New and regenerated primary production in a productive reservoir ecosystem

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Abstract: The concept of new and regenerated production has been used extensively in marine ecosystems but rarely in freshwaters. We assessed the relative importance of new and regenerated phosphorus (P) in sustaining phytoplankton production in Acton Lake, a eutrophic reservoir located in southwestern Ohio, USA. Sources of nutrients to the euphotic zone, including watershed loading, fluxes from sediments, and excretion by sediment-feeding fish (gizzard shad, Dorosoma cepedianum), were considered sources of new P input that support new primary production and were quantified over the course of a growing season. Regenerated production was estimated by the difference between new and total primary production. New production represented 32%–53% of total primary production, whereas regenerated production represented 47%–68% of total primary production. P excretion by gizzard shad supplied 45%–74% of new P and 24% of P required for total production. In summary, fluxes of P from the watershed and those from sediment-feeding fish need to be considered in strategies to reduce eutrophication in reservoir ecosystems.

Résumé : Le concept de production nouvelle et régénérée a été souvent utilisé dans les écosystèmes marins, mais rarement en eaux douces. Nous évaluons l’importance relative du phosphore (P) nouveau et régénéré dans le soutien de la production du phytoplancton dans le lac Acton, un réservoir eutrophe du sud-ouest de l’Ohio, É.-U. Les sources de nutriments vers la zone euphotique, en particulier la charge provenant du bassin versant, les flux issus des sédiments et l’excrétion par un poisson qui se nourrit dans les sédiments (l’aloise à gésier, Dorosoma cepedianum), sont considérées comme des apports de P nouveau qui alimente une nouvelle production primaire; nous les avons quantifiées tout au cours d’une saison de croissance. La production régénérée est représentée par la différence entre les productions primaires nouvelle et totale. La nouvelle production représente 32–53 % de la production primaire totale, alors que la production régénérée constitue 47–68 % de la production primaire totale. L’excrétion de P par l’aloise à gésier fournit 45–74 % de P nouveau et 24 % du P nécessaire à la production totale. En résumé, il est nécessaire de tenir compte des flux de P provenant du bassin hydrographique et de ceux produits par les poissons qui se nourrissent dans les sédiments dans les stratégies pour réduire l’eutrophisation dans les écosystèmes de réservoirs.

Introduction

Algal primary production varies greatly in aquatic ecosystems and can be categorized as either new or regenerated production (Dugdale and Goering 1967; Clark et al. 2008). New primary production is supported by nutrients coming into the ecosystem or habitat from other ecosystems or habitats (new nutrients). Conversely, regenerated primary production is supported by nutrients that are already present and cycle within the ecosystem or habitat (regenerated nutrients). In assessing new and regenerated production in pelagic aquatic ecosystems, the euphotic zone is often designated as the “ecosystem” of interest, as this is the area in which primary production takes place. Thus, nutrients delivered to the euphotic zone are considered new nutrients, whereas those recycled back to primary producers within the euphotic zone are considered regenerated nutrients. The distinction between nutrient sources to the euphotic zone is important because new nutrients have the potential to directly increase algal biomass in the system. As a consequence, new nutrients can enhance productivity and biomass of upper trophic levels, increase nutrient sedimentation rates, and contribute directly to the trophic status of the ecosystem. In contrast, regenerated nutrients can only maintain biomass in the ecosystem.

The relative contributions of new and regenerated production have been extensively studied in marine pelagic systems (Dugdale and Goering 1967; Eppley and Peterson 1979; Clark et al. 2008). In contrast, this concept has rarely been applied in freshwater ecosystems (Caraco et al. 1992; Hudson et al. 1999), perhaps because of the belief that distinguishing new and regenerated production in freshwaters may be more difficult than in marine pelagic ecosystems. In nitrogen-limited marine systems, new and regenerated nu-
Nutrients have historically been distinguished by the chemical form of nitrogen (N). Specifically, this distinction has relied on the assumption that nitrate supports new production, whereas ammonium supports regenerated production. This view derives from earlier observations that nitrate is supplied mostly from upwelling of deep water, which delivers nutrients from outside the mixed layer where phytoplankton reside. In contrast, ammonium is supplied by recycling within the mixed layer, mainly by microbial decomposition of organic matter or excretion by heterotrophic grazers. Thus, oceanographers have distinguished new and regenerated production by comparing nitrate and ammonium uptake rates of phytoplankton (Clark et al. 2008). However, this approach has been questioned recently by studies showing that nitrification can produce nitrate at high rates within the mixed layer, i.e., some nitrate is actually regenerated and is not new (Dore and Karl 1996; Yool et al. 2007; Clark et al. 2008). In addition, fixation of atmospheric N can be an important source of new N in some pelagic systems (Chen et al. 2008; Duce et al. 2008), i.e., nitrate is not the only form by which new N is delivered. These complexities warrant alternative or complementary approaches to estimating new and regenerated production, such as measuring nutrient inputs from various sources, as well as demand for nutrients. In addition, new and regenerated nutrients cannot be distinguished by chemical form when phosphorus is the limiting nutrient, which is often the case in freshwater ecosystems (Caraco et al. 1992).

To our knowledge, no studies have applied the concept of new and regenerated production to reservoirs, despite the importance of these ecosystems to regional and global nutrient and carbon cycles (Cole et al. 2007; Downing et al. 2008; Harrison et al. 2009). Because primary producers in reservoirs (and freshwater systems in general) receive nutrients from a variety of external and internal sources, quantification of new and regenerated production requires the measurement of nutrient sources, as well as nutrient demand. Nutrient sources to the mixed layer of reservoirs are diverse and potentially include watershed and (or) atmospheric inputs, fluxes from sediments and from the hypolimnion, and recycling within the mixed layer.

The relative importance of new and regenerated nutrient sources may also be influenced by biotic communities within the reservoirs. In the US Midwest, reservoirs often contain high biomass of gizzard shad (Dorosoma cepedianum), an omnivorous fish that can be a significant source of nutrients (Vanni et al. 2005, 2006a). Omnivores such as gizzard shad can be sources of either new or regenerated nutrients, depending on their feeding habits. During the larval period and immediately thereafter, gizzard shad are important zooplanktivores in reservoirs (Stein et al. 1995: Bremigan and Stein 2001). Excretion by this age class provides new nutrients (new production) and regenerated nutrients (regenerated production), and (ii) what proportions of total production and new production are sustained by gizzard shad excretion? Because these questions are largely unexplored for midwestern reservoirs and for freshwaters, in general, we feel that this study will improve our understanding of the relative importance of new and regenerated production in freshwater ecosystems. Furthermore, the study will elucidate the relative support of primary production by a single fish species in comparison with other new and regenerated nutrient sources within and outside of the reservoir entire ecosystem.

Materials and methods

Study site and general approach

The study was conducted at Acton Lake, a eutrophic reservoir located in Hueston Woods State Park, southwestern Ohio, USA (Vanni et al. 2005, 2006a). Acton Lake phytoplankton are typically P-limited (Vanni et al. 2006a, 2006c), including during this study. Because the lake has high phytoplankton biomass, the euphotic zone is almost always shallower than the mixed layer, and there is insufficient light penetration to sustain benthic primary production. Therefore, we focused on nutrient inputs to and within the mixed layer, where all primary production occurs. Nutrient input from stream inflows is substantial, as the...
lake’s watershed area is more than 100 times the surface area of the lake, and agricultural land comprises 89% of watershed land area (Knoll et al. 2003; Vanni et al. 2005, 2006c). However, watershed nutrient inputs strongly depend on storm events, which deliver large quantities of nutrients (Vanni et al. 2001). P excretion by gizzard shad can also be an important flux and supports on average ~25% (and up to >40%) of total phytoplankton primary productivity in late summer (Vanni et al. 2006a, 2006b). Our sampling period began on 17 June and ended on 10 September 2004, which covers most of the thermally stratified period.

New production is often derived from estimates of export production, which is often quantified with sediment traps (e.g., Dugdale and Goering 1967; Eppley and Peterson 1979; Caraco et al. 1992). Thus, over a given time period, new production equals export production plus any increase in standing stock of the limiting nutrient (i.e., if there is no change in standing stock, new production equals export production). We did not employ the approach of using sediment traps to quantify export because sediment resuspension accounts for >70% of sediment trap flux (Laurich 2005).

Rather, we quantified all known major fluxes of P into and out of the euphotic zone, as well as phytoplankton primary production and stoichiometry, to estimate new and regenerated production.

**Sampling**

When compared with a typical lake, it is sometimes difficult to define the mixing layer of a reservoir because lateral flow of water affects thermal stratification patterns. However, in a productive system, where waters below the mixed layer are often anoxic or hypoxic, the mixing layer can be delineated using oxygen profiles. Therefore, we measured dissolved oxygen at 0.5 m intervals using a YSI-57 meter (YSI Inc., Yellow Springs, Ohio) two to three times per week (Melack 1978; Dickman et al. 2006). Furthermore, the depth of the mixing layer was used instead of the euphotic zone, because phytoplankton circulate within this layer and the mixing layer was always equal to or slightly deeper than the euphotic zone. To calculate change in standing stocks in the mixing layer over the sampling period ($\Delta_{\text{mass}}$), water samples were collected twice per week at 1 m increments at the deepest part of the reservoir near the dam (8 m, the “outflow site”). We collected samples from this location because it should have relatively less suspended sediment and detrital matter in the water column compared with other areas that are shallower or closer to the input streams. Therefore, samples taken from this location should best represent the algal community.

Water samples were analyzed for particulate organic carbon (POC), particulate phosphorus (PP), total phosphorus (TP), and chlorophyll $a$ (Chl). POC and PP were assessed to calculate the C:P of seston in the mixed layer, and TP $\Delta_{\text{mass}}$ in the mixed layer was estimated. We measured Chl to enable us to calculate daily primary production rates (see below). Total particulate C (organic plus inorganic) mass was obtained by filtering water samples through replicate pre-ashed Pall A/E filters (Pall Corp., Port Washington, New York), the C contents of which were quantified with a Perkin-Elmer Series 2400 CN analyzer (PerkinElmer Inc., Waltham, Massachusetts). Particulate inorganic C mass was obtained similarly, except that each corresponding replicate filter (with sample) was ashed at 550 °C for 4 h before analysis. Particulate organic C was determined by subtracting particulate inorganic C from total particulate C (POC usually comprised >95% of total particulate C). PP was obtained by filtering water samples through a pre-ashed Pall A/E filter, which was then digested with HCl, whereas TP was estimated by digesting unfiltered water samples with potassium persulfate. For both PP and TP, phosphate liberated from digestion was quantified using a Lachat FIA+ QuikChem 8000 Series auto-analyzer (Lachat Instruments (Hach Company), Loveland, Colorado). For chlorophyll analysis, replicate water samples were each filtered onto a Pall A/E glass fiber filter; Chl was extracted with acetone and quantified using a Turner TD-700 fluorometer (Turner BioSystems, Inc., Sunnyvale, California). Mixing-layer concentrations (mg m$^{-2}$) were estimated by multiplying concentration by the volume of the appropriate layer, summing these products, and dividing the sum by surface area of the lake. We assume that the mixing-layer depth does not vary horizontally across the lake.

Concentrations of exported material exiting over the spillway were estimated from samples collected in the 0–1 m layer at the outflow sampling site (Caraco et al. 1992). Linearly interpolated P concentrations were assigned to days when lake samples were not collected (typically interpolations were over 3–4 days). Discharge over the dam was estimated on a daily basis by subtracting the daily change in lake volume from daily estimates of discharge into the lake (via inflow of streams). Lake volume was estimated by continuous measurements of lake level (using a chart recorder) and bathymetric data. Daily export of material over the spillway was estimated by multiplying P concentrations by daily discharge over the dam.

**Total, new, and regenerated production**

Total primary production throughout the study period was calculated by measuring $^{14}$C fixation rates on seven dates at both the outflow site and another shallow site near stream inflows. We followed methods of Fee (1990), as described in detail in Knoll et al. (2003). Briefly, on each date, photosynthesis was measured in the lab at a range of photosynthetically available radiation (PAR) levels to generate a chlorophyll-specific photosynthesis versus irradiance (PI) curve. Additionally, we measured irradiance (PAR) at 0.5 m intervals at both sites in the reservoir using a LI-COR spherical sensor (LI-COR Biosciences, Lincoln, Nebraska) two to three times per week. Reservoir-wide daily primary production rates (mg m$^{-2}$ day$^{-1}$) were obtained by integrating morphometrically corrected depth-specific rates using the PI curves, as well as depth-specific data on PAR and chlorophyll. The Fee (1990) program generated seasonal primary production rates by interpolating between dates of measured production and incorporating light and chlorophyll data obtained between dates of production measurements. Hourly readings of incident solar radiation for the sampling period were obtained from a meteorological station at the Miami University Ecology Research Center, located about 5 km from Acton Lake, using data that are part of the US Environmental Protection Agency Clean Air Status and Trends Network (CASTNET) program (www.epa.gov/castnet). We
assumed that 6% of incident light was reflected from the surface of the lake water and that the remainder entered the water column (Davies et al. 2004). PAR at each lake depth was then estimated using incident radiation and light attenuation coefficients. Note that although we measured primary production seven times during the study period, we measured light attenuation and Chl concentration at least every week, and all attenuation data were used to obtain production estimates. To estimate primary production in terms of P (mg P m⁻² day⁻¹), daily integrated primary production rates (mg C m⁻² day⁻¹) were divided by the corresponding dissolved phosphorus (TDP) concentrations for each stream. Because we obtained the organic carbon and phosphorus samples from the outflow site, where suspended sediment particle concentrations are relatively low, this C:P should best represent the algal community and thus provide an accurate estimate of primary production rates in terms of P.

We quantified P fluxes from new nutrient sources, including watershed input (i.e., from inflow streams), gizzard shad excretion, and benthic–pelagic fluxes. To estimate watershed input, water samples were collected every 6 h from gauging stations located at three inflow streams just before their entry to the reservoir (representing 86% of the lake’s watershed) (see Vanni et al. (2001) and Renwick et al. (2008) for detailed methods). Because streamwater nutrient concentrations increase greatly during storm events (Vanni et al. 2001), all samples during such events were processed, whereas during base flow, about five to six samples per week were processed. Stream samples were analyzed for PP and soluble reactive phosphorus (SRP). As hundreds of stream samples are analyzed per year, measurements of total dissolved phosphorus (TDP) concentrations for each stream were not measured because SRP samples require less labor and TDP can be accurately predicted using SRP. Therefore, the concentration of TDP was derived from stream-specific linear regressions using SRP as the independent variable ($R^2 > 0.81$ in all three streams; Vanni et al. 2001) and was added to PP to yield TP. A daily mean concentration was used on days when storm events occurred, and interpolated concentrations were assigned to days when stream samples were not collected (1–2 days per week). Discharge in all three streams was obtained every 10 min with a datalogger that measured stage and a rating curve relating stage and discharge (Vanni et al. 2001). Daily loading of material into the reservoir from each stream was estimated by multiplying daily discharge ($Q$) by the mean concentration for that day, and loading rates from the three streams were then summed. Because 14% of the watershed is not gauged, these loading rates were divided by 0.86 to estimate total watershed loading, and this loading rate was converted to an areal lakewide flux rate by dividing loading by lake area. To relate nutrient inputs to storm-generated discharge events, we obtained hourly precipitation data during the study period from the same weather station from which we obtained solar radiation data (also part of the CASTNET database).

Gizzard shad excretion rates at the whole-lake scale were obtained by multiplying per-fish excretion rate for each size class (50 mm bins) by the number of fish in that size class and summing these products, as detailed in Vanni et al. (2006a) for previous years. Per-fish excretion rates for each size class were obtained from regressions of P excretion rate versus body mass derived at temperatures similar to those during our study (regression equations are given in Vanni et al. (2006a)). The number of gizzard shad individuals in each size class was estimated using hydroacoustics in May, June, August, and October (detailed hydroacoustics methods are explained in Vanni et al. (2006a)). Lake-wide excretion rates (mg P m⁻² day⁻¹) were linearly interpolated between the hydroacoustics sampling dates.

We did not directly measure the rates at which SRP is released from sediments (via microbial–geochemical processes) for this study. Rather we used data from Nowlin et al. (2005), who measured release rates from aerobic and anoxic sediments several times in Acton Lake in earlier years. Based on their data, we assumed a constant rate of release and subsequent flux into the mixing layer (0.34 mg P m⁻² day⁻¹) over the entire study period (hereafter referred to as sediment release). This includes 0.33 mg P m⁻² day⁻¹ from aerobic sediments and 0.01 mg P m⁻² day⁻¹ from hypolimnetic entrainment of SRP released from anoxic sediments transferred to the euphotic zone (Nowlin et al. 2005).

We assume that watershed loading is quantitatively the most important source of P from outside the lake because Acton Lake is a reservoir with a large, agricultural watershed and because nutrient inputs are high (Vanni et al. 2001). In addition, we assume that gizzard shad excretion is also an important source of new P because of their abundance and high excretion rates (Schaus et al. 1997; Vanni et al. 2006a). The measured new P inputs (watershed loading, gizzard shad excretion, and sediment release) most likely comprise the majority of all possible new P inputs to the reservoir. Compared with these measured sources, atmospheric deposition, groundwater inputs, and other sources are likely to contribute little to P inputs and hence total primary production. For example, given the watershed area to lake area ratio of >100 and assuming that stream discharge is about 40% of precipitation (Vanni et al. 2001), water inputs via streams exceed precipitation inputs directly hitting the lake surface by >40 times. Furthermore, P concentrations in stream water are likely much higher than those in precipitation. Also, changes in lake volume can be accurately predicted using data on stream water inputs and evaporation (W.H. Renwick and M.J. Vanni, unpublished data), suggesting that groundwater inputs are not substantial.

To estimate new production, we assumed that the proportional supply of new and regenerated P is equal to the proportions of new and regenerated production. In other words, the rate of new and regenerated P supply equals the rate of new and regenerated production, respectively. This assumption should be valid as long as phosphorus remains the limiting nutrient (which it was over the course of the study). Consequently, the proportion of primary production supported by new inputs over the sampling period was determined by dividing the new P supply (mg P m⁻² day⁻¹) by total primary production in P units (mg P m⁻² day⁻¹). One possible source of uncertainty with this direct approach is the bioavailability of the various forms of P. To address this issue, we calculated a lower and upper bound of the new production rate using new SRP and TP inputs. We used new TP inputs to estimate the upper bound of new production, because it assumes that all P (particulate and dissolved) is available to phytoplankton. This degree of
availability is unlikely and probably overestimates new P supply to phytoplankton; however, it does provide the highest rate of new production possible. To calculate the lowest rate of new production possible, we used new SRP inputs. In contrast to TP, this approach most likely underestimates new P supply because some of the particulate inputs are possibly available to phytoplankton (or become available soon after being delivered to the lake). In conclusion, we present new and regenerated P as a range, using both approaches (i.e., using SRP and TP inputs as new P supply).

Regenerated P supply was determined by subtracting new P supply from the primary production rate (the latter expressed in P units). Proportional regenerated production was then estimated by dividing the regenerated P supply by the total primary production rate. Lastly, the proportion of total primary production supplied by gizzard shad excretion was determined by dividing gizzard shad excretion rate by total primary production rate.

**Results**

Watershed P loading rates from the streams were high at the beginning of the study period then declined to lower levels, following patterns of stream discharge. Most of the high peaks in stream inputs are associated with high runoff due to storm events (Fig. 1). Over the course of this study, the reservoir received about 1.4 times as much volume from the streams as lake volume, which equates to about six flushings per year, or a water residence time of two months. Approximately 65% of this flushing occurred during the first two weeks of the study. On average, there was a loss of 5.8 mg P m\(^{-2}\) day\(^{-1}\) over the spillway. The average gizzard shad excretion rate of 14.3 mg P m\(^{-2}\) day\(^{-1}\) was similar to rates from previous studies (Schaus et al. 1997; Vanni et al. 2006a). Based on seasonal data on size distributions and per capita excretion rates, we estimate that during our study period ~93% of P excretion by gizzard shad was mediated by detritivorous age classes and only 7% by zooplanktivorous young-of-the-year (YOY) fish. Thus, >90% of P excretion by shad can be considered new P.

Total primary production, averaged over the study period, was 2346 mg C m\(^{-2}\) day\(^{-1}\), whereas seston C:P averaged 42.9 by mass; both were temporally variable (Fig. 2). In P units, total primary production averaged 59.8 mg P m\(^{-2}\) day\(^{-1}\). The new nutrient supply from the watershed ranged from 4.7 mg P m\(^{-2}\) day\(^{-1}\) to 17.3 mg P m\(^{-2}\) day\(^{-1}\) (using SRP and TP inputs, respectively), and the aerobic and anaerobic sediments contributed 0.33 mg P m\(^{-2}\) day\(^{-1}\) and 0.01 mg P m\(^{-2}\) day\(^{-1}\) to the euphotic zone, respectively (assuming rates equal to those in Nowlin et al. (2005)). Taking into account the two different new P supply estimates, 32% (using SRP inputs) to 53% (using TP inputs) of total primary production was supported by new nutrients (P inputs = 19.3 mg SRP m\(^{-2}\) day\(^{-1}\) or 31.9 mg TP m\(^{-2}\) day\(^{-1}\)). This includes all three sources of new P (watershed, gizzard shad excretion, and sediment release). Consequently, 47%–68% of total primary production was supported by regenerated nutrients (28.1–40.7 mg P m\(^{-2}\) day\(^{-1}\)). P excretion by gizzard shad contributed 45%–74% of new P inputs (depending on whether all TP or all SRP inputs are used as a measure of new P) and 24% of P demand needed to sustain total primary production (Fig. 3).

**Discussion**

Our results demonstrate that new P supply has the potential to sustain about one-third to one-half of the total primary production in Acton Lake. Caraco et al. (1992) found that new production accounted for ~35% of total primary production in Mirror Lake, a small oligotrophic glacial lake. We expected this percentage to be higher in Acton Lake.
Fig. 2. (a) Primary production and (b) C–P (mass) ratios (C:P). Primary production was used to determine the proportion of new and regenerated production. C:P are lake-wide averages and were used to convert primary production in terms of C into production in terms of P for each day of the study period. Days on which C:P were not measured were assigned interpolated values (interpolation terms of P for each day of the study period. Days on which C:P used to convert primary production in terms of C into production in and regenerated production. C:P are lake-wide averages and were used to convert primary production in terms of C into production in terms of P for each day of the study period. Days on which C:P were not measured were assigned interpolated values (interpolation was typically between 3–6 days).

than in Mirror Lake, because Acton is a reservoir with a relatively large agricultural watershed and a large population of sediment-feeding fish. Thus, Acton (and other reservoirs) should receive relatively large quantities of new nutrients. If we evaluate the contribution of new P using TP inputs, as did Caraco et al. (1992), the relative contribution of new production is indeed higher in Acton than in Mirror Lake (53% vs. 35%). Thus, our results seem to support this prediction. However, as mentioned above, more than half of the new P inputs from streams are in the form of particulate P, which are likely not as bioavailable as dissolved P. Thus, even if ~20% or more of the particulate P inputs from streams become available to phytoplankton over the study period, new production would exceed 35% of total production. Furthermore, it is not clear to what extent the export estimates made by Caraco et al. (1992) accounted for sediment reuspension. They used sediment traps to estimate export production, and if trap material included both permanently exported and resuspended material, their estimates of export and hence new input may have been inflated, which would further support our expectation that a reservoir would have a higher percentage of primary production supported by new nutrients than natural lakes. Nonetheless, it is evident that new production accounts for a large proportion of total primary production in Acton Lake.

Estimates of the importance of P supply (new or regenerated) in sustaining primary production may be overstated if uptake of P by pelagic bacteria is significant (Cotner and Biddanda 2002), because in this case, a fraction of the P supply would be used by bacteria and not by phytoplankton. We did not measure bacterial P uptake, but we can estimate it using data from 2005, when bacterial production and the C:P of bacteria-sized particles (<1 μm) in the mixing layer were quantified. In 2005, bacterial production in Acton Lake was, on average, equal to 10.4% of primary production, and the C:P of particles <1 μm was 40.1 by mass (Caston et al. 2009). Using these numbers, we estimate that bacterial production in the mixing layer during 2004 was 6.05 mg P–m–2·day–1, i.e., about 10% of phytoplankton P demand. If we estimate total planktonic P demand as bacterial plus phytoplankton demand, new P inputs account for 29%–48% of planktonic P demand (depending on whether SRP or TP inputs are used).

Gizzard shad accounted for about 74% of new SRP inputs and 45% of total P inputs and therefore supplied enough P to support 24% of total primary production. The support of total production by gizzard shad is virtually identical to that estimated by Vanni et al. (2006a, 2006b), who found that shad supported, on average, 23% of late summer production in Acton Lake during the previous four years (2000 to 2003). It is also similar to the proportion of primary production supported by gizzard shad in a Kentucky reservoir (Shostell and Bukaveckas 2004). Gizzard shad excretion can have a substantial influence on phytoplankton growth, as newly available P is supplied at a fairly steady rate throughout the summer, in contrast to the more sporadic input from the streams (Vanni et al. 2001, 2005; Shostell and Bukaveckas 2004).

Although excretion by fish can be considered a P supply, it is also possible that fish can represent a sink for P if growth leads to P sequestration in fish biomass (Kitchell et al. 1979; Vanni 2002). However, Vanni et al. (2006a) showed that during the growing season in Acton Lake, P excretion by gizzard shad exceeded P sequestration via gizzard shad population growth by more than eight times (10.5 mg P–m–2·day–1 vs. 1.3 mg P–m–2·day–1; mean of 4 years). Thus, although rapid growth could dampen P flux rates through the gizzard shad population, much more P is excreted than sequestered in biomass production.

It may be instructive to compare our indirect estimate of P regeneration with that of a general model that predicts P regeneration using TP. Hudson et al. (1999) quantified “planktonic” P regeneration rate (P regeneration rate in the water column by microbes and zooplankton) in several lakes and found that it can be predicted with water column TP according to the formula log(RR) = (1.0077·log(TP)) + 0.7206, where RR is P regeneration rate (in ng P·L–1·h–1) and TP is water column total P (in μg P·L–1). Using data on Acton...
Lake water column TP (collected about weekly during the study), we estimated P regeneration using the Hudson et al. model. This yielded a mean P regeneration rate of 494 ng P L⁻¹ h⁻¹ or 43.7 mg P m⁻² day⁻¹. We can now compare this with our derivation of P regeneration using estimates of new and total P supply, as well as P demand. We estimate overall water column demand for soluble reactive P (SRP) to be 66.6 mg P m⁻² day⁻¹, assuming that phytoplankton primary production (59.8 mg P m⁻² day⁻¹), bacterial P uptake (6.05 mg P m⁻² day⁻¹), and export via the lake’s outflow (0.75 mg P m⁻² day⁻¹) account for all SRP demand in the water column. Assuming that SRP supply = SRP demand (reasonable for the limiting nutrient), we can estimate P regeneration by subtracting new P supply (19.5 mg P m⁻² day⁻¹, including watershed inputs, gizzard shad excretion, and sediment release) from demand (66.6 mg P m⁻² day⁻¹), which yields an estimate of P regeneration of 47.1 mg P m⁻² day⁻¹, very similar to that predicted by the Hudson et al. (1999) model.

Interestingly, Hudson et al. (1999) used their model to estimate planktonic P regeneration in Acton Lake and compared it with a previous estimate (1994) of P excretion by Acton Lake gizzard shad (Schaus et al. 1997). They concluded that fish are not important in P supply because planktonic P regeneration exceeded gizzard shad P excretion by a factor of ~9. This seems at odds with our conclusion here that gizzard shad are an important source of P. However, this apparent discrepancy can be reconciled by considering differences between studies and perspectives. Our gizzard shad biomass estimates from 2004 (the present study) are considerably higher than estimates presented by Schaus et al. (1997) for 1994. Most likely, we underestimated gizzard shad population density and biomass in 1994 because we used sampling methods (a combination of quadrat rotenone and electrofishing) that are less accurate than hydroacoustics. Our estimates of shad biomass (and P excretion) in 2004 are similar to those in 2000–2003, which were also estimated with hydroacoustics (Vanni et al. 2006a), suggesting that 2004 excretion rates are not atypical. Using data from the present study, planktonic P regeneration exceeded gizzard shad P excretion by a factor of ~3 in 2004 (47.1 mg P m⁻² day⁻¹ vs. 14.4 mg P m⁻² day⁻¹). Although this indicates that planktonic supply more P than gizzard shad, the difference is not nearly as great as that estimated by Hudson et al. (1999). In addition, it is important to emphasize that P excretion by gizzard shad is a new source of P, unlike planktonic P regeneration. As mentioned earlier, new P inputs are important for increasing phytoplankton biomass. Without new inputs, water column TP and, hence, phytoplankton biomass would gradually decline over the stratified period due to sedimentation, even if sediment resuspension is considerable (Baines and Pace 1994; Hudson and Taylor 2005). Indeed, new inputs provide P that subsequently can be recycled by microbes and zooplankton within the water column (Vanni 2002). Thus, when judging the importance of fish (or other sources), it is important to carefully consider the yardstick by which importance is measured. Almost two decades ago, Shapiro and Carlson (1982) suggested that excretion by benthic-feeding fish should be evaluated against external P inputs and not against P recycling within the mixing layer, because excretion by these fish delivers nutrients from outside the pelagic food chain. Although they did not couch their argument in the context of new vs. regenerated nutrients, they essentially argued, as we do here, that excretion by benthivorous fish can be a significant source of new nutrients. By incorporating many nutrient sources and by explicitly distinguishing between new and regenerated production, we hope that our study will help clarify the role of benthivorous animals in nutrient cycling.

Although previous work on Acton Lake and other reservoirs showed that gizzard shad can be an important nutrient source (Schaus et al. 1997; Vanni et al. 2005, 2006a), this study allows for a more comprehensive view of this fish,
and other nutrient sources, in sustaining primary production. To our knowledge, this is the first published study that compares gizzard shad excretion with all other nutrient sources known or suspected to be important (and one of the few to accomplish this for any fish species or assemblage). By taking this approach, we were able to evaluate the importance of gizzard shad in comparison with watershed inputs, as well as internal nutrient sources. Also, the consistent results of the new and regenerated production approach and the Hudson et al. (1999) method of estimating planktonic P recycling, in estimating regenerated production, imparts a high level of confidence in our conclusions about the relative importance of new and regenerated production. Our study also makes it clear that even though inputs of new nutrients (including gizzard shad excretion) sustain a significant proportion of primary production, regenerated P likely sustains half or more (47%–68%) of this production. Vanni et al. (2006a) concluded that gizzard shad excretion is relatively more important in productive reservoirs than in less productive reservoirs, in terms of sustenance of primary production. Thus, even in reservoirs in which gizzard shad are dominant in supporting production, regenerated nutrients are still of great importance in sustaining this production. In addition, our study may shed light on the role of bacterioplankton in recycling nutrients. A recent study (Caston et al. 2009) shows that the relative importance of pelagic bacteria production (BPr) in comparison with phytoplankton production (PPr), i.e., BPr/PPr, declines with increasing productivity in reservoirs, as is the case in natural lakes (Biddanda et al. 2001). Yet, assuming that bacteria account for a significant proportion of planktonic P regeneration (Hudson et al. 1999), our study suggests that bacterioplankton are important agents of P recycling in Acton Lake, a highly eutrophic ecosystem. This suggests that bacterioplankton may even be more important in recycling nutrients in less productive lakes. Future studies should evaluate the relative importance of new and regenerated nutrients along a productivity gradient.

This study is one of the few to evaluate new and regenerated production in freshwater ecosystems and the first to evaluate new and regenerated production in a reservoir. We found that the nutrient supply from a single fish species is the most important and continuous source of new nutrients in sustaining ecosystem production over the stratified period. Thus, the role played by fish and other animals in supplying new or regenerated nutrients depends largely on feeding habits of the animals, as well as the fate of nutrients in the absence of animal-mediated excretion. Because fish rely heavily on benthic food sources in most lakes (Vander Zanden and Vadeboncoeur 2002), their excretion may represent an important source of new nutrients in many systems, especially in small and shallow lakes where the littoral zone comprises a high proportion of lake surface area (Schindler and Scheuerell 2002; Mehner et al. 2005).

Our study and others suggest that removal, or greatly reduced biomass, of gizzard shad should lead to lower phytoplankton production and perhaps higher water clarity. Schaus et al. (2002) showed that in Acton Lake, years with lower shad biomass had lower seston C concentration when compared with years with higher gizzard shad biomass. Similar results were found in enclosure experiments in the lake (Schaus and Vanni 2000). Water quality managers may be able to utilize this knowledge to improve water quality. Indeed, the St. John’s River Water Management District in Florida is currently conducting whole-lake gizzard shad reduction experiments to assess if this can reduce phytoplankton biomass and improve water quality and fishing (www.sjrwmd.com/streamlines/2008summer/page3.html). Thus, lake and reservoir managers need to consider both external inputs to the reservoir (via streams) and the biota present within the reservoir to manage the level of eutrophication in these ecosystems.

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