Detritivory and the stoichiometry of nutrient cycling by a dominant fish species in lakes of varying productivity

Karen A. Higgins, Michael J. Vanni and Maria J. González


Little is known about the stoichiometry of nutrient cycling by detritivores. Therefore, we explored stoichiometric relationships in an omnivorous/detritivorous fish (gizzard shad, Dorosoma cepedianum) in three lakes that differed in productivity. Gizzard shad can feed on plankton and sediment detritus, but in all three lakes adult gizzard shad derived >98% of carbon (C) and phosphorus (P), and >90% of nitrogen (N) from sediment detritus, and the remainder from zooplankton.

Gizzard shad selectively consumed detritus with higher C, N and P concentrations than ambient lake sediments. Selective detritivory (i.e. the nutrient content of consumed detritus divided by the nutrient content of ambient detritus) was most pronounced in the lake with the lowest detrital nutrient concentrations. N and P cycling rates per fish were also consistently higher in this lake, in agreement with the prediction of stoichiometry theory that excretion rates should increase with food nutrient content. Among-lake differences in nutrient cycling rates were unrelated to inter-lake variation in fish body nutrient contents, which was minimal. The N:P ratio excreted was near Redfield (~14:1) in all three lakes.

Stoichiometric analyses showed that the C:N and C:P ratios of sediment detritus were much higher (~2.8 ×) than ratios of gizzard shad bodies, revealing substantial N and P imbalances between consumers and their food source. Gizzard shad alleviate N imbalance by selectively feeding on high N detritus (low C:N, high N:P), and apparently alleviate P imbalance by excreting nutrients at a higher N:P than that of their food or their bodies. Thus, this detritivore apparently regulates nutrient acquisition and allocation via both pre-absorption processes (selective feeding) and post-absorptive processes (differential N and P excretion).

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Ecological stoichiometry has emerged as a framework for understanding nutrient limitation of consumers and consumer-mediated nutrient cycling (Sterner and Elser 2002, Frost et al. 2005, Hessen and Elser 2005, Moe et al. 2005). Stoichiometry theory predicts that nutrient cycling by a consumer depends on the imbalance between the nutrient content of the consumer and its food. All else being equal, a consumer will release more nutrients if its food nutrient content is high than if its food nutrient content is low. Similarly, given equivalent food, a consumer with high body nutrient content should release less of that nutrient than a consumer with low body nutrients. Nutrient ratios should also behave according to stoichiometric principles, i.e. a consumer with low body nitrogen:phosphorus (N:P) ratio should excrete nutrients at a higher N:P ratio.
than a consumer with high body N:P, if the two consumers eat the same food (Elser and Urabe 1999, Sterner and Elser 2002).

Most studies addressing the stoichiometry of consumer–resource interactions focus on herbivore–plant interactions (Sterner and Elser 2002, Moe et al. 2005). In contrast, few studies have examined stoichiometric relationships between detritivores and detritus (Cross et al. 2003, Moe et al. 2005, Frost et al. 2005). Detritus is often poor quality in terms of nutrient:carbon ratios; thus, detritivores may be particularly nutrient-limited because of a relatively strong stoichiometric imbalance (Moe et al. 2005). This potential imbalance also has implications for nutrient cycling, because the rates and ratios by which detritivores release nutrients should depend on this imbalance (Vanni 1996, Vanni et al. 2002).

Consumers have several potential strategies for dealing with stoichiometric imbalances (Anderson et al. 2005, Frost et al. 2005). For example, consumers may selectively feed on high nutrient resources. Even detritivores feeding on apparently amorphous detritus can exhibit selectivity for high nutrient detritus (Bowen 1983). Consumers can also alleviate stoichiometric imbalances via post-ingestion processes, e.g. by selectively assimilating, or allocating to growth, nutrients in short supply (Anderson et al. 2005, Frost et al. 2005). Yet, little is known about how consumers, especially detritivores, compensate for stoichiometric imbalances and how these imbalances mediate nutrient cycling.

In freshwater ecosystems, animals can play important but variable roles in nutrient cycling (Vanni 2002). The role of fish in nutrient cycling seems particularly variable among ecosystems (Vanni 2002, Mehner et al. 2005, Sarnelle and Knapp 2005). In lakes, benthic-feeding detritivorous fish are often important in nutrient cycling (Brabrand et al. 1990, Schaus et al. 1997, Zimmer et al. 2006, Vanni et al. in press), and some evidence suggests that these detritivores are more consistently important than planktivorous fish in nutrient cycling (Sarnelle and Knapp 2005). Yet, little is known about the stoichiometry of nutrient acquisition, incorporation, and release by these important consumers (Schindler and Eby 1997, Hood et al. 2005, Moe et al. 2005).

In this study, we investigated the stoichiometry of nutrient cycling by a dominant omnivorous/detritivorous fish species, the gizzard shad (Dorosoma cepedianum). Gizzard shad are widespread throughout the midwestern and southern US, and often dominate fish biomass in reservoirs (Vanni et al. 2005, in press) and warm-water natural lakes (Bachmann et al. 1996). Several studies show that gizzard shad can be important in nutrient cycling and/or food web regulation (reviewed by Vanni et al. 2005). Gizzard shad are omnivores, displaying both ontogenetic shifts in diet as well as omnivory within individuals. Larvae are obligate zooplanktivores, but post-larval individuals (i.e. those >2 or 3 months old) consume detritus (sediments) and zooplankton (and occasionally phytoplankton). Understanding the extent to which gizzard shad consume zooplankton versus sediments is important, because detritivorous shad translocate nutrients from sediments to the water column, thereby providing “new” nutrients for phytoplankton (sensu Dugdale and Goering 1967, Caraco et al. 1992). In contrast, planktivorous shad recycle nutrients already in the water column (Vanni 2002). In addition, the stoichiometric relationships between gizzard shad and their food resources are likely to differ depending on whether shad are zooplanktivorous or detritivorous.

Our objective in this study was to quantify the stoichiometric relationships between gizzard shad, their food resources, and their excreta. Towards that end, we quantified gizzard shad diet composition, the nutrient (N and P) contents and ratios of gizzard shad bodies and their food resources, and the rates and ratios at which gizzard shad excrete nutrients. We then evaluated the extent to which excretion rates and ratios can be explained by stoichiometric constraints. We evaluated these stoichiometric relationships in three lakes that differ in productivity, so that we can assess the generality of our findings. Several aspects of gizzard shad biology and their food resources may vary with productivity, such as gizzard shad abundance and diets (Vanni and Headworth 2004, Vanni et al. 2005) and the nutrient content of sediment detritus (Nürnberg 1988). The three study lakes span a regional lake productivity gradient, and are representative of low, moderate and high productivity lakes (Vanni et al. 2005). Thus, generalities discovered here are likely to apply to the productivity gradient in this geographic region. In a complementary study, we used the nutrient cycling results we report here, and other information, to assess the extent to which nutrient cycling by gizzard shad sustains whole-lake primary productivity in these and four other lakes (Vanni et al. in press).

Methods

Study sites

This study was conducted in three reservoirs in Ohio, USA (Table 1). Burr Oak is mesotrophic and resides in a mostly forested watershed, Pleasant Hill is eutrophic and has a watershed with nearly equal proportions of forest and agriculture, and Acton Lake is hypereutrophic and located in an agricultural watershed (Knoll et al. 2003). These lakes span a representative productivity gradient for lakes in this region (Knoll et al. 2003, Vanni et al. 2005). They also exhibit a gradient with respect to zooplankton assemblages. Burr Oak has the highest cladoceran biomass and the lowest rotifer biomass, while...
Acton has the lowest cladoceran biomass and the highest rotifer biomass; Pleasant Hill is intermediate (Bunnell et al. 2003). The study lakes are typical of most midwestern reservoirs in that they are comparatively warm and shallow with relatively large watersheds relative to lake surface area (Knoll et al. 2003).

### Gizzard shad diet analyses

To quantify diets, 10 adult gizzard shad were collected from each lake via electrofishing on three dates June, July, and October 2000, for a total of 90 fish (148–275 mm total length; median = 189). Fish were immediately placed on dry ice. In the laboratory, we dissected the fish, removed the contents of the foregut, and split the contents into two samples. One was analyzed microscopically to quantify zooplankton in diets (recognizable phytoplankton were rarely observed in guts and were not quantified), and the other was used for nutrient analyses.

To calculate the number of zooplankton in guts, two subsamples were taken from the sample set aside for microscopic analysis (each subsample = 5% of total sample) and examined under a microscope. All taxa were counted, and cladocerans and non-naupliar copepods were also measured. Biomass of individuals was obtained using published weights for particular rotifer species, and from length/mass regressions for cladocerans and copepods (Sigler 2002). Then the entire sample used to quantify zooplankton, including processed subsamples, was filtered onto a Gelman AE 47-mm glass fiber filter, dried and weighed to obtain total dry mass.

The half set aside for nutrient analyses was used to quantify particulate phosphorus (P), carbon (C), and nitrogen (N). Subsamples were placed in a drying oven at 60° C for 24 h and then weighed to obtain dry mass. The P content was then determined by ashing in a muffle furnace, followed by HC1 digestion and subsequent analysis of liberated soluble reactive P (Stainton et al. 1977). C and N contents were determined using a Perkin Elmer Series 2400 elemental analyzer. Fish presumably do not assimilate inorganic C (i.e., C associated with carbonates), but the sediments of these lakes contain considerable amounts of carbonates. Therefore, we obtained the organic carbon content of food in the gut as the difference between total C and inorganic C. To obtain inorganic C, subsamples were placed in a muffle furnace at 550° C for 4 h to burn off organic matter, then analyzed for C. Total C was obtained by analyzing nonashed subsamples. These methods provide a measure of total nutrient mass in guts (i.e., detrital and zooplankton nutrients). To estimate the amounts of nutrients that gizzard shad obtained from detritus, we subtracted nutrients in zooplankton from the total nutrient mass in gut samples. To estimate nutrients in zooplankton, we multiplied zooplankton biomass times the C, N and P concentration (nutrient mass dry mass–1) for each zooplankton group and then summed these products. Nutrient concentrations of zooplankton were assumed to be 0.45 (C), 0.10 (N) and 0.01 (P), except for Daphnia, which was assumed to have a P concentration of 0.015 (Andersen and Hessen 1991).

To determine potential detrital food quality available to shad, three sediment cores were collected at shallow areas in the “upstream” portion of each lake (i.e., gizzard shad habitat) in mid summer, late summer, and early fall in 2000 and 2001 (total N = 18 for each lake). The top two cm of sediment (the layer most likely consumed by gizzard shad) was scraped off and ground to a fine powder. Subsamples were processed for nutrients in exactly the same manner as gut nutrient samples. Sediment nutrient concentrations did not vary over time within a lake (ANOVA, P > 0.05, log-transformed data), so we pooled all samples from all dates and examined differences in nutrient concentrations and ratios among the three lakes using ANOVA and Tukey-Kramer HSD tests on log-transformed data.

We also evaluated gizzard shad feeding selectivity within each of the general food categories (i.e., detritus and zooplankton). To evaluate detritivorous feeding selectivity, we calculated a selectivity index for each element (C, N and P), defined as the concentration of that element in gut detritus (total nutrients in foregut minus nutrients derived from zooplankton) divided by nutrient concentration of the sediment (Marais 1980). Ratios that were at least two standard errors greater than 1.0 were taken as evidence of selective feeding. Differences in selectivity indices among elements and lakes were tested by performing a two-way ANOVA (α = 0.05) on log-transformed data. To quantify zooplanktivorous feeding selectivity, Chesson’s (1983) coefficient of selectivity was calculated for each zooplankton group (rotifers, copepods, nauplii, and cladocerans) as \( \tau = (r_i/p_i) / \Sigma (r_i/p_i) \), where \( r_i \) is the proportion of total zooplankton individuals in gizzard shad guts comprised of group i, \( p_i \) is the proportion of total zooplankton individuals comprised of group i in zooplankton samples taken with a plankton net (63 μm mesh) at “upstream” sites where shad were collected. Chesson’s coefficient varies

<table>
<thead>
<tr>
<th>Burr Oak</th>
<th>Pleasant Hill</th>
<th>Acton</th>
</tr>
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<tbody>
<tr>
<td>Surface area (ha)</td>
<td>266</td>
<td>312</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>4.5</td>
<td>4.8</td>
</tr>
<tr>
<td>Chlorophyll a (μg P l–1)</td>
<td>24</td>
<td>71</td>
</tr>
<tr>
<td>Phytoplankton primary production (mg C m–2 d–1)</td>
<td>239</td>
<td>1087</td>
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Table 1. Characteristics of the three study lakes. Total phosphorus, chlorophyll and primary production data are epilimnetic values at the deepest area near the dam, from May through September 1998–2000, and are taken from Knoll et al. (2003).
from 0–1, and a value >1/number of prey items (in this case, 0.25) indicates selective feeding on that group.

### Excretion experiments

We measured the rates at which gizzard shad excreted N (as ammonium) and P (as soluble reactive phosphorus) in the three study lakes in July 1999 (temperature ~24°C), June 2000 (~24°C), July 2001 (~28°C), and October 2001 (~15°C), using methods similar to those of Schaus et al. (1997). Our goal was to measure rates on ~30 fish of varying size per lake per experiment, but this was not always possible given the availability of fish on any given date. We included fish of age 0–3 years, although we did not include any larvae.

Gizzard shad were collected by electrofishing at the upstream end of each reservoir during midday, i.e. after shad had been feeding for several hours (Pierce et al. 1981). Individual fish were placed for ~30 min in coolers with 4 l of lake water prefiltered (0.3 μm glassfiber filter) to remove algae and bacteria that could take up released nutrients. Samples for final nutrient concentrations were collected and immediately filtered (Gelman AE filters). Excretion rates were obtained as the difference between initial and final N and P concentrations (Schaus et al. 1997). Comparisons of excretion rates using this method and bioenergetics/mass balance models show that the two approaches yield similar rates (Vanni 1996, Schaus et al. 1997, Schindler and Eby 1997, Hood et al. 2002). Zooplanktivorous feeding selectivity varied considerably among lakes and dates, but there was no general trend towards selectivity of large taxa (Fig. 1). Burr Oak gizzard shad strongly selected rotifers on all three dates, as did those in Pleasant Hill in October 2001 (Fig. 1). Nauplii were strongly preferred in Pleasant Hill in July 2001. In Acton, cladocerans were selected in June 2000 and were also selected (along with cladocerans) in Pleasant Hill in July 2001. In Acton, cladocerans were selected in June 2000, copepods were selected in July 2001, and no taxon was preferred in October 2001 (Fig. 1).

### Results

#### Gizzard shad diets

**Diet composition**

Gizzard shad diets in all three lakes were comprised largely of sediment detritus. In all three lakes, shad derived >99% of their organic C, >98% of their P, and >90% of their N from sediments. Differences among lakes in these percentages were slight and not significant (P > 0.05 for all 3 elements).

**Zooplanktivorous feeding selectivity**

The few zooplankton that occurred in the guts were mostly rotifers, followed by nauplii, copepods, and cladocerans in order of descending frequency (Sigler 2002). Zooplanktivorous feeding selectivity varied considerably among lakes and dates, but there was no general trend towards selectivity of large taxa (Fig. 1). Burr Oak gizzard shad strongly selected rotifers on all three dates, as did those in Pleasant Hill in October 2001 (Fig. 1). Nauplii were strongly preferred in Pleasant Hill in June 2000 and were also selected (along with cladocerans) in Pleasant Hill in July 2001. In Acton, cladocerans were selected in June 2000, copepods were selected in July 2001, and no taxon was preferred in October 2001 (Fig. 1).

**Nutrient contents of sediment detritus**

Acton sediments tended to have the highest nutrient concentrations, although differences in N concentration were not significant (Fig. 2). Burr Oak sediments had the lowest C concentration, while Pleasant Hill sediments had the lowest P concentration. Nutrient ratios of sediments differed little among lakes. Neither the C:N...
nor the N:P ratio differed significantly among lakes, while the C:P ratio was higher in Pleasant Hill than the other two lakes (Fig. 2).

Nutrient contents of ingested detritus
C, N and P concentrations in ingested sediment detritus were significantly higher in Burr Oak than in Pleasant Hill, with Acton intermediate (Fig. 2). In all three lakes, nutrient concentrations of ingested detritus were higher than those of ambient lake sediments, indicating selective feeding on relatively high quality detritus (see also next section). The C:N ratio of ingested detritus was higher in Pleasant Hill than in Burr Oak, but other differences in nutrient ratios were not significant (Fig. 2).

Fig. 1. Chesson’s index of feeding selectivity for zooplanktivorous feeding by gizzard shad. Values above dashed lines indicate selective feeding on that group.

Fig. 2. C, N and P contents and ratios (mean ± SE) in ambient lake sediment detritus (left-hand column) and in detritus ingested by gizzard shad (right-hand column). Error bars represent variation among fish in a particular lake. All ratios are molar. Within a panel, means that are not significantly different from each other have common letters at the base of bars. Numbers above bars in the panels depicting C, N and P concentrations represent detritivorous feeding selectivity indices (SE in parentheses). Index values significantly >1 indicate selective feeding on detritus that is enriched with that element, compared to lake sediments.
**Detritivorous feeding selectivity**

For all elements, detritivorous feeding selectivity indices were significantly >1.0, indicating selective feeding on nutrient-rich detritus (Fig. 2). Two-way ANOVA revealed significant main effects of lake and element (P < 0.0001) and no lake × element interaction. Thus, we deleted the interaction term, re-ran the ANOVA and explored differences in main effects by examining paired contrasts. This revealed that feeding selectivity was higher in Burr Oak than in Pleasant Hill or Acton (which did not differ significantly from each other) and that feeding selectivity was higher for N than for C or P (which did not differ significantly from each other). Nutrient ratios provide additional evidence of higher feeding selectivity for N than for C or P. In all three lakes, the C:N ratio of ingested detritus was lower than that of lake sediments, while the N:P ratio of ingested detritus was higher than that of lake sediments. In contrast, C:P ratios were similar in ingested sediments and lake sediments (Fig. 2).

**Nutrient excretion**

For all ANCOVAs on excretion rates, the lake × body mass interaction was not significant, so we deleted the interaction term and re-ran ANCOVAs. The ANCOVA models explained >54% of the variance in excretion rates in all cases except July 2001 (R² = 0.49 for P and 0.23 for N). N and P excretion rates of individual gizzard shad were significantly (P ≤ 0.0001 in all cases) and positively (Fig. 3) correlated with fish wet mass. N and P excretion rates differed significantly among lakes during all experiments (P < 0.031 in all cases). N excretion rates in Burr Oak were higher than those in Pleasant Hill on all dates, and higher than those in Acton on all dates except one (Fig. 3). N excretion rates differed between Acton and Pleasant Hill on two dates, but the ranking of these two lakes was not consistent among experiments. Burr Oak P excretion rates were higher than at least one other lake on all dates, while Acton and Pleasant Hill differed on only one date (Fig. 3). Among-lake
differences in excretion rates corresponded to among-lake differences in nutrient contents of detritus ingested by gizzard shad. That is, fish in Burr Oak had the highest excretion rates as well as the highest gut nutrient contents, while Pleasant Hill fish tended to have the lowest excretion rates and the lowest gut nutrient contents (Fig. 2, 3). Overall, excretion rates were lowest in the October experiment, corresponding to the lower temperature during this time. However, N excretion rates of larger fish were also relatively low in July 2001, when temperatures were highest (Fig. 3).

Differences in N:P excretion ratios among lakes were not nearly as consistent as those for excretion rates, and variance explained was much less for ratios (R² always <0.36; Sigler 2002) than for excretion rates. N:P excretion ratio differed among lakes in two experiments (June 2000 and October 2001) and varied significantly with body mass in only one experiment (October 2001). In the October experiment, the N:P excretion ratio was significantly higher in Pleasant Hill than in the other two lakes. However, in the June 2000 experiment, a significant lake × body mass interaction precluded specific comparisons among lakes. Averaged over all experiments, mean N:P excretion ratios were very similar among lakes (14.0, 14.5 and 13.6 (molar) for Acton, Pleasant Hill, and Burr Oak, respectively).

Gizzard shad body nutrients

We found several differences among lakes in gizzard shad body nutrient contents and ratios, as well as significant effects of fish body mass in most cases. However, differences among lakes were generally small (Fig. 4), as was the amount of variance explained by these relationships (R² <0.17 in all cases). Body C and P, as well as body C:N and C:P ratios, varied significantly with fish mass. The relationship between mass and body P was positive, while mass was negatively correlated with body C, C:N and C:P (Fig. 4); however, slopes were relatively shallow. Body C, as well as C:N and C:P ratios, were significantly higher in Pleasant Hill than in the other lakes, while fish in Burr Oak had the highest N content. Body P content was not significantly different among lakes.

We observed relatively little variation among tissue samples (i.e. within a fish) in C and N contents and the C:N ratio (Table 2). Pooling all lakes, the mean coefficient of variation (CV) among replicate tissue samples (i.e., within-fish variation) was only 2.9% for C and 4.4% for N, whereas the mean CV among fish was 12.7% for C and 7.1 for N (Table 2). For the C:N ratio, the CV among fish was also much higher than that within fish (17.3 vs 2.8%, Table 2). Thus, for C, N and C:N, variation among fish was much greater than among samples.

Fig. 4. Gizzard shad body C, N and P contents and ratios in the three study lakes. Each point represents an individual fish. Percentages are expressed per unit dry mass, and ratios are molar.
that within fish (i.e., among replicate tissue samples) (Table 2). In contrast, within-fish variation in P was nearly as great as among-fish variation in P (Table 2), even though we analyzed more tissue samples per fish for P (3 samples) than for C and N (2 samples). Note that we cannot quantify within-fish CVs for N:P or C:P ratios, because within a fish we assayed P on different tissue samples from those used to assay C and N.

### Discussion

#### Detritivory versus zooplanktivory

Gizzard shad obtained nearly all ingested C, N, P from sediment detritus in all three lakes. This contrasts with the prediction of Vanni and Headworth (2004) that these fish would consume relatively more detritus and less zooplankton at high productivity. The prediction is based on the assumptions that large-bodied (hence energetically preferred) zooplankton are relatively more available at low productivity, and that gizzard shad prefer zooplankton over detritus, because the former are more nutritious. Cladocerans are in fact relatively more abundant, and rotifers less abundant (in terms of both percent individuals and biomass), in Acton than in Burr Oak, with Pleasant Hill intermediate. This pattern holds on the dates we sampled as well as in general in these lakes (Bunnell et al. 2003, Vanni et al. 2005). However, we found no evidence that adult gizzard shad selectively preyed on large zooplankton. However, “large” taxa were exceedingly scarce in these lakes. For example, *Daphnia* never comprised >10% of total zooplankton biomass, and only comprised >5% in 2 of 9 samples.

The observations that zooplankton comprised a small fraction of shad diets, and that shad did not select large-bodied zooplankton, suggest that these fish may more easily capture small-bodied zooplankton as they feed on detritus. As larvae, gizzard shad visually select individual zooplankters. However, when they are a few months old (~25–30 mm in length), gizzard shad become pump filter feeders (Drenner et al. 1984), at which time they also obtain the capacity to consume and digest detritus (Pierce et al. 1981, Heinrichs 1982). Small zooplankton that are weak swimmers (i.e. nauplii and many rotifers) may be easier to capture in this feeding mode (Drenner et al. 1984). Alternatively, zooplankton species composition may be different near the sediments (where shad feed) than in integrated water column samples (where zooplankton samples were collected).

We observed selective detritivory in all three lakes. That is, shad consumed detritus that was relatively nutrient rich compared to lake sediments. Selectivity was highest in Burr Oak, where sediment C and nutrient concentrations were also lowest (Fig. 2), suggesting that gizzard shad exhibit higher selectivity when feeding on poorer quality detritus. Such a pattern was also observed by Mundahl and Wissing (1988), who found that gizzard shad feeding on Acton Lake sediments had a selectivity index for N of 6.1, while gizzard shad fed a low-quality laboratory diet had a selectivity index for N of 13.2, similar to the range we observed (Fig. 2).

Other detritivorous fish also have the capacity to selectively feed, particularly on detritus with high N concentrations (Odum 1970, Bowen 1983, Ahlgren 1996). The behavioral and/or morphological mechanisms by which detritivorous fish accomplish this are not well known (Bowen 1983). In Acton Lake, gizzard shad feed selectively on sediment particles of low density, which contain higher concentrations of organic matter, C and N (Smoot 1999). Thus, relatively light, organically enriched sediment particles may be selectively filtered over heavier particles such as inorganic sediments, as has also been observed for mullet, a detritivorous fish common in estuaries (Odum 1970). Little is known about the stoichiometric relationships between detritivores and their food (Sterner and Elser 2002). However, it has been suggested that detritivorous fish are more likely to be nutrient-limited (as opposed to energy-limited) than other fish because of the large imbalance between the nutrient contents of detritus and fish (Schindler and Eby 1997, Sterner and Elser 2002). While
detritivorous fish may in fact be nutrient-limited, selective feeding on high quality detritus can at least partially alleviate nutrient limitation, and must be considered in models of detritivore stoichiometry (Vanni 1996).

We assessed detrital resources using 2-cm deep sediment cores, but gizzard shad may forage in a thinner layer of freshly deposited surficial sediments that may be more enriched in carbon and nutrients than a 2-cm core sample. It is therefore possible that the “selectivity” we observed resulted from inadequate sampling of food resources. However, we do not think this is the case, based on the work of Mundahl and Wissing (1988). They quantified C and N feeding selectivity of detritivorous Acton Lake gizzard shad using the same methods we used, except that they collected freshly deposited sediments using sediment traps that were deployed in the lake for just 18-20 h. The C and N contents of these freshly deposited sediments were similar to, or lower than, those we observed. For example, Mundahl and Wissing (1988) report a range of 0.1 – 0.4% N (as dry mass) in their sediments, whereas we observed a mean of 0.18% N (range 0.13 – 0.23) in our Acton sediment samples. Mundahl and Wissing (1988) report a range of total C (they did not quantify organic C) of 2.8 – 3.4%, whereas we observed somewhat higher C concentrations (mean total C = 4.6% [range 4.3 – 4.9]; mean organic C = 2.1% [range 1.7 – 2.6]) in our sediment samples. In addition, as mentioned above, Mundahl and Wissing (1988) observed C and N selectivity indices similar to those we observed (they did not quantify P in sediments or shad guts). Thus, gizzard shad appear able to selectively consume high C and N detritus, even compared to freshly deposited sediments.

Nutrient excretion

N and P excretion rates were always higher in Burr Oak than in at least one other lake, and fish in Burr Oak also consumed detritus with the highest nutrient concentration. This relationship supports stoichiometry theory, which predicts that excretion rates will increase with food nutrient content, as long as other factors (e.g. consumer body nutrient content, feeding rate, growth rate) remain constant (Sterner and Elser 2002). We found no significant among-lake differences in fish body P contents, so the higher P excretion rates of Burr Oak fish cannot be explained by differences in body P. Burr Oak gizzard shad actually had higher body N contents than fish in the other lakes, yet still had higher N excretion rates. While this relationship appears to contradict stoichiometry theory, differences among lakes in fish body N were relatively small, especially in relation to variation within a lake (Fig. 4). In addition, we observed considerable variation among fish in body nutrient contents, and for P, considerable variation among replicate tissue samples within a fish (Table 2). This variation among and within fish may have made it more difficult to detect differences among lakes in body nutrients. Variation among fish in C content may be due to variable lipid storage; we noticed considerable variation in oil content among fish as they were ground for nutrient analyses. Higher within-fish variation for P (compared to that for C or N) may result from variation in the contribution of small bone or scale fragments (which are P-rich) to samples.

The positive association between the nutrient contents of ingested detritus and nutrient excretion rates are consistent with the predictions that nutrient release rates increase with food nutrient content. However, alternative explanations are possible. For example, feeding rates and/or assimilation efficiencies (for N and/or P) of Burr Oak gizzard shad may have been higher than in the other lakes. If either feeding rates or assimilation efficiencies were higher in Burr Oak, the total amount of nutrients assimilated per fish would be higher, which could potentially lead to higher nutrient excretion rates. We have no information on how feeding rate or assimilation efficiency varies among lakes, so we cannot explicitly evaluate these alternative mechanisms. Recent models suggest that post-assimilation mechanisms (i.e. adjustment of excretion rates) may be more effective than differential assimilation for generalist consumers (Anderson et al. 2005), but much more work is needed to test this hypothesis (Frost et al. 2005).

Assuming that the observed among-lake differences in excretion rates are due to stoichiometric constraints, our results suggest that variation in food nutrient content is more important than variation in consumer body nutrient content in determining excretion rates. Few studies have explicitly quantified how nutrient excretion varies with these two factors. Elser and Urabe (1999) analyzed data from several zooplankton studies and concluded that variation in food (phytoplankton) nutrient content was more important than variation in zooplankton body nutrients in determining N:P excreted by zooplankton, in agreement with our results. In contrast, Vanni et al. (2002) found that interspecific variation in body P accounted for a large fraction of interspecific variation in P excretion rates and N:P excreted of fish and tadpoles in a tropical stream. These apparently contradictory findings probably relate to the relative variation in food nutrient content versus consumer nutrient content. Phytoplankton exhibit tremendous variation in nutrient content compared to zooplankton, so variation in phytoplankton may be relatively important in determining variation in zooplankton nutrient excretion. Regarding nutrient cycling by fish, body nutrient content may have had a stronger effect on excretion in the Vanni et al. (2002) study than in our study because interspecific variation in body P was much greater than the among-lake variation we
observed in gizzard shad body nutrients. More studies under natural conditions and with controlled, realistic diets are needed to help elucidate how diet and consumer nutrient contents modulate excretion rates and ratios (Frost et al. 2005).

Although per capita N and P excretion rates were highest in the lake of lowest productivity (Burr Oak), at the ecosystem scale nutrient flux through gizzard shad increases with lake productivity (Vanni et al. in press). This is because gizzard shad biomass increases greatly with productivity in these ecosystems (Vanni et al. 2005, in press), and this increase in biomass outweighs the opposing trend we found here of decreasing per capita rates with increasing productivity. Thus, in terms of regulating ecosystem-scale nutrient cycling, gizzard shad may have stronger impacts in high-productivity lakes, although this will depend on how the magnitude of other nutrient supplies varies along the productivity gradient.

Selective detritivory, stoichiometry, and nutrient excretion by gizzard shad

We observed substantial imbalances between ambient sediments and shad bodies for both N and P, relative to C. Thus, the C:N and C:P of ambient sediments were both $\sim 2.8 \times$ that of shad bodies (Fig. 5). Gizzard shad apparently have different strategies for dealing with N versus P imbalances, yet strategies appear to be the same in all three lakes. Selective feeding on high N detritus reduces the imbalance for N by roughly half, but selective feeding does not substantially reduce the imbalance for P, relative to C (Fig. 5). As a consequence, the N:P of consumed sediment is $\sim 1.5 \times$ higher than the N:P of ambient sediment or shad bodies. Thus, once sediments are consumed, shad apparently must selectively incorporate P, relative to N, to maintain their body N:P. This is also apparent from N:P excretion ratios, which are $\sim 2.1 \times$ higher than shad bodies and somewhat higher ($\sim 1.2 \times$) than consumed detritus (Fig. 5). N:P ratios also support stoichiometry theory, which predicts that if food N:P is higher than body N:P, the consumer will excrete at an N:P that is even higher than ingested food (Sterner and Elser 2002).

Note that the N:P relationships we observed conform to stoichiometry theory only when we consider the N:P of detritus actually consumed by shad, and not just ambient lake sediments. Ambient sediments and shad bodies have similar N:P. Thus if we had considered ambient sediments as “food,” we would have predicted excretion N:P and body N:P to be similar (Sterner and Elser 2002). Once again, this highlights the importance of selective detritivory in mediating the stoichiometry of nutrient cycling by gizzard shad, and more generally, the need to carefully consider nutrient contents and ratios of material actually ingested by consumers rather than relying on the nutrient status of ambient food sources as a measure of dietary nutrient content.

Consumers release nutrients via egestion (feces) as well as excretion. We did not measure egestion rates, but it is useful to estimate how egestion and excretion rates may compare and how they relate to stoichiometry. To do so, we used a mass–balance approach to estimate egestion rates in Acton Lake, where we have considerable data on gizzard shad growth rates. First we estimated ingestion rates of detritivorous gizzard shad in midsummer using the model described in Vanni and Headworth (2004); most parameters of this model derive from Acton gizzard shad. Ingestion of sediment detritus (g dry mass

Fig. 5. Mean nutrient ratios of ambient lake sediments, detritus ingested by gizzard shad, gizzard shad bodies, and (for N:P) nutrients excreted by shad. Arrows represent flow of nutrients and energy in the lakes. All ratios are molar.
consumed fish$^{-1}$ d$^{-1}$) of a 55 g (wet mass) fish in late July 2000 was estimated using daylength and temperature. We converted this rate to N and P ingestion rates (g N or P consumed fish$^{-1}$ d$^{-1}$) using data on gut sediment N and P during the summer experiments reported here. We then estimated N assimilation by multiplying N ingestion by 0.77, the N assimilation efficiency reported for detritivorous Acton Lake gizzard shad (Mundahl and Wissing 1988). This yielded N ingestion and assimilation rates of 67.6 and 52.0 mg N fish$^{-1}$ d$^{-1}$, respectively. Egestion was then calculated as ingestion minus assimilation (15.6 mg N fish$^{-1}$ d$^{-1}$). We then compared that to excretion using the mass balance approach and using data from the experiments we report here. To use the mass balance approach, we first estimated the amount of N allocated to growth using estimated growth rate of gizzard shad of this size and the mean body N content observed for Acton shad (9% of dry mass). This yielded an estimate of N allocated to growth of 2.0 mg N fish$^{-1}$ d$^{-1}$, and a predicted excretion rate of 50.0 mg N fish$^{-1}$ d$^{-1}$ (excretion = assimilation - growth, or 52.0 – 2.0). Thus, according to the mass balance approach, shad excreted 3.2 × as much N as they egested. The N excretion rate predicted by the mass balance approach was ~19% lower (50.0 vs 62.1) than the rate predicted from the mass vs N excretion regression generated from our July 2000 experiment (Fig. 3), but was within the confidence interval of the regression generated by the experiment.

We did the same calculations for P; however, we have scant data on P assimilation efficiency, so for this exercise we used the same value (0.77) as for N assimilation efficiency. P ingestion, assimilation and egestion were estimated to be 11.1, 8.5 and 2.6 mg P fish$^{-1}$ d$^{-1}$, respectively. Allocation of P to growth was estimated to be 0.7 mg P fish$^{-1}$ d$^{-1}$ (using a mean body P of 3.0% of dry mass), yielding a predicted excretion rate of 7.9 mg P fish$^{-1}$ d$^{-1}$, or ~3.0 × as much as P egestion. The P excretion rate predicted by the mass balance approach was 35% lower than the rate predicted from the mass vs P excretion regression generated from our July 2000 experiment (Fig. 3), but was within the confidence interval of this regression.

Thus it appears that excretion is quantitatively more important than egestion, in terms of nutrient flux through gizzard shad. In addition, excreted N and P are dissolved and hence more bioavailable (to phytoplankton) than egested nutrients, and should thus have a greater impact on primary producers. Both excretion and egestion may be important in the post-ingestion regulation of consumer body nutrient composition and nutrient cycling (Anderson et al. 2005, Frost et al. 2005). However, we cannot adequately evaluate the stoichiometry of egestion because we do not have sufficient data on P assimilation efficiencies. Future studies need to quantify both egestion and excretion so that these post-ingestive processes can be explicitly compared.

Conclusions

Many aspects of gizzard shad diets and nutrient cycling parameters were similar in three lakes that differ considerably in productivity. In all three lakes, nearly all nutrients ingested by shad and thus excreted into the water column, were derived from sediment detritus. We did observe among-lake variation in excretion rates, which appears to be mediated by selective detritivory. However, the ratio at which gizzard shad excreted nutrients was relatively constant among lakes, and appears to be driven by stoichiometric constraints, in particular the relative imbalances between nutrients ingested and sequestered in fish bodies. Because detritivores are critical in nutrient cycling in many ecosystems, it is important that we quantify stoichiometric constraints on these consumers, and how these constraints mediate the many linkages between detritus-based and primary producer-based food chains (Moore et al. 2004).

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References

Ahlgren, M. O. 1996. Selective ingestion of detritus by a north temperate omnivorous fish, the juvenile white sucker, Catostomus commersoni. — Environ. Biol. Fish. 46: 375–381.


Sterner 1990. Please provide further details.


