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Nutrient excretion by fish supports a variable but significant proportion of lake primary productivity over 15 years

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Abstract. Animals play an important and sometimes overlooked role in nutrient cycling. The role of animals in nutrient cycling is spatially and temporally variable, but few studies have evaluated the long-term importance of animal-mediated nutrient cycling in meeting nutrient demand by primary producers. We quantified the proportion of phytoplankton nutrient (phosphorus, P) demand met by excretion by gizzard shad (*Dorosoma cepedianum*) in a eutrophic reservoir where this species dominates fish biomass. From 2000 to 2014, gizzard shad excretion supported a variable proportion of phytoplankton P demand, averaging 7–27% among years over the growing season (spring and summer). Temporal patterns emerged, as gizzard shad consistently supported a higher proportion of demand during summer (mean 31%) than spring (8%). In spring, the proportion of demand met from gizzard shad excretion was best predicted by gizzard shad population biomass, stream discharge, and temperature. In summer, this proportion was best predicted only by biomass of the young-of-year (YOY) gizzard shad. Thus, variation in YOY shad biomass significantly alters nutrient supply, and future studies should explore the long-term role of animal population dynamics in nutrient cycling. Our study shows that several years of data are needed to perform a critical evaluation of the importance of animals in meeting ecosystem nutrient demand.

Key words: animal-mediated nutrient cycling; gizzard shad; hypereutrophic; long term; phosphorus; reservoir.

INTRODUCTION

Animals can have strong effects on nutrient cycling in ecosystems. For example, excretion by animals is an important nutrient source for primary producers in ecosystems as diverse as coral reefs (Allgeier et al. 2014), savannas (le Roux et al. 2020), and streams (McIntyre et al. 2008). In aquatic ecosystems, excretion by animals can play an important yet variable role in supplying nutrients that limit primary production. Although other sources, such as watersheds and microbially mediated recycling, may represent larger annual fluxes, nutrient excretion by animals sometimes supports a nontrivial fraction of primary production (Allgeier et al. 2017, Atkinson et al. 2017). The importance of animal excretion depends largely on the consumer's abundance, but also on body size, diet, and environmental factors (e.g., temperature), all of which affect the quantity, timing, and duration of animal-mediated nutrient subsidies (Subalusky and Post 2018). Few studies have quantified the importance of animal excretion over long timescales, that is, more than a couple of growing seasons (Atkinson et al. 2017). Animal body size, metabolic rates, abundance, and species composition all vary temporally at multiple scales. Thus, short-term studies provide only a snapshot view, and quantifying animal excretion over long periods is necessary to reveal the variation in the role of animal-mediated nutrient cycling.

The importance of animal excretion for primary producers can be quantified several ways (Vanni 2002, Atkinson et al. 2017). Experiments manipulating animal abundance can provide insight, but because animals have many direct and indirect effects on primary producers, it may be difficult to ascertain mechanisms. Another approach is to compare excretion by animals to

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other nutrient fluxes; however, it is often not possible to measure all nutrient fluxes, potentially limiting the utility of this approach. A third approach, which we use here, is to compare excretion of the limiting nutrient by animals to ecosystem demand for that nutrient. This avoids the need to measure other fluxes, and the proportion of nutrient demand met by animal excretion provides a quantitative measure of importance. Relatively few studies have employed this supply:demand approach, but they reveal a highly variable role for animals. For example, among different streams fish excretion supplies 5% to >90% of nutrient demand (McIntyre et al. 2008, Small et al. 2011, Wilson and Xenopoulos 2011). In these and other studies, variation in the importance of animals was largely explained by variation in their biomass (Atkinson et al. 2017). Population sizes of fish often fluctuate greatly across years, largely because of variation in recruitment (Ludsin et al. 2014), so it is likely that their importance in nutrient cycling varies interannually.

In our study system (Acton Lake, a eutrophic reservoir), as well as many other lakes in the midwestern and southeastern United States, gizzard shad (*Dorosoma cepedianum*) are the dominant fish based on biomass (Vanni et al. 2006). Gizzard shad (except for their zooplanktivorous larvae) consume detritus from the sediments to meet their nutritional needs and excrete unneeded nutrients into the water column in forms that are highly available to phytoplankton. Thus, most nutrients excreted by gizzard shad are “new” nutrients (sensu Dugdale and Goering 1967); that is, they are supplied from outside the euphotic zone (Williamson et al. 2018). Most of these nutrients would otherwise remain in sediments or the aphotic hypolimnion, unavailable to phytoplankton (Nowlin et al. 2005). In a study of seven lakes across a watershed land use gradient, the proportion of nutrient demand supplied by gizzard shad excretion (supply:demand) increased with lake productivity and the amount of watershed agriculture (Vanni et al. 2006). That study showed that gizzard shad support ~25%–30% of phytoplankton nutrient demand in Acton Lake, but data were restricted to summer. Excretion by gizzard shad also is an important nutrient source for phytoplankton in summer in other reservoirs and natural lakes (Gido 2002, Shostell and Bukaveckas 2004, Schaus et al. 2010). However, none of these studies examined long-term variation in supply:demand. Gizzard shad excretion rates are temporally variable. In Acton Lake, gizzard shad excretion often provides more phosphorus to the water column than does the watershed in summer when shad biomass is high and watershed inputs are small, but reverse is true in spring when stream runoff is high (Williamson et al. 2018). Thus, we expect that the proportion of nutrient demand supplied by gizzard shad excretion also varies seasonally.

Our goal was to quantify seasonal and interannual variation in the relative importance of a dominant fish in supplying nutrients to phytoplankton. Thus, we used the supply:demand approach to evaluate the contribution of gizzard shad excretion to primary production in Acton Lake over 15 yr. To our knowledge, Williamson et al. (2018) is the only long-term study (>10 yr) to quantify the importance of animal-mediated excretion. That study compared nutrient supply by gizzard shad vs. the watershed in Acton Lake, but did not quantify nutrient supply relative to phytoplankton demand. We addressed the following questions: (1) How does the proportion of primary production supported by gizzard shad excretion vary over seasonal and interannual time scales? (2) What are the drivers of variability among seasons and across years in nutrient supply:demand? We predicted that gizzard shad would support more primary production in summer, when both their per capita excretion rates and biomass are likely to be maximal. Alternatively, primary production supported by gizzard shad may not increase seasonally if there is not a large influx of young-of-year fish, or if there is an unusual precipitation pattern (i.e., a dry spring or wet summer) in a particular year. We also predicted that fish biomass will explain most of the variability in the proportion of primary production supported.

Methods

Study site

Acton Lake is a hypereutrophic reservoir located in southwest Ohio (39°34′ N, 84°44.5′ W). The lake has a large agricultural watershed (~110× lake surface area) that provides large nutrient subsidies via inflow streams (Kelly et al. 2018). As already mentioned, gizzard shad are by far the dominant fish in terms of biomass (Vanni et al. 2006).

Field and lab methods

We quantified nutrient supply (excretion) and demand from 2000 to 2014. Methods for estimating gizzard shad excretion rates are detailed in Williamson et al. (2018). Briefly, larval gizzard shad were sampled weekly during May–July, and hydroacoustic surveys were conducted every August to quantify abundance of all age classes. Using these data, we estimated the number of gizzard shad in each age class (0–4+ yr) on a daily basis. Daily per fish P excretion rates were estimated using regressions with fish wet mass and temperature as predictor variables, derived from experimentally measured excretion rates of gizzard shad in Acton Lake. Methods for phytoplankton nutrient demand are detailed in Vanni et al. (2006). Weekly, we collected water samples integrated through the euphotic zone and at discrete 1-m intervals and measured photosynthetic active radiation (PAR; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at 0.5-m intervals, at a site near the deepest part of the lake. Water from the integrated samples was used to measure phytoplankton photosynthetic rates and phytoplankton (seston) nutrient concentrations. Depth-specific samples were used to estimate phytoplankton biomass as chlorophyll a using a fluorometer (Turner Designs, San Jose, California, USA). To quantify seston carbon (C) and phosphorus (P) concentrations, samples were collected on Pall A/E glass fiber filters. Seston P concentrations were quantified by digesting filters and measuring liberated soluble reactive P with a Lachat autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Seston C concentrations were analyzed with an elemental analyzer (PerkinElmer, Wellesley, Massachusetts, USA or CE Elantech, Lakewood, New Jersey, USA). Photosynthetic rates were estimated, usually every 2 weeks, by measuring ^{14}C uptake of phytoplankton (from integrated samples) incubated at various PAR levels in the lab. These rates were used to create a photosynthesis-irradiance (PI) curve. Then, the PI curves, solar radiation from a nearby weather station, light attenuation in the water column, and depth-specific chlorophyll concentrations were used to calculate daily primary production in the lake. Phytoplankton phosphorus demand (mg $P{\cdot}m^{-2}{\cdot}d^{-1}$) was then calculated by dividing primary production (mg $C{\cdot}m^{-2}{\cdot}d^{-1}$) by seston C:P ratio. We focused on P supply and demand because Acton Lake phytoplankton were usually P limited during our study. Phytoplankton N limitation was relatively rare during this study, occurring mainly in summers of drought years, and when phytoplankton were N-limited, they were also co-limited by P (Hayes et al. 2015). Thus, P demand is a valid estimate of nutrient demand needed to sustain primary production.

Data analysis

To estimate the proportion of primary production supported by gizzard shad (supply:demand), we divided population P excretion rate by P demand (both in mg $P{\cdot}m^{-2}{\cdot}d^{-1}$). Daily P supply rates were summed over the growing season (April–October) and divided by P demand summed over the same period, to obtain the "annual" (growing season) P supply:demand. We also calculated weekly means for supply and demand, as well as other predictor variables (e.g., temperature and fish biomass) that we expected to impact excretion. Discharge (Williamson et al. 2018) was included as a possible predictor because stream-derived nutrients may increase overall supply (potentially decreasing the relative importance of excretion), but large streamflow

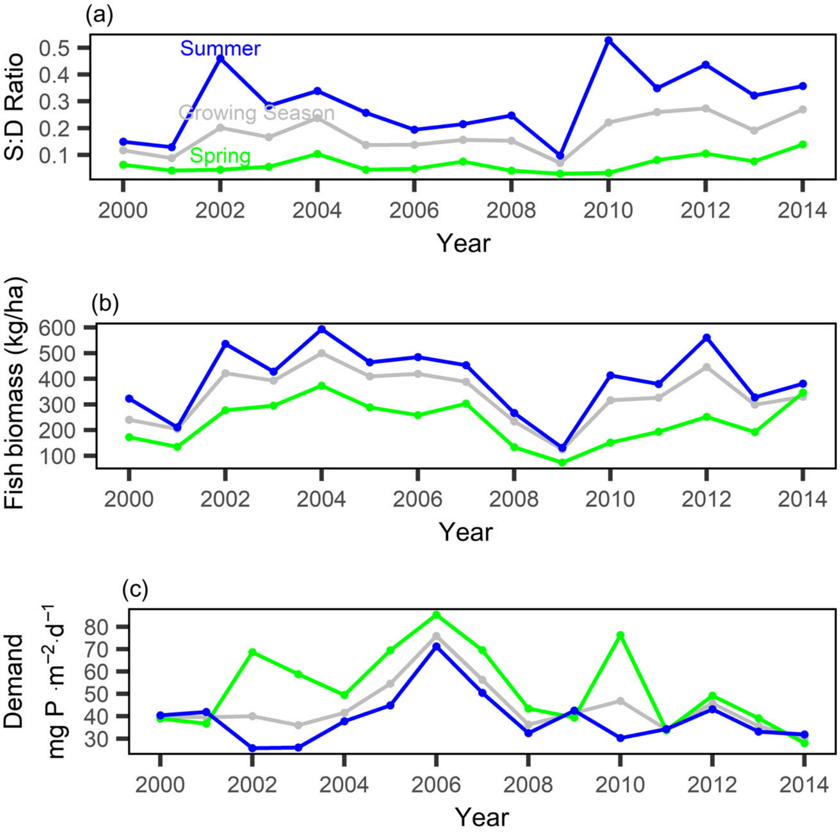

FIG. 1. Long-term trends in Acton Lake from 2000 to 2014 of nutrient excretion by gizzard shad as a proportion of nutrient demand by phytoplankton (supply:demand S:D (a)), gizzard shad biomass (b), and phytoplankton P demand (c).

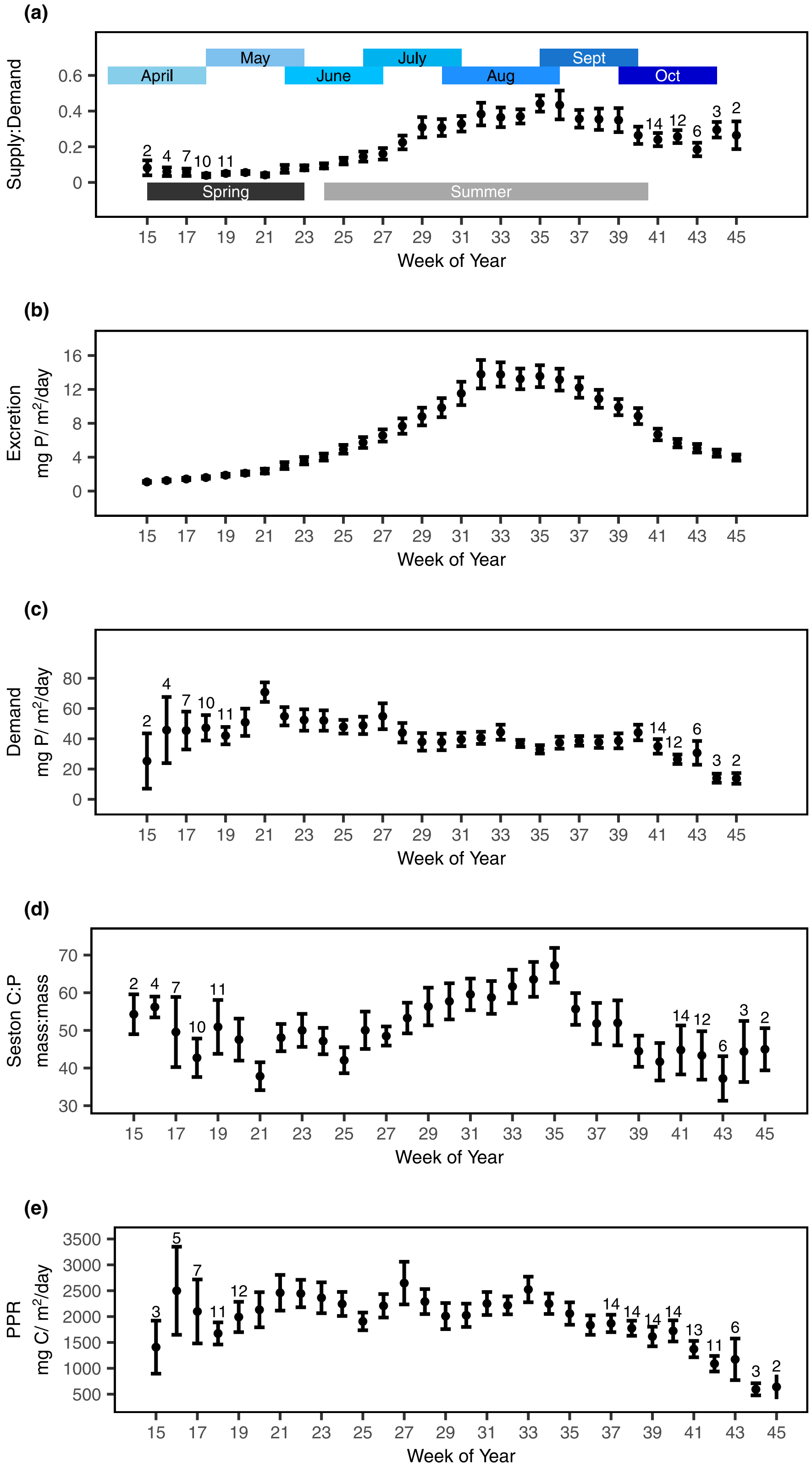

FIG. 2. Weekly patterns in supply:demand (a), P excretion rate (b), P demand by phytoplankton (c), seston C:P ratio (d), and phytoplankton primary production (PPR) (e). The solid symbols are weekly means over 15 yr (2000–2014), and the vertical lines represent the standard error. The numbers over the bars represent the number of years for which data were included for that week, for years when we had fewer than 15 yr of data.

events can also wash phytoplankton from the lake, thereby decreasing demand.

Spring and summer are relatively distinct seasons in Acton Lake. Nutrient supply by the watershed is typically higher in spring than summer, whereas gizzard shad excretion rates are higher in summer (Williamson et al. 2018). Thus, we conducted multiple regressions separately for spring (April–June) and summer (July–September) to determine drivers of interannual variation in supply:demand. Regressions used means for that season (mean of data for that period) to avoid autocorrelation and sample size inflation. Regressions included these predictors: total shad biomass, young-of-year shad biomass, stream discharge, temperature, and hatch size (number of larval gizzard shad hatching that year). The top models for each season were selected based the lowest Akaike information criterion (AIC; Burnham and Anderson 2002).

RESULTS

The proportion of phytoplankton nutrient demand supported by gizzard shad (supply:demand ratio, or S:D) in Acton Lake was highly variable over the 15 yr. Averaged over the growing season (April–September), gizzard shad supported a wide range of primary production, from 7% in 2009 to 27% in 2012 (Fig. 1a). Similar trends were observed in gizzard shad biomass (Fig. 1b). Demand was usually highest during the spring, and averaged over the growing season, demand was highest in 2006 and lowest in 2014 (Fig. 1c). Meanwhile, S:D was lower in spring than summer, which was also true for total fish biomass and excretion (Fig. 1b). In spring, S:D varied from 3% to 19%, with a mean among years of 8%, whereas in summer (July–September), S:D varied from 9% to 53% with a mean of 31% (Fig. 1a).

Although S:D varied greatly among years, its seasonality was consistent across years (Fig. 2). Weekly S:D, averaged across years, was 5.5% in April–May, increased rapidly in June, and averaged 30%–40% from mid-July to mid-September before declining to ~25% by the end of September (Fig. 2a). Gizzard shad excretion followed a similar trend, increasing from ~1 mg $P \cdot m^{-2} \cdot d^{-1}$ in April to >13 in early August, followed by a gradual decline to ~5 by October (Fig. 2b). Compared to excretion rate, phytoplankton P demand was much less variable seasonally, and was generally highest in late May–early June (Fig. 2c). Regarding the two components of demand, primary production increased during the spring and remained high from late May–mid August before declining, and seston C:P ratio was highest late summer (Fig. 2d).

In spring, the best model to predict S:D included total gizzard shad biomass, temperature, and stream discharge (Table 1). In summer, the best model only included young-of-year gizzard shad biomass, which on average accounts for ~22% of total gizzard shad biomass in summer.

DISCUSSION

Temporal variability

Our 15-yr study shows that long-term data are needed to understand the importance of animal-mediated nutrient cycling fully. Throughout our study period, gizzard shad made important, yet variable, contributions to nutrient supply to phytoplankton; on average their excretion supported 18% of primary production averaged over the growing season (April–September). They supported 31% of primary production, on average, in summer (July–September) when phytoplankton biomass is high and dominated by cyanobacteria, that is, when water quality problems are likely to be most severe. Thus, as predicted, gizzard shad consistently supported much more primary production during the summer than the spring. Yet, interannual variability in our study was high, spanning about a six-fold range across all years in both spring and summer, and varying as much as three-fold between two successive years (2009 and 2010).

As expected, gizzard shad biomass explained much of the interannual variation in supply:demand. Interestingly, the best model during the spring included not only total fish biomass but also temperature and stream discharge. We hypothesized that discharge would be important because streams provide large nutrient subsidies during spring when runoff is high (Williamson 2018), which should reduce the relative importance of gizzard shad. Other studies have linked nutrient excretion by consumers to increasing temperatures, so it was surprising that temperature was not more important during the summer months (Atkinson et al. 2017). In summer, variability was largely explained by the biomass of the young-of-year (YOY) fish, which is often the largest gizzard shad age class, in terms of biomass and excretion rates, during summer (Williamson et al. 2018). By using the seasonal approach in the analysis, we gain clarity on the strong impact of YOY, especially in years such as 2002 and 2010 which had large YOY classes that supported a relatively high proportion of primary production.

We recognize that characterizing animal-mediated excretion as "important" based on supply:demand is somewhat subjective. However, any nutrient source that supports >30% of primary production, as gizzard shad excretion does in summer, would be considered important by most ecologists. In addition, new nutrients were first deemed as important for the open ocean on the basis of new sources supporting 8%–40% of phytoplankton demand (Dugdale and Goering 1967), a range very similar to that supported by gizzard shad in Acton Lake.

Although gizzard shad excretion supports a significant fraction of primary production in Acton Lake, our results clearly show that other P sources must be important. Even in summer, gizzard shad supported >50% of demand in just 1 of 15 yr (Fig. 2). We estimated P

TABLE 1. Results from the multiple regressions predicting supply: demand in Acton Lake during the spring and summer.

Model	Model rank	Coefficients	SE	T	P value	Adj. R^2	AIC$_c$	ΔAIC$_c$
Spring								
SD ~ FishBio + Discharge + Temp	1	1.65×10^{-4} 7.45×10^{-3} 2.36×10^{-2}	4.19×10^{-5} 1.94×10^{-3} 3.94×10^{-3}	3.932 3.833 6.02	<0.001	0.8235	−75.4336	0
SD ~ FishBio + Temp	2	2.00×10^{-4} 1.38×10^{-2}	5.97×10^{-5} 4.36×10^{-3}	3.355 3.158	<0.01	0.6221	−67.3756	8.06
SD ~ Temp + Discharge	3	2.76×10^{-2} 9.16×10^{-3}	5.65×10^{-3} 2.82×10^{-3}	4.893 3.252	<0.01	0.6108	−66.9337	8.5
SD ~ YOYbio + Discharge + Temp	4	1.82×10^{-3} 9.58×10^{-3} 2.65×10^{-2}	9.88×10^{-4} 2.58×10^{-3} 5.19×10^{-3}	1.839 3.17 5.11	<0.01	0.6753	−66.9189	9.14
SD ~ HatchSize + Discharge + Temp	5	-1.10×10^{-3} 9.35×10^{-3} 2.80×10^{-2}	1.11×10^{-2} 3.55×10^{-3} 7.4×10^{-3}	−0.099 2.635 3.983	<0.01	0.5759	−62.2805	13.15
Summer								
SD ~ YOYbio	1	1.56×10^{-3}	3.33×10^{-4}	4.675	<0.0001	0.5983	−27.438	0
SD ~ YOYbio + Temp	2	1.27×10^{-3} 2.95×10^{-2}	4.16×10^{-4} 2.62×10^{-2}	3.59 1.125	<0.01	0.6064	−25.1234	2.32
SD ~ YOYbio + Discharge	3	1.55×10^{-3} -1.63×10^{-3}	3.67×10^{-4} 1.92×10^{-2}	4.213 −0.085	<0.01	0.5651	−23.6288	3.81
SD ~ FishBio + Temp	4	4.20×10^{-4} 5.76×10^{-2}	-2.00×10^{-4} 2.57×10^{-2}	2.098 2.242	<0.01	0.4873	−21.161	6.18
SD ~ YOYbio + Discharge + Temp	5	1.27×10^{-3} 9.54×10^{-3} 3.56×10^{-2}	4.31×10^{-4} 2.11×10^{-2} 3.4×10^{-2}	2.958 0.451 1.174	<0.01	0.5784	−20.7317	6.71

Notes: Data from 2000 to 2014 were used, and the predictors included total fish biomass (FishBio), stream discharge into the lake (Discharge), temperature (Temp), and young-of-year biomass (YOYbio). The top five models for each season were included.

recycling (by microbes and zooplankton) in the euphotic zone and compared this to P supply by gizzard shad and the lake's watershed (Appendix S1: Table S1), which revealed trends similar to our supply:demand estimates. Considering the sum of these three sources (recycling, shad excretion, and watershed) as "aggregate P supply," recycling supplied ~77% of P over the growing season, and this fraction was similar in spring and summer (Appendix S1: Table S1). Averaged over all 15 yr, shad excretion and watershed inputs supplied similar amounts of P, but the relative importance of these two sources differed in spring vs. summer (as shown by Williamson et al. 2018). However, as we have discussed elsewhere (Vanni 2002, Vanni et al. 2006, Domine et al. 2010), gizzard shad excretion and the watershed provide new P, which supports new production, whereas recycling provides P already in the water column. Without inputs of new P, sinking of phytoplankton from the water column would reduce the mass of P, and hence overall production, in the euphotic zone (Vanni 2002). In terms of new P, gizzard shad excretion and the watershed are the dominant sources (Domine et al. 2010).

Drivers of variation in supply:Demand

Although most studies of consumer-mediated nutrient cycling explore only the supply from the consumer (excretion), our study explicitly considered supply relative to demand by primary producers over multiple years. In terms of the quantity, quality, timing, and duration framework (Subalusky and Post 2018), the quality of the excretion subsidy provided by gizzard shad is consistently high, as P and N are both excreted in inorganic forms that are readily available to phytoplankton, and the N:P ratio excreted is much closer to the optimum required by algae (i.e., close to the Redfield ratio) than supply from the watershed (Williamson et al. 2018). Per individual gizzard shad excretion rates are also fairly similar, for a given body mass, across different ecosystems (Gido 2002, Shostell and Bukaveckas 2004, Vanni et al. 2006, Schaus et al. 2010). However, at the ecosystem level, the quantity and timing of gizzard shad excretion rates, and hence its importance in supporting primary production, varies greatly both seasonally and among years. The biomass of the gizzard shad was obviously an important predictor for the quantity and timing of the subsidy over multiple years. Furthermore, we were able to explore both organismal and ecosystem drivers during this long-term study. Although population-level factors including the number and biomass of fish are clearly the most critical drivers of nutrients from animals, ecosystem processes, such as stream discharge, may influence the relative importance of these subsidies, especially during years with limited inputs from the watershed.

Gizzard shad YOY biomass is a major driver of supply:demand in summer, when excretion rates and phytoplankton biomass are at their seasonal highs

(Williamson et al. 2018). Thus, even though fish are born in May and June, YOY biomass increases greatly in summer as these fish grow. Similarly, a long-term study found that the biomass of YOY amphibians (tadpoles) strongly affected whether their populations were net importers or exporters of nutrients to/from ponds. Yet, short-term data sets (1–3 yr) would not accurately capture ecosystem dynamics because of highly variable juvenile recruitment (Capps et al. 2015). These results illustrate the need to understand population recruitment dynamics in terms of ecosystem impacts. Fish recruitment is quite variable, and little is known about the factors driving it in small lakes, where both biotic and physical factors (e.g., temperature) are likely to influence recruitment directly or indirectly (Ludsin et al. 2014). In a study examining 12 midwestern reservoirs, gizzard shad recruitment was positively correlated with reservoir productivity, consumption of small copepods, and the number of YOY hatching (Bremigan and Stein 2001). However, understanding the relationships between zooplankton and gizzard shad is difficult, as zooplankton biomass was hard to predict and phenological mismatches were common (Bremigan and Stein 2001), and we observed great variation in YOY abundance in a single productive reservoir. Thus, future studies should explore the abiotic and biotic factors that impact YOY survival. Understanding the role of these factors may be especially important for gizzard shad, as they transition to detritivory during their first summer of life.

Studies in aquatic and terrestrial systems show that body size, both across and within species, is an important predictor of nutrient excretion by individual animals (Doughty et al. 2016, Vanni and McIntyre 2016, Atkinson et al. 2017, le Roux et al. 2020). Additionally, despite great interannual variation, fish communities often show “loose equilibrium” dynamics; that is, over many years communities tend to return to a central region of community space, but not exactly to one average community (Matthews and Marsh-Matthews 2016). This suggests that nutrient cycling by fish communities will show similar dynamics. On the other hand, invasive species can increase ecosystem-level nutrient cycling (e.g., armored catfish; Capps et al. 2013). Gizzard shad are native to our study watershed, but their abundance increases greatly in human-made reservoirs, and their high biomass can render them native invasive species. For example, gizzard shad are actively being removed from some Florida lakes to reduce nutrient flux and improve water quality (Schaus et al. 2010). Therefore, it is important to consider how both the loss and redistribution of animals due to anthropogenic forces impacts nutrient cycling.

In conclusion, nutrients provided by animals in lakes can support a substantial amount of nutrient demand from phytoplankton, and the quantity of this subsidy is largely dependent on the biomass of the consumer. In the case of gizzard shad in Acton Lake (and likely fish on other ecosystems), variation is driven by the young-of-year age class. YOY biomass impacts both interannual variation and seasonality of the nutrient subsidy, resulting in consistent peaks in nutrient supply in summer as YOYs are recruited, but great variation among years.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3364/suppinfo