Stoichiometry of nutrient excretion by fish: interspecific variation in a hypereutrophic lake

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This study investigates how nutrient cycling rates and ratios vary among fish species, with a particular focus on comparing an ecologically dominant detritivore (gizzard shad) to other fishes in a productive lake. We also examined how nutrient cycling rates are mediated by body size (as predicted by allometry theory), and how variation in nutrient cycling is related to body and food nutrient contents (according to predictions of ecological stoichiometry). As predicted by allometry, per capita nitrogen and phosphorus excretion rates increased and mass-specific excretion rates decreased, with increasing mass. Body phosphorus content was correlated with body mass only in one species, bluegill. Contrary to stoichiometric predictions, there was no relationship between body P and mass-normalized P excretion rate, or between body N:P and excreted N:P, when all individuals of all species were considered.

However, at the species level, we observed some support for a body nutrient content effect on excretion as predicted by stoichiometry theory. For example, gizzard shad had lower body P (high body N:P) and also excreted P at higher rates (lower N:P) than bluegill, which had high body P (lower body N:P). We applied the Sterner (1990) homeostatic stoichiometry model to the two most common species in the study – gizzard shad and bluegill - and found that food N:P had a greater effect than consumer body N:P on excreted N:P. This indicates that, in terms of variation among these species, nutrient excretion may be more of a function of food nutrient content than the nutrient content of the consumer. These results suggest that stoichiometry can provide a framework for variation among species in nutrient cycling and for evaluating the ecosystem consequences of biodiversity loss.

Human-induced decreases in biodiversity may cause functional shifts in ecosystem processes, leading to a debate among ecologists as to the relative importance of how biodiversity mediates ecosystem functioning (Hooper et al. 2005). Some authors have concluded that differential impacts of species (i.e. species identity) on their environment and the types of interactions that take place may be the most important mechanisms by which biodiversity enhances ecosystem functioning (Hooper et al. 2005). To evaluate the importance of species identity in regulating ecosystem processes, more information is needed on how different species mediate such processes.

Ecological stoichiometry theory (sensu Sterner and Elser 2002) has emerged as a conceptual framework for how species vary in mediating nutrient cycling, an important ecosystem process. This theory predicts that nutrient release by a consumer is a function of the imbalance between the consumer’s body nutrient content and its food’s nutrient content as well as the efficiency at which the consumer assimilates nutrients into biomass (Sterner and George 2000, Vanni et al. 2002). Of particular interest is the ratio at which nutrients are released. A model proposed by Sterner (1990) suggests that the N:P ratio of nutrient release (hereafter excretion N:P) by a consumer will increase curvilinearly with food N:P and will decrease with consumer N:P, assuming that the consumer is homeostatic with respect to body N and P contents and has an equal maximum gross growth efficiency (GGE$_{max}$) for each nutrient.

Animals such as fish and invertebrates are often important in nutrient cycling within freshwater ecosystems, but few studies have explicitly examined inter-
specific variation (Vanni 2002). Fish species vary greatly in their diets (Mathews 1998) and in their body nutrient contents (Davis and Boyd 1978, Tanner et al. 2000, Vanni et al. 2002). Thus, the potential exists for substantial interspecific variation in the rates and ratios by which they release nutrients (Elser et al. 1996, Vanni et al. 2002). However, more studies are needed to explore how nutrient release by fish follows stoichiometric predictions.

Gizzard shad (Dorosoma cepedianum) are facultative detritivores (Yako et al. 1996) that are found in most reservoirs, natural lakes and large rivers in the lower midwest and southern United States (Johnson et al. 1988, Vanni et al. 2005). Larval shad are obligate zooplanktivores, but when they reach a total length of ~30 mm, they can consume sediment detritus (Heinrichs 1982, Mundahl 1991, Smoot and Findlay 2000, Schaus et al. 2002). In reservoirs, gizzard shad often comprise a large portion of fish biomass, and diets of non-larval shad are dominated by sediment detritus (Mundahl and Wissing 1986, Vako et al. 1996, Vanni et al. 2005, Higgins et al. 2006). A negative correlation has been found between gizzard shad and bluegill (Lepomis macrochirus) abundances in these systems, with bluegill densities being consistently low when gizzard shad densities are high (Garvey and Stein 1998, Vanni et al. 2005). If these two fishes recycle nutrients at different rates and/or ratios, then it is possible that a shift in the abundance of one of these species could lead to an important alteration in consumer-mediated nutrient fluxes within a reservoir.

Through nutrient excretion, gizzard shad populations can represent a significant source of N and P for phytoplankton in reservoirs (Schaus et al. 1997, Shostell and Bukaveckas 2004, Vanni et al. 2005, 2006). Due to the low N:P ratios at which they excrete, these fish can alter phytoplankton communities, possibly favoring the growth of cyanobacteria (Schaus et al. 1997, Shostell and Bukaveckas 2004). To some extent, the importance of gizzard shad in nutrient cycling in reservoir ecosystems is probably due to their relatively high biomass (Vanni et al. 2005, 2006). Yet, it is not known whether the ecosystem-level importance of shad in nutrient cycling is due simply to their great abundance, or also because they have higher per capita excretion rates than other species. Information on how different species vary in nutrient cycling is thus essential.

We investigated the effect of species identity and abundance on ecosystem functioning by measuring the variation among fish species in nutrient excretion rates and ratios in a hypereutrophic reservoir. The objectives were to quantify and compare excretion rates of several species (over a range of body sizes), including gizzard shad, and to understand the stoichiometric factors underlying interspecific variation in nutrient excretion rates and ratios. Body nutrient contents and diets were quantified to correlate them with excretion rates and to test predictions of ecological stoichiometry theory. Because gizzard shad dominate fish biomass and have strong community- and ecosystem-level effects in many reservoirs, and because we already know a great deal about nutrient cycling by this species, we explicitly focused on comparisons between gizzard shad and other species. We addressed several hypotheses. Our first null hypothesis was that fish species other than gizzard shad would have similar excretion rates and ratios (per individual or per biomass) as shad. The alternative hypothesis was that fish species vary significantly in nutrient excretion rates and/or ratios. If the alternate hypothesis was supported, we further hypothesized that variation among species could be explained by ecological stoichiometry theory (i.e. by the imbalance between consumer and body nutrient contents). Finally, we tested the hypothesis that gizzard shad are important in nutrient cycling simply because of their high abundance vs the alternative hypothesis that they are important because they excrete nutrients at high rates or at unique N:P ratios. While we quantified nutrient excretion by five fish species in four families, we focus particular attention on gizzard shad and bluegill due to the inverse relationship between their abundances in reservoir ecosystems.

Methods

Nutrient excretion experiments

Nutrient excretion experiments were conducted July-September 2004 in Acton Lake, a 231-ha hypereutrophic reservoir in southwestern Ohio. Excretion rates were measured on a total of 164 fish of various body sizes, collected via electroshocking in the upstream portion of the reservoir. We studied five fish species – gizzard shad (D. cepedianum, family Clupeidae, n = 49), bluegill (L. macrochirus, family Centrarchidae, n = 52), longear sunfish (Lepomis megalotis, family Centrarchidae, n = 23), logperch (Percina caprodes, family Percidae, n = 23), and golden shiner (Notemigonus crysoleucas, family Cyprinidae, n = 17). The fish assemblage was dominated by shad and bluegill, and sample sizes varied according to seasonal availability.

Excretion experiments followed established methods (Schaus et al. 1997, Gido 2002, Shostell and Bukaveckas 2004, Higgins et al. 2006). Each fish was transferred to a container filled with Acton water that was pre-filtered using Advantec high-volume filters (0.3 µm nominal pore size) (Advantec MFS, Dublin, California) that removed phytoplankton and bacteria that could take up excreted nutrients. Containers with fish and controls without fish were kept at epilimnetic temperatures that ranged from 23-28°C throughout the
study. Initial water samples were taken from 50-l carboys before filling the containers to quantify initial nutrient concentrations prior to fish addition. Fish and controls were incubated for 45–60 min. The water was then filtered through Pall A/E glass-fiber filters (1.0 µm pore size) (Pall Corporation, Ann Arbor, Michigan) and analyzed for NH$_3$-N and SRP using the phenol-hypochlorite technique (Solorzano 1969) and molybdenum blue method (Stainton et al. 1977), respectively, using a Lachat (Loveland, Colorado) Series 8000 autoanalyzer. Excretion rates were determined as the difference between initial and final nutrient concentrations, corrected for controls (Schaus et al. 1997).

Body nutrient analysis

Upon completion of excretion experiments, fish were measured for total length, weighed, euthanized, and then frozen for analysis of tissue C, N, and P. The entire gastrointestinal tract was dissected and removed for later gut content analysis. The fish were then oven-dried at 60°C until they reached a stable weight. Entire fish bodies (minus the gut) were ground into powder, using a Retsch (Haan, Germany) Model ZM100 tissue grinder (for large individuals) and a mortar and pestle (for small individuals), and homogenized. These samples were analyzed for C and N using a Perkin Elmer (Oak Brook, Illinois) Series 2400 elemental analyzer (1 sample per fish), and for P using HCl digestion followed by SRP analysis (2 replicate samples per fish) (Vanni et al. 2002).

Correlation of body nutrient content, nutrient excretion and gut contents

Per capita nutrient excretion rates and ratios were regressed against body mass and against corresponding body nutrient content and body nutrient ratios to determine if nutrient excretion was a function of body nutrient content, as predicted by stoichiometry theory. Log-log plots were used in certain instances to stabilize the variance among species and to explicitly examine allometric relationships. Log per capita excretion rates were expected to be correlated with log body mass, with an exponent $<1$, according to allometry theory (Peters 1983, West et al. 1997).

Because excretion rates are a function of size, it is desirable to remove size effects when comparing species or when trying to ascertain the effect of body nutrient contents. Therefore, mass-normalized rates were obtained to explicitly evaluate the relationship between body nutrient contents and excretion using the following formula:

$$X_n = \frac{X}{W^b}$$

where $X$ is the non-normalized excretion rate, $X_n$ is the mass-normalized excretion rate, $W$ is body mass, and $b$ is the scaling exponent relating log body mass and log per capita excretion rate for a particular species (Brown et al. 2002). The scaling exponent, $b$, was obtained empirically from log-log plots generated by our data and accounted for the fact that this scaling exponent may be species-specific.

According to stoichiometric predictions, diet nutrient content and ratios can affect excretion rates and ratios (Sterner 1990). Because we wished to explore how both body nutrients and dietary nutrients affect excretion rates and ratios, the gut contents of 21 gizzard shad, gizzards, and 32 bluegill stomachs, which were randomly chosen to represent a range of dates and sizes, were removed. We focused only on shad and bluegill because they were the dominant species in Acton Lake (and thus, had the largest sample sizes), and because of the aforementioned inverse relationship between their abundances in reservoir ecosystems. We examined diets of more bluegill than gizzard shad because earlier work had revealed that non-larval shad feed almost entirely on sediment detritus (Mundahl and Wissing 1986, Schaus et al. 2002, Sigler 2002, Higgins et al. 2006). Gut contents were examined under a dissecting scope to identify and quantify food items. N and P contents of food items were estimated from the literature rather than from direct quantification because gut material from fish used in excretion experiments may have been partially digested during the experiments, leading to possible biases in nutrient contents.

To further evaluate the potential roles of body N:P and food N:P in driving excretion N:P, we applied the Sterner (1990) homeostatic stoichiometry model to gizzard shad and bluegill. This curvilinear model predicts N:P recycling ratios as a function of food N:P and consumer body N:P using two equations based on the nutrient limitation of the consumer. If P is deficient in the food (i.e. food N:P > body N:P), then the recycled N:P ratio is described by:

$$\left(\frac{N}{P}\right)_f = \frac{\left(\frac{N}{P}\right)_c - GGE_{max} \times \left(\frac{N}{P}\right)_c}{1 - GGE_{max}}$$

where $(N/P)_f$ is the nutrient ratio of the consumer, $(N/P)_c$ is the nutrient ratio of the food, GGE$_{max}$ is the maximum gross growth efficiency for the limiting nutrient, and $(N/P)_c$ is the consumer nutrient recycling ratio. When N is scarce in food relative to the consumer’s body, then the following equation applies:
The model assumes that individuals maintain a constant body N:P, which is reasonable given the temporal scale over which diets and excretion rates were measured (diets reflect food consumed within a few hours and excretion rates were measured over 45–60 min).

We used the body N:P ratios we observed for shad and bluegill and initially set GGE$_\text{max}$ for N and P to 0.70. Data on GGE$_\text{max}$ for N and P are not available for either fish species, to our knowledge. Therefore, GGE$_\text{max}$ was estimated from maximal growth efficiencies and body nutrient content data presented in Fig. 1 in Schindler and Eby (1997). From this figure, GGE$_\text{max}$ for wet mass (maximum growth in wet mass/consumption of prey in wet mass) for fish consuming Daphnia was estimated to be 0.24. Then we used body P contents of fish and Daphnia to convert GGE$_\text{max}$ for wet mass to GGE$_\text{max}$ for P, yielding a value of 0.71. GGE$_\text{max}$ is much higher for P than for wet mass because fish have much higher body P content than zooplankton. Using the same approach, we also calculated GGE$_\text{max}$ for P for fish feeding on other zooplankton and found slightly lower values (0.65 when feeding on Bosmina and 0.64 when feeding on copepods). Because GGE$_\text{max}$ represents maximal efficiency for the most limiting nutrient (Sterner 1990), we used 0.70 in our calculations.
initial approach and assumed that P is limiting since prey items have a higher N:P than fish bodies.

Based on our gut analyses, bluegills fed mainly on chironomids (Results). Therefore, in our simulations, we set N:P ratios for bluegill prey equal to 29 (molar), based on an average of values for dipterans from Cross et al. (2003) (n = 11 individuals from a reference stream) and Frost et al. (2003) (n = 8 Canadian lakes differing in productivity, number of individuals collected not presented). We set the N:P ratio of detritus consumed by gizzard shad to be 12 (molar) based on aerobic detritus actually consumed by shad in Acton Lake, not ambient detritus, as shad selectively feed on detritus that has higher C, N, and P content than ambient detritus (Higgins et al. 2006).

Statistical analyses

Data were log-transformed when appropriate to equalize variances and were analyzed using an analysis of covariance (ANCOVA) with Bonferroni (slopes) and Dunnett (intercepts) adjustments for multiple comparisons with gizzard shad (proc glm – SAS, Version 9.1). In all cases, species was considered the categorical variable. Nutrient excretion rates and ratios, as well as fish body nutrient contents and ratios, were considered dependent variables in ANCOVAs (separate ANCOVAs for each dependent variable), with wet mass as a covariate. To examine the relationship between body N:P and excretion N:P, excretion N:P was modeled as a dependent variable using ANCOVA with body N:P as a covariate. To examine the relationship between body nutrient content and excretion rate without the potentially confounding influence of size effects, mass-normalized N and P excretion rates were used as dependent variables and body N and P, respectively, used as covariates. Regression lines were also fitted to the data for all variables, using least squares regression, to obtain the slopes and intercepts for each species.

Results

Nutrient excretion experiments

Per capita N excretion was highly and positively correlated with mass for all 164 fish analyzed together (Fig. 1a, p = 0.0295, ANCOVA). There was also a significant species effect (p < 0.0001) as well as a mass × species interaction (p < 0.0001). As predicted by allometry theory, all slopes of log-log plots were found to be <1 (Appendix A). Logperch and golden shiner were the only species with slightly negative slopes, but the size ranges of these two species were quite narrow and slopes thus need to be interpreted with caution. Gizzard shad had higher N release rates than logperch and shiner but shad N excretion rates were not statistically different from other fish species (Fig. 1a, Appendix B). The presence of a very small gizzard shad in the dataset (Fig. 1) had minimal influence on the regression analysis conducted for N excretion as well as for all other dependent variables.

The presence of a significant species × size interaction precludes direct interspecific comparisons of N excretion rates using all data. Thus, we separated gizzard shad and bluegill into two size classes (small and large), within which fish of both species were similar in size. Then we calculated species means for each size class to look at how size of a particular species can influence interspecific differences in excretion. We found that large shad tended to excrete more N than longear sunfish, small bluegill, and logperch (p < 0.05) but that N excretion rates of large shad were statistically similar to large bluegill and shiner. Small shad had lower N release rates than large bluegill (p < 0.05) but were not statistically different from the other fishes.

Per capita P excretion was also a function of increasing mass for all fishes (Fig. 1b, p = 0.0437). There was a significant species effect (p < 0.0001) as well as a mass × species interaction (p = 0.0015). Slopes were <1, again indicating allometric scaling for all fish species. Once again, logperch had a slightly negative slope that was statistically different from shad. The slope for gizzard shad was statistically indistinguishable from all other fish species (Fig. 1b, Appendix B). When considering species means, large and small shad tended to excrete more P per capita than other fish of the same body size (Fig. 1b; also see section on mass-normalized rates below).

Body nutrient analysis

Mass had no effect on fish body N content (Fig. 2a, p = 0.9088) but there was an effect of species (p = 0.0001) and a mass × species interaction (p = 0.0051). This was also seen for body C:N and body C:P ratios (Torres 2005). Bluegill was the only species in which N content increased with mass, and this increase was slight (Fig. 2a, m = 0.06, p = 0.0001). Gizzard shad had less body N than bluegill but was statistically similar to all other species (Appendix C).

There was a significant effect of mass (Fig. 2b, p = 0.0258), species (p < 0.0001), and mass × species interaction (p < 0.0001) on body P content. This was also seen for C body content (Appendix C, Torres 2005). Bluegill was the only species for which body P content increased with mass (p < 0.0001, Fig. 2b). A marginally significant increase in body P with mass was observed for longear sunfish (p = 0.0787). Similarly, bluegill had
a greater increase in body P content with mass (i.e. steeper slope) than gizzard shad; body P and mass were unrelated in shad (Fig. 2b, Appendix C).

Considering all species combined, there was a significant effect of mass (Fig. 2c, \( p = 0.0034 \)) and mass \( \times \) species interaction (\( p = 0.0006 \)), but there was no species effect (\( p = 0.2730 \)). Both gizzard shad (\( p = 0.0198 \)) and bluegill (\( p < 0.0001 \)) showed decreasing body N:P with mass, but the decrease was steeper for bluegill than it was for shad (Fig. 2c, Appendix D). The slope for gizzard shad body N:P was statistically similar to all other fish species (Appendix D).

### Relationships between body nutrients and nutrient excretion

For mass-normalized N excretion rates, there was a non-significant body N \( \times \) species interaction (Fig. 3a, \( p = 0.0741 \)). However, there was a significant species effect (\( p < 0.0001 \)) and a main effect of body N (\( p = 0.0078 \)). Gizzard shad and logperch were the only species in which mass-normalized N excretion varied with body N; in both cases, body N and N excretion were positively related (\( p = 0.0217 \) for shad and \( p = 0.0271 \) for logperch). Gizzard shad was found to have a lower N excretion rate than logperch and golden shiner but a higher N excretion rate than bluegill and longear sunfish (Fig. 3a, Appendix E). For mass-normalized per capita P excretion rates, there was no body P \( \times \) species interaction (\( p = 0.7789 \)) or effect of body P (\( p = 0.1079 \)) but there was an effect of species (Fig. 3b, \( p < 0.0001 \)). Mass-normalized P excretion rates of shad were higher than all other fishes except logperch (Fig. 3b, Appendix E).

There was a significant effect of species on excreted N:P (Fig. 3c, \( p < 0.0001 \)), but no effect of body N:P (\( p = 0.5254 \)) and no body N:P \( \times \) species interaction (\( p = 0.9064 \)). Overall, gizzard shad had a lower, and less variable, excretion N:P than the other fish species (Fig. 3c, Appendix E).

### Dietary nutrients

Five out of 32 bluegills examined for gut contents had empty stomachs. The other 27 fish had gut contents that were comprised primarily of benthic invertebrates, with 60–99% of the identifiable food items being chironomid larvae. As for gizzard shad, 7 out of 21 individuals were found with empty gizzards. The rest of the shad had gut contents consisting of only sediment detritus obtained from sediments of Acton Lake that are overlain with well-oxygenated water. Although non-larval gizzard shad are primarily detritivorous in this and other reservoirs (Higgins et al. 2006), we do not know whether the origin of the detritus is allochthonous and/or autochthonous.
Discussion

Nutrient excretion

As allometry theory predicts, per capita N and P excretion increased with increasing mass, but with slopes less than 1 on a log-log scale (Elser et al. 1996, Schaus et al. 1997). Mass-specific P excretion rates for gizzard shad in our study were similar to ranges reported for gizzard shad in Taylorsville Reservoir, Kentucky (Shostell and Bukaveckas 2004), and those found in previous studies of shad in Acton Lake (Mather et al. 1995, Schaus et al. 1997, Higgins et al. 2006). However, the slope for P excretion was low compared to other studies on Acton Lake gizzard shad (Schaus et al. 1997, Higgins et al. 2006), despite similarities in lake temperature. Ranges for gizzard shad mass-specific N excretion rates were considerably wider than estimates of prior

Fig. 3. Mass-normalized per capita N (A) and P (B) excretion vs body N and body P content, respectively, for Acton Lake fishes. N excretion is on an arithmetic scale while P excretion is on a log-scale. (C) Nutrient release ratios as a function of fish body N:P.
studies (Appendix F). The ranges for mass-specific P and N excretion for bluegill sunfish (0.01–0.99 μmol P g⁻¹ h⁻¹; 1.7–86.7 μmol N g⁻¹ h⁻¹) were considerably wider than laboratory values reported by Mather et al. (1995) (0.04–0.18 μmol g⁻¹ h⁻¹ for P; 2.5–3.4 μmol g⁻¹ h⁻¹ for N). Nutrient excretion rates for the other fishes in Acton Lake could not be compared to literature values because no previous studies have been conducted using those species.

The null hypothesis that other fish species within Acton Lake would have similar excretion rates and ratios (per individual or per biomass) as gizzard shad was partially supported. We found that gizzard shad was unique in its per capita nutrient excretion as compared to other fishes. Shad had higher N release rates than logperch and golden shiner, and the slope of the P excretion vs. mass relationship was greater for shad than logperch. When excretion rates were mass-normalized, shad had higher P excretion rates than all other fish species except logperch (Fig. 3b). Thus, the effect of body size on nutrient recycling may be species dependent, but, given that logperch are scarce in Acton Lake and other reservoirs, we can conclude that gizzard shad have consistently higher P excretion rates than all other common fish species of similar size.

Body nutrients

We found no significant effect of mass on fish body N content, contrary to Davis and Boyd (1978), who found that N content decreased with increasing mass for bluegill. In fact, we found a slight increase in body N content with mass for bluegill (m = 0.06, P = 0.0001). Bluegill was also the only fish species that had increasing body P with increasing mass, possibly due to stiffer and greater numbers of scales. This suggests that bluegill likely have a greater relative allocation of P to the formation of bones and scales than the other fishes studied here (Sterner and George 2000, Sterner and Elser 2002). A similar trend was reported by Davis and Boyd (1978) and may be characteristic of the family Centrarchidae (Sterner and Elser 2002), though a significant mass vs body P relationship was not seen for longear sunfish in our study (but this may be due to low sample size, as the correlation between body size and body P was marginally significant). It has also been proposed that high and low consumer body P may be a manifestation of evolutionary adaptations in “stoichiometric niches” (e.g. development of reduced body demands for N or P; Hessen et al. 2004). Thus, the body nutrient stoichiometry of freshwater fishes has a phylogenetic component that needs further exploration.

Compared to bluegill, gizzard shad’s higher mean body N:P is a consequence of (1) the low body P content relative to body N for shad and (2) the high body P content of sunfish. Both shad and bluegill had decreasing body N:P with increasing mass, a result that supports Vanni’s (1996) prediction that there should be a decreasing allometric trend for body N:P with increasing fish size. The other fishes in this study did not show the same trend, indicating that fish body N:P may decrease with size only over broad size ranges or that the relationship between body size and body N:P may be species-specific. Ultimately, to evaluate differences in body nutrient stoichiometry among fish, one must consider constituent elements as well as their ratios and their biochemical form (Anderson et al. 2004).

Correlations between body nutrients and excretion

Can ecological stoichiometry theory explain the variation among Acton Lake fishes? With respect to the relationships between body nutrient contents (or ratios) and excretion rates (or ratios), we found mixed support for stoichiometric predictions. Contrary to stoichiometric predictions, per capita N excretion increased with increasing body N, but this trend was driven entirely by bluegill. Unlike Vanni et al. (2002), we found no relationship between body P and mass-normalized P excretion rate, or between body N:P and excreted N:P, when all individuals of all species were considered. Yet, at the species level, we observed some support for a body nutrient content effect on excretion. When mean mass-normalized P excretion rates were plotted against mean body P content for each species (i.e. n = 5) on a log-log scale, there was a significant negative correlation between these two variables (p = 0.0327). For example, gizzard shad had lower body P (high body N:P) and also excreted P at higher rates (lower N:P) than bluegill, which had high body P (lower body N:P). However, golden shiner and logperch showed trends unlike bluegill and shad, with relatively high body N:P and high excretion N:P, possibly due to a higher N:P diet than bluegill (Fig. 3c). This agrees with findings of Vanni et al. (2002), who found a negative correlation between body P and P excretion at the species level. However, we found no relationship between body N content and N excretion rate (p = 0.3696; in agreement with Vanni et al. 2002) or excretion N:P (p = 0.9062, in contrast to the findings of Vanni et al. 2002).

Application of Sterner’s homeostasis model

Comparison of the diets of gizzard shad and bluegill suggests that food N:P may play a strong role in determining excreted N:P, because the N:P ratio of
invertebrates and sediment detritus is quite different. Consistent with other studies, examination of gut contents revealed that gizzard shad primarily ingest detritus (Higgins et al. 2006) whereas bluegills tend to consume chironomids (Olson et al. 2003). Although bluegill diet preference has not been assessed in Acton Lake, it is reasonable to assume that resident bluegills prefer chironomids, as they are very abundant in shallow, oxygenated areas in this lake (Devine and Vanni 2002). It is possible that differences in the nutrient contents of chironomids and detritus may explain the variation in excretion rates between bluegill and shad.

To assess this possibility, we applied the Sterner (1990) homeostasis model, and this produced two noteworthy results (Fig. 4). First, overall, there was close agreement between modeled and measured excretion N:P; N:P excretion ratios predicted by this model were only slightly greater than those obtained in nutrient excretion experiments for both gizzard shad and bluegill (Fig. 4a). Furthermore, the relative difference between species in N:P excretion ratio was preserved. We observed a 3.5 \times difference between N:P excretion ratios of these two species (excretion N:P = 19 for shad and 66 for bluegill) from direct measurement, whereas the model predicted N:P excretion ratios of 23 and 79, which is a 3.4 \times difference. Second, the difference in body N:P between the two species appears to be insufficient to explain the observed variation in excretion N:P. For example, if food N:P is held constant at 12 (equivalent to that of detritus consumed by shad), the model predicts excretion N:P to be only 13\% higher for bluegill than for shad, in contrast to the aforementioned 3.5 \times difference. Similar results were obtained using food N:P values typical of bluegill diets (Fig. 4a).

In contrast, the difference in dietary N:P between shad and bluegill can apparently explain much more of the difference between these two species in N:P excretion ratio (Fig. 4a). By adjusting GGE_{max} for each species until the excretion N:P values in the model corresponded to those found in the nutrient excretion experiments, we were able to generate GGE_{max} values of 0.620 for bluegill and 0.605 for shad, values that seem reasonable given the estimates presented above for bluegill feeding on zooplankton (Fig. 4b).

Results of these model simulations suggest that the observed difference in excretion N:P between shad and bluegill may be more a function of differences in food N:P and GGE_{max} than consumer body N:P (Fig. 4b). Elser and Urabe (1999) also concluded that nutrient release by zooplankton is more a function of food N:P than consumer body N:P, but Vanni et al. (2002) concluded that interspecific variation in N:P excretion ratio among fish in a tropical stream was driven by variation in body N:P (mainly due to body P). Our results thus differ from those of Vanni et al. (2002), most likely because the interspecific range in body P and body N:P was much narrower in our study than that observed by Vanni et al. (2002).

Diet, diet shifts, and growth rates may play vital roles in determining nutrient recycling within aquatic systems. Aquacultural studies have consistently found that body P and P excretion increase as dietary P increases for a few fish species (e.g. rainbow trout *Oncorhyncus mykiss*)-Bureau and Cho 1999; juvenile haddock *Melanogrammus aeglefinus*-Roy and Lall 2003), possibly due to a decrease in the efficiency of P utilization or calcium-limitation. Brabrand et al. (1990) also suggested that P release rates of fish are influenced by the food they consume; in their study, sediment-feeding fish tended to have higher P excretion
rates than fish feeding on invertebrates. This is consistent with our results and may reflect a general tendency for sediment detritus to have lower N:P than invertebrate tissue. Yet, it is possible that fishes within the same feeding guild may affect nutrient recycling differently depending on slight differences in food (e.g. high vs low organic matter) or differences in assimilation efficiencies (Yossa and Araujo-Lima 1998). Lastly, the role of growth rates is not clear. Schindler and Eby (1997) suggest that under most conditions, fish growth rate has little effect on P excretion rate, because fish usually are energy limited (not N or P-limited) and grow at rates that are well below maximal. However, excretion rates of P-limited fish (e.g. herbivorous fish-Schindler and Eby 1997, Hood et al. 2005) may be sensitive to growth rate. Clearly, more work is needed to elucidate how food N:P, body N:P, and physiological parameters (GGE, growth rate, etc.) mediate excretion N:P under various conditions.

Based on our results, gizzard shad may be important in P cycling both because of their abundance and high per capita P excretion rates. In Acton Lake during summer 2004, gizzard shad comprised 66% of total fish biomass but were also responsible for 81% and 95% of all N and P excreted by the fish community (Torres 2005). Thus, shad are disproportionately important to nutrient cycling and, in turn, primary production within the reservoir due to their abundance and the amount of N and P they release. It has been suggested that shad can synergistically regulate primary production in reservoirs with watershed-derived nutrients (Vanni et al. 2005). Since the Acton Lake watershed is >90% agricultural, lake N:P is high due to the high influx of N from fertilizers (Arbuckle and Downing 2001; Vanni et al. 2001), especially in spring-early summer. Thus, the low N:P excreted by shad may provide algae with more P for primary production. This is substantiated by the fact that shad can support up to 50% of primary production in mid-late summer in Acton Lake (Vanni et al. 2006). Nutrient excretion by gizzard shad also supports a substantial proportion (10–20%) of primary productivity in other reservoirs, but the role of shad in supporting production seems greatest in highly productive, agriculturally impacted reservoirs (Vanni et al. 2006).

**Conclusion**

Gizzard shad are important to nutrient cycling in reservoirs, and presumably other ecosystems, because they are abundant and their excretion rates are stoichiometrically unique, excreting P at high rates and at a low N:P ratio. Adult shad can decrease chironomid abundance via bioturbation (Gido 2003) and larval-juvenile shad can reduce zooplankton via predation; these actions can reduce bluegill populations and promote shad population growth (Garvey and Stein 1998, Vanni et al. 2005). At the ecosystem level, they could shift a system that is P-limited to one that is N-limited. This, in turn, could cause the algal assemblage to be dominated by N-fixing cyanobacteria. However, the influence of shad nutrient cycling on primary production may be dependent on nutrient inputs from the watershed (Arbuckle and Downing 2001, Vanni et al. 2005) as well as seasonality and interannual variability in population size and precipitation (Shostell and Bukaveckas 2004, Vanni et al. 2005). Thus, it appears that species identity and abundance must be taken into consideration to prevent, control, or reverse eutrophication in reservoirs and other aquatic systems.

At least in low-diversity systems like Acton Lake, it seems that the abundance of a particular species as well as its per capita effects can mediate its impact on the functioning of an ecosystem. If species identity is found to be crucial to ecosystem functioning in other low and high diversity systems, then the concept of species redundancy (Walker 1992) needs to be reevaluated.

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Appendix A–G can be found as O15268 at www.oikos.ekol.lu.se