakes and reservoirs, in terms of population density, biomass, and abundance relative to other fish species (Bachmann et al. 1996, DiCenzo et al. 1996, Michaletz 1998, Bremigan and Stein 2001, Vanni et al. 2005). Thus, nutrient flux through gizzard shad populations most likely increases with ecosystem productivity (Vanni and Headworth 2004). However, productive lakes also receive large nutrient inputs from watersheds and other sources; indeed, increased watershed inputs are a major reason why these lakes are productive (e.g., Carpenter et al. 1998, 1999). Thus, it is not clear how the relative importance of nutrient flux through gizzard shad varies along productivity gradients.

A model by Vanni and Headworth (2004) predicts that gizzard shad support an increasing proportion of primary production as lake productivity increases. In this paper, we provide the first explicit test of this prediction, using reservoirs in Ohio (USA) as study systems. It is important to test this prediction because reservoirs are the dominant lake type in the United States at latitudes between 30° and 42°, and gizzard shad are often the dominant fish species in these ecosystems. More broadly, our study represents the first explicit test of a hypothesis about how the nutrient-cycling role of a particular species varies along a productivity gradient.

In aquatic ecosystems, potential productivity is often correlated with land use practices in watersheds. As watersheds are converted from native vegetation to agricultural land or urban areas, nutrient export from watersheds to streams and lakes increases, sometimes greatly (e.g., Vitousek et al. 1997, Carpenter et al. 1998). In Ohio reservoirs, primary productivity and its proxies (total phosphorus and chlorophyll concentrations) are correlated with the percentage of watershed land used for agriculture (Knoll et al. 2003). Because watershed processes likely determine potential ecosystem productivity, we adopt a watershed perspective in our quest to understand the role of gizzard shad in nutrient cycling (Vanni et al. 2005). Specifically, we also test the hypothesis that gizzard shad support an increasing proportion of lake primary production as watershed land use becomes increasingly agricultural.

METHODS

General approach

We employed a supply/demand approach. Specifically, we estimated nutrient excretion rates of gizzard shad (supply) and uptake of nutrients by phytoplankton (demand). We then calculated the proportion of primary production supported by gizzard shad, defined as the supply of the limiting nutrient divided by demand for that nutrient (Schindler et al. 1993, Shostell and Bukaveckas 2004). The importance of a particular nutrient flux can also be evaluated by comparing its magnitude to that of other fluxes (Vanni 2002), but it is often difficult or impossible to quantify all nutrient sources, particularly in multiple ecosystems (Caraco et al. 1992, Binkley et al. 2000). The supply/demand approach is advantageous because one need not measure all, or even the majority of, nutrient sources. Rather, it is assumed that total nutrient supply (i.e., from all sources) equals nutrient demand. However, the supply/demand approach is appropriate only for the limiting nutrient, because the total supply of a nonlimiting nutrient may exceed demand for that nutrient. Therefore, we also quantified the magnitude of nitrogen (N) and phosphorus (P) limitation of phytoplankton in our study lakes.

Study sites

We quantified the importance of nutrient cycling by gizzard shad in seven reservoirs in Ohio, USA. These lakes span a wide gradient in watershed land use, in terms of agricultural land vs. forest; other land use types such as urban areas comprise minimal proportions (Table 1). All lakes are shallow and of moderate size in terms of surface area, typical features of most reservoirs in the midwestern United States. Three of our lakes (Burr Oak, Pleasant Hill, and Acton [see Plate 1]) were sampled relatively intensively over a four-year period (2000–2003) for this study. The other four lakes were each sampled twice in 2002. In each lake we estimated the supply of nutrients (N and P) via excretion by gizzard shad, the demand for these nutrients via phytoplankton primary production, and lake trophic status (total P and chlorophyll concentrations). In addition we determined whether N or P limited phytoplankton growth. Our sampling occurred in mid to late summer (early July through mid-September), so our results apply mainly to typical summer conditions. We also characterized land use in each of the lake's watersheds, using data from the U.S. Geological Survey (USGS 2003).

Nutrient supply by gizzard shad

Quantification of nutrient cycling by gizzard shad at the ecosystem scale requires information on the rates at which individual fish excrete nutrients, and the number and sizes of fish. We quantified gizzard shad abundance

TABLE 1. Characteristics of the study lakes and their watersheds.

Lake	Surface area (km^2)	Mean depth (m)	Watershed area (km^2)	Watershed land use (percentage of land area): Total agricultural land	Row crops	Pasture and hay	Forest	Other
Acton	2.32	3.9	257	89.0	76.2	12.8	9.5	1.5
Burr Oak	2.66	4.5	83	11.6	3.1	8.5	88.0	0.4
C. J. Brown	8.15	4.9	228	88.8	67.0	21.8	9.6	1.6
Kiser	1.56	1.9	21	78.3	61.8	16.5	20.9	0.8
O'Shaughnessy	4.05	4.7	1103	86.5	72.2	14.3	10.8	2.7
Piedmont	9.82	4.5	211	39.9	5.2	34.7	55.2	4.9
Pleasant Hill	3.12	4.8	512	52.3	25.6	26.7	47.7	3.9

Notes: Watershed areas and land use percentages do not include the study reservoirs themselves. Total agricultural land is equal to row crops plus pasture and hay. Some land use proportions and lake surface areas differ slightly from those in Knoll et al. (2003), because we used a different GIS database (USGS) here as compared to that used in Knoll et al. (Ohio Department of Natural Resources).

and size distributions in each lake in each year. Excretion rates were directly measured in the three intensively sampled lakes and extrapolated to others.

Population size and size-frequency distributions.—We used acoustic surveys to estimate gizzard shad population size and size-frequency distributions. In a given year, each lake was sampled once (most lakes and years) or twice (Burr Oak and Pleasant Hill in 2002 and 2003, and Piedmont in 2002). All surveys were conducted between 10 July and 4 September, where depth was >1.5 m. Generally this represented $>80\%$ of lake surface area.

A BioSonics DT 6000 echosounder (Biosonics, Incorporated, Seattle, Washington, USA) was used to collect both side-looking and down-looking data with mobile acoustic surveys. We used circular 200-kHz split-beam, 6° cone angle transducers, and sampled at 2.5 m/s and 5 pings/s with a pulse length of 0.2 ms, minimum threshold of -56 dB, source level of 214.1 dB/μPa, and receiver sensitivity of -53.0 dB/μPa. Latitude and longitude coordinates were written to each file via a Trimble (Tulsa, Oklahoma, USA) or Lowrance Electronics (Sunnyvale, California, USA) DGPS unit. The acoustic system was first calibrated by Biosonics, and then field calibrated before each survey with a tungsten carbide reference sphere of known acoustic size (Foote and MacLennan 1984). For side-looking surveys, data were collected from the lake surface to 2 m below the surface, 5–20 m from the transducer. For down-looking surveys, the transducer was mounted 0.5 m beneath the surface and data were collected from 2 m below the surface to just above the bottom. Echo integration processing parameters processed these data to within 0.5 m of the bottom.

Areal estimates of abundance were obtained by echo integration (MacLennan and Simmonds 1992). Acoustic data were processed to obtain the mean size of fish for scaling the echo integration relative densities. Total reflected voltages from echo integration were converted to absolute areal abundance (fish per square meter) by scaling voltages by average back-scattered cross sections from individual fish targets within 4 dB of the center of the beam. Scaling constants were stratified when back-scattered voltages from single targets changed by more than 1.5 dB and the number of targets was sufficient. Lengths of fish were estimated by collecting a random subsample of individual targets from down-looking acoustic surveys and applying Love's dorsal aspect equation (Love 1971). We used this equation to convert individual acoustic target strength ($-$dB) to total length in millimeters.

Acoustic methods cannot distinguish among different species of fish, but rather provide data on the number of fish of all species. Therefore, we used electrofishing surveys to estimate the percentage of fish that were gizzard shad. In each of the three intensively sampled lakes (Burr Oak, Pleasant Hill, and Acton), we conducted electrofishing surveys in areas where depth was >1.5 m (i.e., where acoustics data were gathered). We conducted surveys nine times in each lake (27 total), from July to October 1998–2000. Each survey consisted of several 300-second transects. In total we captured 1697 fish in the three lakes (445, 559, and 693 fish from Burr Oak, Pleasant Hill, and Acton, respectively). Gizzard shad comprised a high, and remarkably consistent, percentage of these fish (93.5%, 94.1%, and 93.7% in Burr Oak, Pleasant Hill, and Acton; overall mean of 93.7%). Therefore, to estimate gizzard shad population size in each lake, we multiplied total fish abundance (from acoustics estimates) by 0.937 in all lakes.

Nutrient excretion rates.—Nutrient excretion rates are dependent on body mass, so gizzard shad sampled with acoustics were grouped into 50-mm (total length) bins. For each bin, we used the length midpoint to estimate mean body mass using length–mass regressions. For Acton, Burr Oak, and Pleasant Hill, we used length–mass regressions specific to each lake. Then we calculated per capita excretion rates (i.e., mg N and P excreted per fish per day) for that size class using regressions of body mass vs. per capita excretion rate, also specific to each of those lakes. The body mass–excretion regressions were derived from direct measurements of excretion rates in Acton made during the summers of 1994 (Schaus et al. 1997) and in Acton, Burr Oak, and Pleasant Hill during summers of 1999–2001 (Higgins et al. 2006), when lake epilimnion temperatures were 24°–28°C (see Appendix). For excretion measurements, individuals of a range of sizes were collected by electrofishing at the upstream end of each reservoir during midday, i.e., after shad had been feeding for several hours. Individual fish were placed for ~30 min in coolers with 4 L of lake water prefiltered (0.3-μm glass fiber filter; Gelman AE filters, Pall Corporation, East Hills, New York, USA) to remove algae and bacteria that could take up released nutrients. Samples for final nutrient concentrations were collected and immediately filtered (Pall A/E filters). Excretion rates were obtained as the difference between initial and final N and P concentrations. Details are provided in Schaus et al. (1997) and Higgins et al. (2006).

In total, size-dependent excretion rates were measured five times during summer in Acton, and three times each during summer in Burr Oak and Pleasant Hill (see Appendix; Schaus et al. 1997, Higgins et al. 2006). For each size class, we calculated excretion rates with each regression equation from that lake, then averaged these rates. The average was then used as an estimate of excretion rate per fish for that size class. Then, we multiplied per fish excretion rate by the number of fish in that size class to obtain a lakewide excretion rate for that size class, and summed size class excretion rates to generate lakewide excretion rates for the entire population.

We do not have direct measures of gizzard shad excretion rates in the other four lakes. Therefore, we estimated per capita excretion rates in these lakes with mass vs. excretion regression equations derived from intensively sampled lakes, by matching lakes based on trophic status (Table 1). Thus, for Piedmont, we used Burr Oak regressions, for C. J. Brown we used Pleasant Hill regressions, and for Kiser and O'Shaughnessy we used Acton regressions. This assumes that fish in lakes of similar trophic status have similar per capita excretion rates; we address the implications of this assumption in the *Discussion*.

Nutrient demand by phytoplankton

Nutrient demand by phytoplankton was quantified by measuring phytoplankton primary production rates and phytoplankton (seston) nutrient ratios (Schindler et al. 1993). Specifically, we divided primary production rate (milligrams of carbon per square meter per day) by seston C:P or C:N ratio (mass : mass) to generate nutrient demand (milligrams of N or P per square meter per day). We also characterized lake trophic status (total phosphorus and chlorophyll concentrations) so that we could examine the relationship between trophic status and nutrient flux through gizzard shad.

Phytoplankton and nutrient sampling.—Each lake was sampled at least twice in each year between early July and early September (see Fig. 1 for the number of dates). For each sampling event, integrated samples were repeatedly collected from the euphotic zone (surface to the depth at which photosynthetically active radiation (PAR) = 1% of surface irradiance) at the deepest part of each lake (near the dam) until sufficient volume of water was obtained to fill two sample containers. One sample was placed in a 2-L amber nalgene bottle and used to quantify primary production rate. The other sample was placed in a 4-L translucent bottle, and was used to estimate total P, chlorophyll, and seston nutrient concentrations. In addition, PAR was measured at 0.5-m intervals (using a LI-COR spherical sensor [Lincoln, Nebraska, USA]), and water was collected at 1-m intervals with a Van Dorn sampler to quantify depth-specific chlorophyll concentrations (see *Primary production* for estimates).

To quantify chlorophyll *a* concentration, phytoplankton samples were filtered onto Pall A/E glass fiber filters (Pall Corporation), frozen, and stored in the dark. Chlorophyll was extracted with acetone in the dark at 4°C, and quantified with a Turner fluorometer (Turner Designs, Sunnyvale, California, USA). Samples for total P were transferred to 125-mL nalgene bottles and acidified with H_2SO_4. They were then digested with potassium persulfate to convert all P to soluble reactive P (SRP), which was then quantified with a Lachat autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Seston carbon, N, and P concentrations were also quantified on integrated samples. Samples were first passed through a 63-μm mesh to remove large zooplankton, then collected onto glass fiber filters. For C and N, samples were collected on 25-mm Pall A/E filters, frozen, and assayed using a PerkinElmer Series 2400 elemental analyzer (PerkinElmer Life And Analytical Sciences, Wellesley, Massachusetts, USA). For P, samples were collected onto 47-mm Pall A/E filters, digested with HCl and assayed for soluble reactive P as for total P samples (Stainton et al. 1977). "Seston" includes phytoplankton as well as bacteria and detritus. We assume that the seston nutrient ratios are reflective of those in phytoplankton (Sterner and Elser 2002).

Primary production.—Primary production rates were quantified by measuring ^{14}C uptake following methods of Fee et al. (1989). Detailed methods are described in Knoll et al. (2003). Briefly, we measured ^{14}C uptake of phytoplankton at a range of PAR levels in the laboratory, and from these generated a chlorophyll-specific photosynthesis vs. irradiance (PI) curve. The PI curves were used with depth-specific PAR and chlorophyll concentrations in the lakes to obtain lake-wide primary production rates, corrected for lake morphometry (i.e., the volume of water at each depth) for each date, using the computer program DPHOTO (Fee 1990). We use cloud-free primary production rates (Fee et al. 1992); these reflect maximal nutrient demand by phytoplankton, and are comparable across sample dates and lakes.

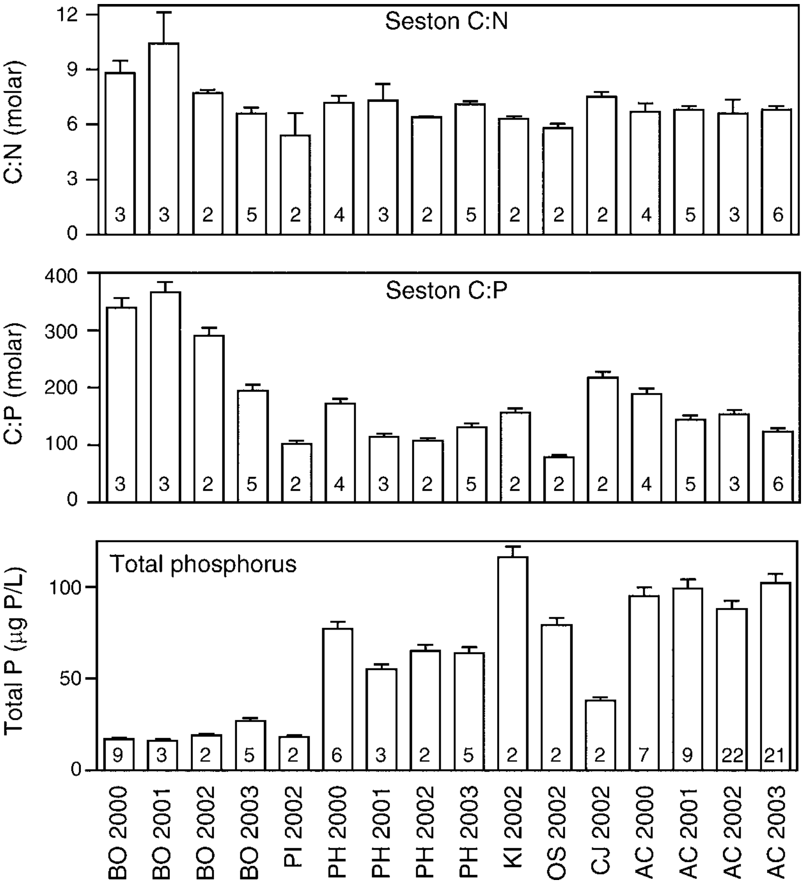

FIG. 1. Lake production parameters, including nutrient supply (excretion by gizzard shad) and demand (uptake by phytoplankton) in the seven study lakes, 2000–2003. Ratios of C:N and C:P are expressed on a molar basis. Lakes are ordered according to the percentage of watershed land composed of agriculture, then by year. Bars are simple means (±SE) of all sample dates. Numbers at the base of each bar represent the number of sampling events that year for that parameter. Nutrient supply and demand panels have no error bars because each was estimated once per year using a composite of sampling dates. Lake abbreviations are BO, Burr Oak; PI, Piedmont; PH, Pleasant Hill; KI, Kiser; OS, O'Shaughnessy; CJ, C. J. Brown; and AC, Acton.

Phytoplankton nutrient limitation

In order to estimate the proportion of primary production supported by nutrient cycling by gizzard shad, information on the identity of the limiting nutrient for phytoplankton is needed. Therefore, we conducted growth bioassay experiments on the same dates we measured primary production rates. Integrated samples were collected as described above, placed in clear plastic containers, and returned to the laboratory for experiments, which were always initiated within 24 hours of sampling. In the laboratory, water was passed through a 63-µm mesh to remove large zooplankton, and then 350 mL water was distributed to each of eight 500-mL Erlenmeyer flasks. We present results from three treatments, each represented by duplicate flasks: Control (no nutrients added); +N (50 µmol/L N added as NH_4NO_3); and +P (2.5 µmol/L P added as $NaH_2PO_4 \cdot H_2O$). Phytoplankton were incubated at an irradiance of 200 µmol PAR$\cdot$m$^{-2}\cdot$s^{-1} for 48 hours, at which time samples from each flask were filtered and analyzed for chlorophyll. We assessed nutrient limitation status in each experiment using ANOVA on final log-transformed chlorophyll concentrations. We then used the Tukey-Kramer HSD test (JMP, SAS 2002) to compare specific treatments. We considered phytoplankton to be limited by N or P if addition of one of these nutrients resulted in final chlorophyll concentrations that were significantly greater than in the control. In some cases, chlorophyll increased significantly in both single-nutrient treatments. In these cases we considered the nutrient eliciting the strongest response to be the primary limiting nutrient.

Statistical analyses of trends

We hypothesized that the relative importance of nutrient cycling by gizzard shad increases with lake productivity, i.e., that the proportion of primary production supported by gizzard shad increases with lake productivity. To test this hypothesis, we used simple linear regressions, with the proportion of primary production supported by nutrient excretion by

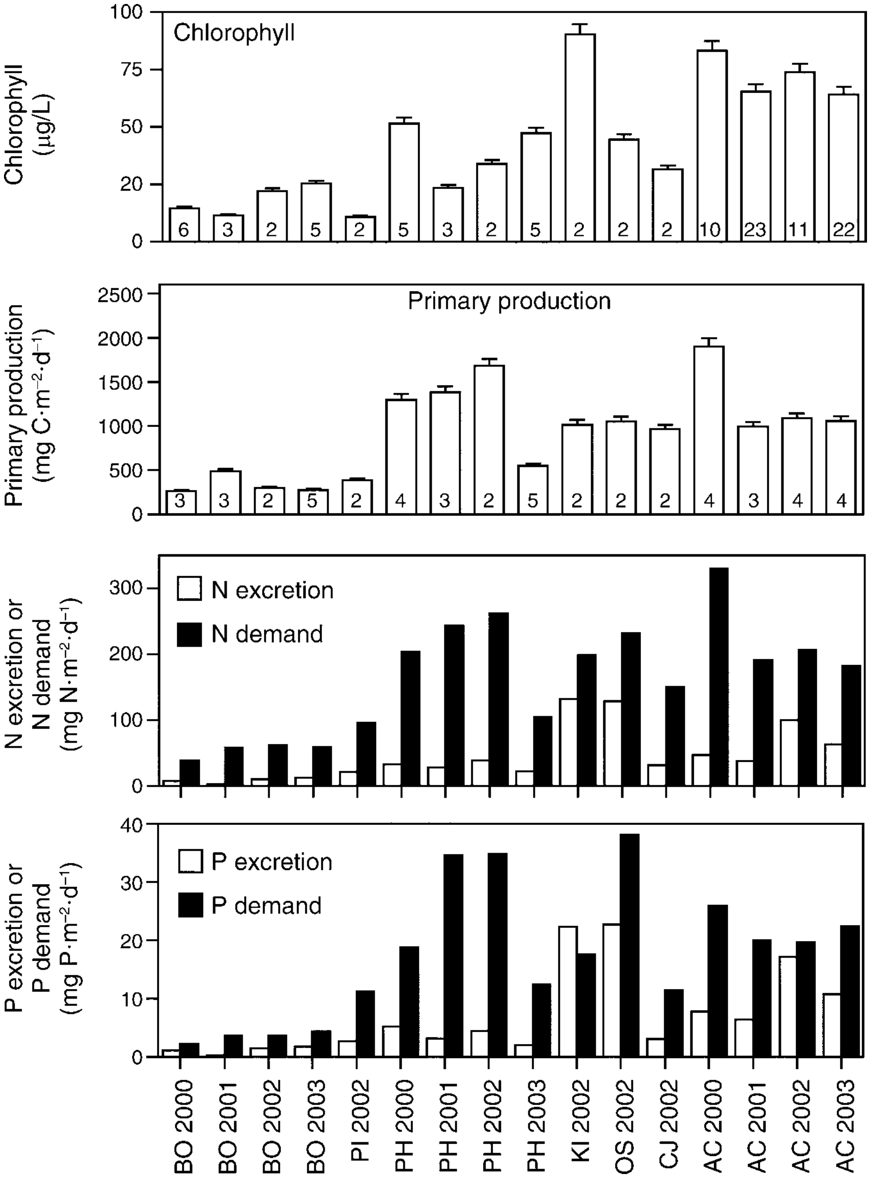

FIG. 1. Continued.

gizzard shad as the dependent variable, and three different indicators of lake productivity as independent variables: TP, chlorophyll, and the percentage of watershed land used for agriculture (hereafter percentage watershed agriculture). The two former independent variables are often used as proxies for productivity (e.g., Smith 1998), and percentage watershed agriculture can serve as a measure of potential lake productivity (Knoll et al. 2003). We did not use primary production as an independent variable in these regressions because of potential autocorrelation problems, i.e., primary production rate would have been used in both independent and dependent variables. We also examined whether the type of agriculture (percentage of row crop vs. pasture; Table 1) was related to the proportion of production supported by gizzard shad. Because nutrient loading to a lake may also be a function of watershed size relative to lake size, we also examined patterns using four different indicators of relative watershed size and/or nutrient loading: the ratio of watershed area to lake surface area (WA:LA); the ratio of watershed area to lake volume (WA:LV); and two "nutrient loading indices." The first loading index was obtained by multiplying WA:LA by percentage watershed agriculture, and the second by multiplying the WA:LV by percentage watershed agriculture. Finally, we also used linear regression to quantify relationships between the various trophic state variables and primary production.

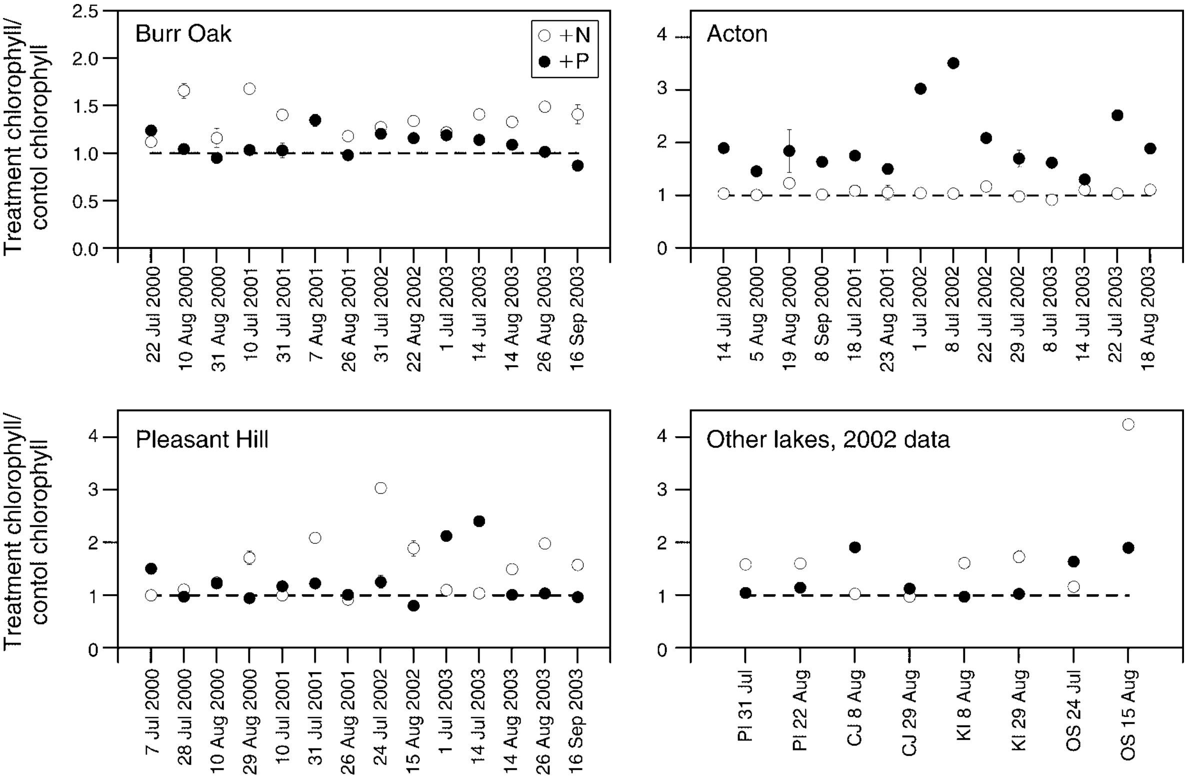

FIG. 2. Results of nutrient limitation experiments for three lakes (2000–2003) and for other lakes (2002 only). For each point, the mean of the control replicates was used as the denominator. Each treatment replicate was then divided by the control mean, and the mean (±SE) of these ratios is plotted here. An apparent lack of error bar on some points indicates that the SE was smaller than the symbol, except in one case (O'Shaughnessy, 24 July 2002, P treatment); in this case only one replicate was employed due to methodological problems. Note that although ratios are presented here, statistical analyses were conducted on actual chlorophyll concentrations, as described in *Methods*. Dashed lines indicate the threshold for nutrient limitation (values above the dashed lines indicate nutrient limitation). See Fig. 1 legend for lake abbreviations.

For all regression analyses, we used weighted regressions with a single value for each lake (i.e., $n = 7$). In each year we obtained simple means for each variable, using all samples collected in a given summer (July–early September). For the lakes sampled for more than one year (Acton, Burr Oak, and Pleasant Hill), we then used a simple mean of these annual means as an observation. In each regression, we weighted the impact of each lake by the number of years it was sampled, i.e., Acton, Burr Oak, and Pleasant Hill were assigned weights of 4, and the other four lakes were assigned weights of 1. The weighting scheme reflects the notion that more confidence should be placed in the lakes sampled most intensively. All data were transformed prior to analyses to stabilize variances. Data on the percentage of watershed used for agriculture, the percentage in row crops, and the percentage in pasture were arcsine square-root transformed, while other variables were log-transformed. For all regressions, we report adjusted r^2 values. Statistical analyses were conducted using JMP software (version 5.0.1a, SAS 2002).

RESULTS

Lake trophic status

Lakes varied ~4–5× in trophic status indicators such as TP, chlorophyll, and primary production (Fig. 1). Within lakes for which we have multiple years of data, trophic status indicators were relatively consistent among years. TP, chlorophyll, and primary production were relatively low in Burr Oak, high in Acton, and intermediate in Pleasant Hill. Within a lake, TP was less variable than chlorophyll or primary production, both within and among years. Seston C:P and C:N ratios showed less variation among lakes than trophic status indicators. C:N ratios varied ~2× and C:P ratios ~3× among lakes.

Phytoplankton nutrient limitation

We observed instances of both N and P limitation (Fig. 2). Burr Oak phytoplankton increased significantly when N was added in 13 of 14 experiments. In five experiments phytoplankton also responded to P, but the response to N was always greater. Thus we conclude that N is the primary limiting nutrient in Burr Oak.

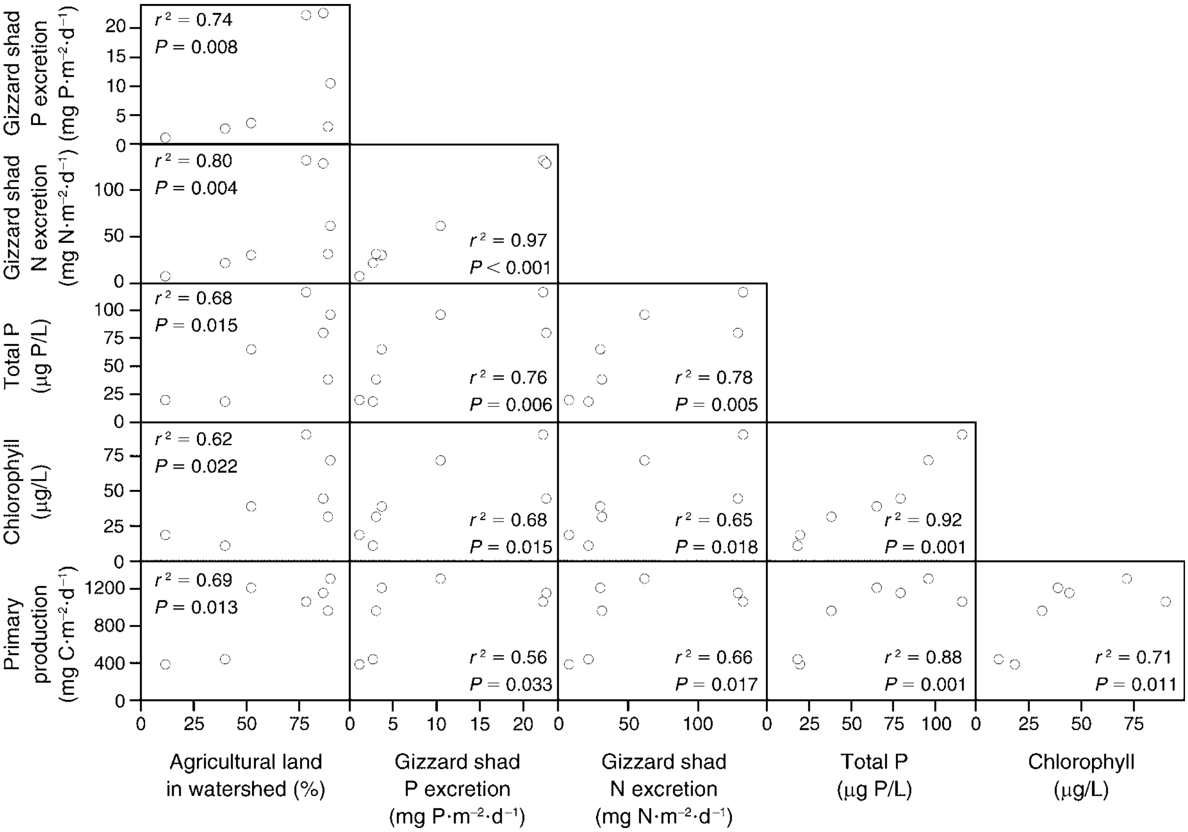

FIG. 3. Matrix of correlations between watershed land use (percentage of watershed land used for agriculture), lake trophic state indicators, and nutrient excretion by gizzard shad. Although untransformed data are presented here, statistics are based on weighted regressions on transformed data (see *Methods* for details).

Acton phytoplankton biomass increased significantly when P was added in 13 of 14 experiments, and never increased in the +N treatment (Fig. 2). Thus we conclude that P is the primary limiting nutrient in Acton. Pleasant Hill phytoplankton biomass responded significantly to additions of N (seven experiments) and P (five experiments; Fig. 2). Thus, N limitation was slightly more frequent than P limitation for Pleasant Hill phytoplankton.

In both Kiser experiments and both Piedmont experiments, phytoplankton responded to N, but not P (Fig. 2). In one Piedmont experiment, addition of P increased biomass, but the response was much weaker than to N addition. We conclude that N was the primary limiting nutrient for both Kiser and Piedmont. In the first C. J. Brown experiment, phytoplankton increased when P was added, and N addition had no effect (Fig. 2). In the second C. J. Brown experiment, phytoplankton did not respond significantly to either N or P (phytoplankton did respond to addition of both N and P; data not shown). In the latter experiment, P addition seemed to have more effect than N addition, but the difference was not significant. We conclude that P is the primary limiting nutrient in C. J. Brown. In the first O'Shaughnessy experiment, addition of P but not N stimulated phytoplankton biomass, while in the second O'Shaughnessy experiment the reverse was true. Thus O'Shaughnessy phytoplankton were equally limited by N or P.

Relationships between trophic status and watershed land use

The trophic status indicators were all significantly correlated with each other, and with the percentage of watershed area composed of agricultural land (Fig. 3). Lake-wide N and P excretion rates of gizzard shad were also significantly correlated with trophic status indicators and with watershed agriculture. Thus, as the extent of watershed agriculture increased, so did lake trophic status (as indicated by TP, chlorophyll and primary production), and N and P flux through gizzard shad populations (Fig. 3). In general, correlations were similar (r^2 within ±0.05) when we used percentage of row crops rather than percentage of agriculture as the independent variable in these regressions. The exception was with chlorophyll as the dependent variable; in this case r^2 was 0.62, with percentage agriculture as the independent variable and 0.73 with percentage of row crops as the independent variable. None of the correlations using percentage of pasture as the independent variable were significant, nor were any of the correlations using the

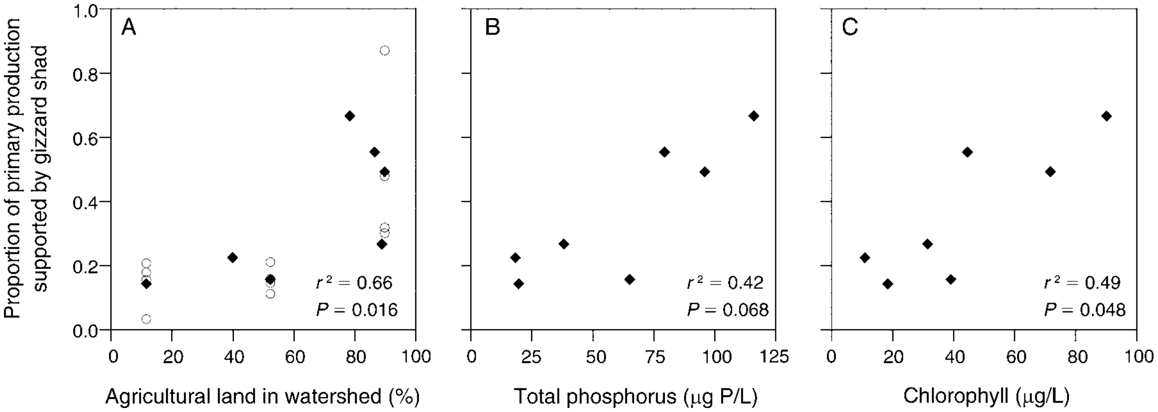

FIG. 4. Relationships between (A) watershed land use (percentage of watershed land used for agriculture), (B) total P, and (C) chlorophyll and the proportion of primary production supported by nutrient excretion by gizzard shad. In (A), the open circles represent individual annual means for (left to right across graph) Burr Oak, Pleasant Hill, and Acton Lakes. In all panels, the diamonds represent overall means for a lake, using all years pooled together. Although untransformed data are presented here, statistics are based on weighted regressions on transformed data (see *Methods* for details).

watershed size or "loading indices" ($r^2 < 0.20$, $P > 0.17$ in all cases).

Nutrient supply and demand

Nutrient flux through gizzard shad accounted for a variable fraction of nutrient demand, ranging from ~3% of phytoplankton N uptake in Burr Oak in 2001 to >100% of P uptake in Kiser (Fig. 1). For a given nutrient (N or P), supply (excretion by gizzard shad) and demand were highly correlated (log N demand = 1.455 + 0.472 log N excretion, $r^2 = 0.646$, $P = 0.0002$; log P demand = 0.762 + 0.585 log P excretion, $r^2 = 0.582$, $P = 0.0006$).

To estimate the proportion of phytoplankton primary production supported by gizzard shad, we divided nutrient supply (excretion by gizzard shad) into demand for the limiting nutrient. As lake trophic status increased, gizzard shad supported an increasing proportion of primary production (Fig. 4). This pattern held regardless of whether percentage agriculture, TP, or chlorophyll was used as the predictor variable, although the trend with TP was only marginally significant (Fig. 4B). The proportion of primary production supported by gizzard shad ranged from ~3% in Burr Oak in 2001 to 87% in Acton Lake in 2002 (Fig. 4A). The association between land use and the proportion of primary production supported by shad was even stronger when percentage of row crops was used as the independent variable ($r^2 = 0.73$, $P = 0.0090$) instead of percentage total land used for agriculture ($r^2 = 0.66$, $P = 0.0162$; Fig. 4A). In contrast, percentage pasture was not correlated with the proportion of primary production supported by gizzard shad ($r^2 = 0.01$, $P = 0.8102$). The relationship between watershed land use and the proportion of primary production supported by shad appears to exhibit a somewhat threshold response (Fig. 4A). Thus, in the four lakes with mostly agricultural watersheds (>78% of land used for agriculture; >60% of land in row crops), shad supported >25% of primary production (mean 51%; range 27–67%). In contrast, in the three lakes in watersheds with ≤53% agricultural land (<26% row crops), gizzard shad supported <25% of production (mean 18%; range 14–23%). These patterns also held among years in the three intensively sampled lakes. Thus, gizzard shad supported >30% of primary production in all four years in Acton, while in Burr Oak and Pleasant Hill, gizzard shad supported <22% in all four years (Fig. 4A).

DISCUSSION

Gizzard shad as a source of nutrients for phytoplankton

Our results show that nutrient cycling by a single animal species, in this case gizzard shad, can support a substantial proportion of primary production in reservoir ecosystems. Furthermore, the proportion of primary production supported by gizzard shad increases as the watersheds of these lakes become more agricultural, and hence as lake trophic status increases. Based on diet analyses in three lakes that span our land use/productivity gradient (Acton, Burr Oak, and Pleasant Hill), gizzard shad derive >90% of their dietary N and P from sediment detritus (Higgins et al. 2006). Thus, nearly all nutrients excreted by gizzard shad are translocated from sediments, and can be considered "new" nutrients (sensu Dugdale and Goering 1967, Caraco et al. 1992), because they are delivered to the euphotic zone from outside this habitat.

The importance of nutrient cycling by a consumer can be evaluated in at least three ways (Vanni 2002): (1) by comparing nutrient flux through the consumer to nutrient demand, as in this study; (2) by comparing consumer-mediated nutrient cycling rates to other nutrient input rates; and (3) by conducting experiments

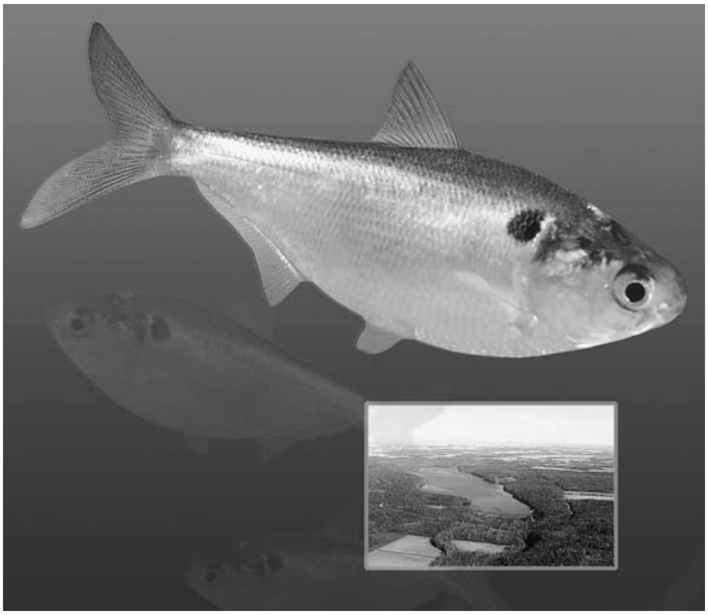

PLATE 1. An adult gizzard shad (*Dorosoma cepedianum*). Gizzard shad are important in cycling nutrients in reservoir ecosystems, and their importance increases with lake productivity (and with the extent of agriculture in lake watersheds). Eutrophic Acton Lake (inset) resides in a forested state park, but 89% of its watershed is agricultural land, and gizzard shad supply, on average, ~50% of the phosphorus needed to support primary production. Photo credits: main photo, M. Vanni; inset, W. H. Renwick.

that isolate and quantify effects of consumer-mediated nutrient cycling on recipient organisms (e.g., primary producers). Evidence from all three approaches suggests that gizzard shad are an important source of nutrients, particularly in productive reservoirs.

Only one other study has quantified the proportion of phytoplankton nutrient demand sustained by gizzard shad. Shostell and Bukaveckas (2004) found that nutrient excretion by gizzard shad supplied 14–20% of P uptake and 31–58% of N uptake by phytoplankton in a reservoir in Kentucky. Agricultural land comprises 76% of the lake's watershed, and the lake is N limited. Thus we can infer that shad supported 31–58% of primary production. This proportion fits well in the relationship we observed between watershed agriculture and support of production (Fig. 4).

Comparison of nutrient fluxes in Acton Lake also shows that gizzard shad are an important source of nutrients. Lake-wide N and P fluxes through gizzard shad substantially exceed the rates at which N and P are supplied to the Acton Lake euphotic zone via release from sediments and entrainment from the hypolimnion (Nowlin et al. 2005). Watersheds are another potentially large source of nutrients to reservoirs, especially during storms when large quantities of nutrients are delivered via inflow streams (Vanni et al. 2001, 2005, Shostell and Bukaveckas 2004). Within a reservoir the relative importance of watershed inputs vs. excretion by gizzard shad depends on stream flow, which in turn depends on precipitation and runoff. During wet periods, watersheds deliver more nutrients than nutrient excretion by shad, but during dry periods (i.e., late summer), excretion by shad often exceeds watershed inputs (Shostell and Bukaveckas 2004, Vanni et al. 2005).

In our study, gizzard shad rarely supported substantially more than 50% of primary production, even in the agriculturally impacted lakes. Yet, as mentioned above, nutrient flux through gizzard shad most likely exceeded other inputs of "new" nutrients (i.e., from the watershed and sediments), at least in Acton Lake. It is probable that nutrient recycling by zooplankton and microbes within the water column ("regenerated" nutrients) supports significant amounts of production in these and other lakes (Hudson et al. 1999). Even in lakes in which nutrient excretion rates of gizzard shad are >50% of primary producer nutrient demand, recycling within the water column may exceed excretion by shad, even for the limiting nutrient. This may seem contradictory, because it implies that supply exceeds demand, which should not be the case for the limiting nutrient. However, it is important to note that uptake by phytoplankton is not the only sink for nutrients in the water column. In particular, bacteria may be important in nutrient uptake (Cotner and Biddanda 2002), and in hard-water lakes such as these, precipitation of P with calcium may also be a sink for P (e.g., Kleiner and Stabel 1989, Nürnberg 1998*a*). Thus, even for the limiting nutrient, total supply probably exceeds demand by primary producers (but presumably not total demand).

Numerous experiments in ponds and mesocosms show that gizzard shad can increase phytoplankton biomass and/or water column nutrients (Drenner et al. 1986, 1996, Schaus and Vanni 2000, Watson et al. 2003). In addition, in a comparative study of 20 Illinois reservoirs, Aday et al. (2003) found that phytoplankton biomass was ~1.7× higher in reservoirs with gizzard shad than in those without gizzard shad. Enhancement of phytoplankton by gizzard shad can occur via nutrient translocation and/or trophic cascades. However, an experiment in Acton Lake showed that gizzard shad enhance water column nutrient concentrations and phytoplankton biomass only when they have access to sediments (i.e., when they can translocate nutrients), and not when they are experimentally prevented from feeding on sediments (Schaus and Vanni 2000).

Thus nutrient flux measurements, supply/demand studies, and field experiments all support the notion that gizzard shad are a substantial source of new nutrients. Although most of this evidence derives from reservoirs, gizzard shad are also abundant in warmwater natural lakes (e.g., in Florida [Bachmann et al. 1996]) and rivers, and may be important in these ecosystems as well.

Nutrient flux through gizzard shad along a productivity gradient

Gizzard shad sustained an increasing proportion of primary production as watershed agriculture increased. As landscapes are degraded from forest to agricultural land, watersheds deliver more nutrients to downstream lakes (e.g., Carpenter et al. 1998). Yet our results imply that with increasing agriculture, nutrient translocation by gizzard shad reinforces the effects of increased nutrient loading from watersheds. That is, an increase in watershed agricultural land causes an increase in nutrient loading, which causes both an increase in phytoplankton production and an increase in gizzard shad biomass. Increased gizzard shad biomass causes a further increase in phytoplankton production.

The positive relationship between watershed agricultural land and nutrient flux through gizzard shad is driven largely by increased gizzard shad biomass. In our study, shad biomass and nutrient excretion were highly correlated (N excretion: $r^2 = 0.89$; P excretion: $r^2 = 0.93$; log-log regression, $n = 7$). Other studies in reservoirs (DiCenzo et al. 1996, Michaletz 1998) and natural lakes (Bachmann et al. 1996) have found that gizzard shad abundance increases with ecosystem productivity (although no other studies have explicitly related gizzard shad abundance to watershed land use). Thus, there likely exists a general, positive relationship between ecosystem productivity and nutrient flux through gizzard shad populations. We cannot evaluate the magnitude of nutrient flux through gizzard shad in the two other reservoir studies (DiCenzo et al. 1996, Michaletz 1998) because these studies only present relative abundance (catch per unit effort), not actual biomass. Bachmann et al. (1996) present data on gizzard shad biomass in 65 natural lakes in Florida; gizzard shad were completely absent from oligotrophic lakes, common in lakes of moderate productivity, and by far the most abundant fish species in highly productive lakes. Based on the data in Bachmann et al. (1996), it appears that gizzard shad biomass is lower in the Florida lakes than in our study reservoirs, at a given level of productivity (chlorophyll or total P). This difference may be due to the fact that gizzard shad receive a greater subsidy of terrestrially derived detritus in reservoirs (because reservoirs have larger watersheds than natural lakes), or because of methodological differences. (Bachmann et al. [1996] estimated fish biomass in a single cove in each lake using rotenone, a fish poison.) As the use of hydroacoustics becomes more common in reservoirs and natural lakes, we should be able to more generally assess how nutrient flux through fish varies with productivity and along other ecological gradients.

In some lakes, substantial amounts of nutrients are tied up in fish biomass (Vanni 2002). If gizzard shad function increasingly as nutrient sinks along the land use gradient (because of greater abundance), this could theoretically moderate their role in nutrient cycling. Thus it is useful to explore the extent to which gizzard shad act as a sink for nutrients. We evaluated this at the scale of a growing season (spring to late summer) in Acton Lake by examining seasonal changes in nutrients stored in shad biomass. For all age classes, we used the acoustics data as an estimate of late-summer abundance. For all age classes except young-of-year (YOY), we estimated the abundance of shad in spring (May) by interpolating the number of fish observed in consecutive late summer acoustics surveys. For YOY, we used the peak estimate of larval gizzard shad abundance (obtained with ichthyoplankton tows; M. J. González and M. J. Vanni, *unpublished data*) as our spring estimate. At each time period, we multiplied the biomass of shad in each age class by body P content of Acton Lake gizzard shad (1% of dry mass for larvae and 3% of dry mass for other ages; A. Pilati, L. E. Torres, and M. J. Vanni, *unpublished data*) to obtain the mass of P tied up in shad biomass; the change in this mass from spring to late summer represents net sequestration of P by shad growth.

During the four years of this study, growth of the entire Acton Lake gizzard shad population sequestered on average 1.3 mg $\text{P}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (range 0.7–2.4 mg $\text{P}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) from mid-May through mid-September. In comparison, gizzard shad excreted on average 10.5 mg $\text{P}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (range 6.4–17.1 mg $\text{P}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) in late summer (Fig. 1). The ratio of P excreted to P sequestered was on average 8.6 (range 7.1–10.3). Thus, over the scale of a growing season, gizzard shad excreted much more P than they sequestered in biomass. Because there was no trend in mean annual biomass over these four years, it is also unlikely that the gizzard shad population sequestered P from year to year. It seems quite reasonable that shad excreted much more P than they sequestered, because assimilated P has only two fates, allocation to growth or excretion, and fish usually assimilate much more P than they allocate to growth (Schindler and Eby 1997). Thus, even though a substantial amount of nutrients can be tied up in gizzard shad biomass, and this amount increases with lake productivity, the amount excreted by shad appears to greatly exceed that sequestered by the population. Unfortunately, we do not have data on larval shad in the other lakes to estimate nutrient sequestration (in Acton, YOY fish accounted for ~68% of P seasonal P sequestration). However, because shad biomass is high in Acton, we would expect nutrient sequestration also to be high compared to most other lakes.

Drenner et al. (1996) suggested that the stimulatory effects of benthic-feeding fish (such as gizzard shad) on phytoplankton increase with productivity in reservoir ecosystems, and therefore that nutrient in inputs and benthivorous fish synergistically regulate phytoplankton biomass. This hypothesis is supported by mesocosm experiments in which gizzard shad had greater effects on phytoplankton, zooplankton, and nutrients at high productivity than at low productivity (Drenner et al. 1996). Drenner et al. (1996) also proposed nutrient translocation as a potential mechanism accounting for this interactive effect, but did not have the data necessary to assess this mechanism. Our finding that gizzard shad support an increasing proportion of primary production as watershed agriculture increases is consistent with this synergism hypothesis, and implicates nutrient translocation as a mechanism by which external nutrient loading (driven by watershed land use) and omnivorous fish jointly control realized reservoir productivity. However, it is possible that trophic interactions may contribute to the patterns we observed with respect to regulation of productivity by gizzard shad. High densities of YOY gizzard shad can depress the abundance of zooplankton grazers (e.g., DeVries and Stein 1992, Dettmers and Stein 1996), which could lead to reduced grazing pressure on phytoplankton and ultimately increased phytoplankton abundance. However, we feel that the nutrient translocation mechanism is more likely in our study, because in late summer (when we conducted our study), all age classes of gizzard shad including YOY are detritivorous in these reservoirs (Higgins et al. 2006), and an experiment in Acton Lake showed that detritivorous gizzard shad increase phytoplankton biomass by translocating nutrients and not via a trophic cascade (Schaus and Vanni 2000). Whether the mechanism involves nutrient translocation and/or trophic cascades, the potentially synergistic relationship between productivity and gizzard shad effects has important implications for the functioning of reservoir ecosystems and for managing eutrophication (Drenner et al. 1996, Power et al. 2004, Vanni et al. 2005).

Our finding that the proportion of primary production supported by gizzard shad increases with lake productivity agrees with predictions of a model developed by Vanni and Headworth (2004), even though one potentially important model assumption was not met. Specifically, the Vanni-Headworth model predicted that P excretion rates of individual gizzard shad (i.e., per fish or per gram fish mass) would increase with productivity because sediment P content increases with productivity (Nürnberg 1988*b*), and stoichiometry predicts increasing P excretion rates with increasing food P content (Sterner and Elser 2002). In contrast, per capita excretion rates were higher in Burr Oak (low productivity) than in Acton (high productivity) and usually intermediate in Pleasant Hill (moderate productivity), apparently because selective feeding on high-nutrient detritus was more pronounced in Burr Oak (Higgins et al. 2006). However, N and P flux through shad populations (i.e. at the ecosystem scale) nevertheless increased with lake productivity because shad population size increased so greatly with increasing productivity.

Assumptions and limitations of the supply/demand approach

Supply/demand studies such as these rely on several assumptions that may strongly influence results. We assumed that mass-specific excretion rates of gizzard shad obtained from a lake of given productivity could be applied to other lakes of similar productivity (e.g., that Burr Oak rates apply to Piedmont, and Acton rates apply to other high-productivity lakes). The other approach (short of measuring excretion rates in all lakes, which was not practical) would be to use a single mass vs. excretion rate relationship for all lakes, derived from all regressions from all lakes. Had we used that approach, we would have observed an even steeper trend in the relationship between trophic status (or percentage watershed agricultural land) and the proportion of primary production supported by gizzard shad. This is because the use of a "global" mass-specific rate for all lakes would yield lower excretion rates in the low-productivity lakes and higher excretion rates in the high-productivity lakes, relative to the rates we estimated in this paper (see Appendix). Thus the positive correlation between trophic status and the proportion of production supported by shad appears to be robust against variations in how individual excretion rates are obtained.

Another potentially important assumption relates to the identity of the limiting nutrient in the lakes that shifted between N and P limitation, i.e., O'Shaughnessy and Pleasant Hill. We assumed N limitation for both, even though they were nearly as likely to be P-limited. However, simulations show that the trends are robust to assumptions about the identity of the limiting nutrient in these lakes. We reran the linear regressions presented in Fig. 4 under all four combinations of nutrient limitation (i.e., both lakes N-limited; both lakes P-limited; one N-limited but the other P-limited). The regression statistics were quite insensitive to these variations; within each of the three regressions (i.e., with percentage watershed agricultural land, total P, and chlorophyll as the independent variable), r^2 values varied no more than 0.04 units across the four scenarios. These relationships were robust because within each of these two lakes, shad supported similar fractions of N and P demand (Fig. 1).

Our study was conducted in mid to late summer, and thus we need to be careful about applying findings to other times of the year. In fact, shad may be most important in sustaining primary production during this time, when temperature-dependent mass-specific excretion rates are maximal (Schaus et al. 1997, Higgins et al. 2006) and nutrient inputs from inflow streams are minimal due to low runoff (Vanni et al. 2001, Shostell and Bukaveckas 2004, Vanni et al. 2005). However, primary production rates and the symptoms of eutrophication (algal blooms, hypoxic bottom waters) are most pronounced in mid to late summer, so it is important to quantify the relative importance of nutrient sources during this time.

Conclusions

In reservoirs spanning a wide range of watershed land use, nutrient translocation by gizzard shad supported an increasing proportion of primary production as watersheds became more agricultural and lakes became more eutrophic. This may imply a synergism between watersheds and gizzard shad in regulating reservoir productivity. Future studies need to quantify the importance of gizzard shad across other environmental gradients. For example, gizzard shad abundance is probably higher in relatively small, shallow lakes with extensive oxygenated areas, and in lakes with large watershed : lake area ratios. Thus nutrient translocation may be more important in these lakes as compared to lakes that are deep and/or have relatively small watersheds (Vanni et al. 2005). In addition we need to assess whether nutrient translocation by shad is important in other ecosystems (rivers and natural warmwater lakes) and, more generally, if other dominant detritivore species can exert similar controls on productivity in other ecosystem types.

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LITERATURE CITED

Aday, D. D., R. J. H. Hoxmeier, and D. H. Wahl. 2003. Direct and indirect effects of gizzard shad on bluegill growth and population size structure. Transactions of the American Fisheries Society **132**:47–56.

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. Canadian Journal of Fisheries and Aquatic Sciences **53**:842–855.

Belovsky, G. E., and J. B. Slade. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. Proceedings of the National Academy of Sciences (USA) **97**: 14412–14417.

Binkley, D., Y. Son, and D. W. Valentine. 2000. Do forests receive occult inputs of nitrogen? Ecosystems **3**:321–331.

Bracken, M. E. S., and K. J. Nielsen. 2004. Diversity of intertidal macroalgae increases with nitrogen loading by invertebrates. Ecology **85**:2828–2836.

Bremigan, M. T., and R. A. Stein. 2001. Variable gizzard shad recruitment with reservoir productivity: causes and implications for classifying systems. Ecological Applications **11**: 1425–1437.

Caraco, N. F., J. J. Cole, and G. E. Likens. 1992. New and recycled primary production in an oligotrophic lake: insights for summer phosphorus dynamics. Limnology and Oceanography **37**:590–602.

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. Ecological Applications **8**:559–568.

Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecological Applications **9**:751–771.

Cotner, J. B., and B. A. Biddanda. 2002. Small players, large role: microbial influence on biogeochemical processes in pelagic aquatic ecosystems. Ecosystems **5**:105–121.

Dettmers, J. M., and R. A. Stein. 1996. Quantifying linkages among gizzard shad, zooplankton, and phytoplankton in reservoirs. Transactions of the American Fisheries Society **125**:27–41.

DeVries, D. R., and R. A. Stein. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. Canadian Journal of Fisheries and Aquatic Sciences **49**:1216–1227.

DiCenzo, V. J., M. J. Maceina, and M. R. Stimpert. 1996. Relations between reservoir trophic state and gizzard shad population characteristics in Alabama reservoirs. North American Journal of Fisheries Management **16**:888–895.

Drenner, R. W., J. D. Smith, and S. T. Threlkeld. 1996. Lake trophic state and the limnological effects of omnivorous fish. Hydrobiologia **319**:213–223.

Drenner, R. W., S. T. Threlkeld, and M. D. McCracken. 1986. Experimental-analysis of the direct and indirect effects of an omnivorous filter-feeding clupeid on plankton community structure. Canadian Journal of Fisheries and Aquatic Sciences **43**:1935–1945.

Dugdale, R. C., and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnology and Oceanography **12**:196–206.

Elser, J. J., E. R. Marzolf, and C. R. Goldman. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the fresh-waters of North America—a review and critique of experimental enrichments. Canadian Journal of Fisheries and Aquatic Sciences **47**:1468–1477.

Fee, E. J. 1990. Computer programs for calculating in situ phytoplankton photosynthesis. Canadian Technical Report of Fisheries and Aquatic Sciences 1740. Canada Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Fee, E. J., R. E. Hecky, M. P. Stainton, P. Sandberg, L. L. Hendzel, S. J. Guildford, H. J. Kling, G. K. McCullough, C. Anema, and A. Salki. 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 Sciences 1662. Canada Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Fee, E. J., J. A. Shearer, E. R. DeBruyn, and E. U. Schindler. 1992. Effects of lake size on phytoplankton photosynthesis. Canadian Journal of Fisheries and Aquatic Sciences **49**:2445–2459.

Foote, K. G., and D. N. MacLennan. 1984. Comparison of copper and tungsten carbide spheres. Journal of the Acoustical Society of America **75**:612–616.

Frank, D. A., P. M. Groffman, R. D. Evans, and B. F. Tracy. 2000. Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. Oecologia **123**:116–121.

Higgins, K. A., M. J. Vanni, and M. J. González. 2006. Detritivory and the stoichiometry of nutrient cycling by a dominant fish species in lakes of varying productivity. Oikos, *in press*. [doi: 1111/j.2006.0030-1299.14745.x]

Hudson, J. J., W. D. Taylor, and D. W. Schindler. 1999. Planktonic nutrient regeneration and cycling efficiency in temperate lakes. Nature **400**:659–661.

Kleiner, J., and H. H. Stabel. 1989. Phosphorus transport to the bottom of Lake Constance. Aquatic Sciences **51**:181–191.

Knoll, L. B., M. J. Vanni, and W. H. Renwick. 2003. Phytoplankton primary production and photosynthetic parameters in reservoirs along a gradient of watershed land use. Limnology and Oceanography **48**:608–617.

Kuenzler, E. J. 1961. Phosphorus budget of a mussel population. Limnology and Oceanography **6**:400–415.

Love, R. H. 1971. Dorsal-aspect target strength of an individual fish. Journal of the Acoustical Society of America **49**:816–823.

Lovett, G. M., L. M. Christenson, P. M. Groffman, C. G. Jones, J. E. Hart, and M. J. Mitchell. 2002. Insect defoliation and nitrogen cycling in forests. BioScience **52**(4):335–341.

MacLennan, D. N., and E. J. Simmonds. 1992. Fisheries acoustics. Chapman and Hall, New York, New York, USA.

Michaletz, P. H. 1998. Population characteristics of gizzard shad in Missouri reservoirs and their relation to reservoir productivity, mean depth, and sport fish growth. North American Journal of Fisheries Management **18**:117–123.

Mundahl, N. D., and T. E. Wissing. 1987. Nutritional importance of detritivory in the growth and condition of gizzard shad in an Ohio reservoir. Environmental Biology of Fishes **20**:129–142.

Nowlin, W. H., J. L. Evarts, and M. J. Vanni. 2005. Release rates and potential fates of nitrogen and phosphorus from sediments in a eutrophic reservoir. Freshwater Biology **50**: 301–322.

Nürnberg, G. K. 1998*a*. Prediction of annual and seasonal phosphorus concentrations in stratified and polymictic lakes. Limnology and Oceanography **43**:1544–1552.

Nürnberg, G. K. 1988*b*. Prediction of phosphorus release rates from total and reductant soluble phosphorus in anoxic lake sediments. Canadian Journal of Fisheries and Aquatic Sciences **45**:453–462.

Power, M. E., M. J. Vanni, P. T. Stapp, and G. A. Polis. 2004. Subsidy effects on managed ecosystems: implications for sustainable harvest, conservation, and control. Pages 387–409 *in* G. A. Polis, M. E. Power, and G. R. Huxel, editors. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois, USA.

SAS. 2002. JMP software, version 5.0.1a. SAS Institute, Cary, North Carolina, USA.

Schaus, M. H., and M. J. Vanni. 2000. Effects of gizzard shad on phytoplankton and nutrient dynamics: role of sediment feeding and fish size. Ecology **81**:1701–1719.

Schaus, M. H., M. J. Vanni, T. E. Wissing, M. T. Bremigan, J. E. Garvey, and R. A. Stein. 1997. Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. Limnology and Oceanography **42**:1386–1397.

Schindler, D. E., and L. A. Eby. 1997. Stoichiometry of fishes and their prey: implications for nutrient recycling. Ecology **78**:1816–1831.

Schindler, D. E., J. F. Kitchell, X. He, J. R. Hodgson, and S. R. Carpenter. 1993. Food web structure and phosphorus recycling in lakes. Transactions of the American Fisheries Society **122**:756–772.

Shostell, J., and P. A. Bukaveckas. 2004. Seasonal and interannual variation in nutrient fluxes from tributary inputs, consumer recycling and algal growth in a eutrophic river impoundment. Aquatic Ecology **38**:359–373.

Sirotnak, J. M., and N. J. Huntly. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: Voles in riparian areas. Ecology **81**:78–87.

Smith, V. H. 1998. Cultural eutrophication of inland, estuarine, and coastal waters. Pages 7–49 *in* M. L. Pace and P. M. Groffman, editors. Successes, limitations and frontiers in ecosystem science. Springer, New York, USA.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of fresh-water. Miscellaneous Special Publication 25. Freshwater Institute, Canada Department of Fisheries and Oceans, Winnipeg, Canada.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: The biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey, USA.

USGS (United States Geological Survey). 2003. National Land Cover Characterization. ⟨http://landcover.usgs.gov/natllandcover.asp⟩

Vanni, M. J. 1996. Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. Pages 81–95 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics **33**: 341–370.

Vanni, M. J., K. K. Arend, M. T. Bremigan, D. B. Bunnell, J. E. Garvey, M. J. González, W. H. Renwick, P. A. Soranno, and R. A. Stein. 2005. Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems. BioScience **55**:155–167.

Vanni, M. J., and J. L. Headworth. 2004. Cross-habitat transport of nutrients by omnivorous fish along a productivity gradient: integrating watersheds and reservoir food webs. Pages 43–61 *in* G. A. Polis, M. E. Power, and G. R. Huxel, editors. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois, USA.

Vanni, M. J., 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. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications **7**:737–750.

Watson, D. L., D. R. Bayne, D. R. DeVries, and J. Williams. 2003. Influence of gizzard shad on phytoplankton size and primary productivity in mesocosms and earthen ponds in the southeastern U.S. Hydrobiologia **495**:17–32.

Yako, L. A., J. M. Dettmers, and R. A. Stein. 1996. Feeding preferences of omnivorous gizzard shad as influenced by fish size and zooplankton density. Transactions of the American Fisheries Society **125**:753–759.

APPENDIX

Equations used to estimate N and P excretion rates of gizzard shad (*Ecological Archives* E087-098-A1).