

Biomass-Dependent Diet Shifts in Omnivorous Gizzard Shad: Implications for Growth, Food Web, and Ecosystem Effects

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Abstract.—We examined diet patterns of omnivorous gizzard shad *Dorosoma cepedianum* in Acton Lake, Ohio, during 1994–1997 using a multiple stable isotope analysis to quantify the role of this species in the system. On most dates, zooplankton were relatively depleted in $\delta^{13}\text{C}$ (about –30‰ to –25.5‰) compared with sediments (–25‰), permitting construction of a mixing model to determine the proportion of C derived from benthic detritus and from planktonic productivity. During periods of greater gizzard shad biomass (>35 kg/ha), gizzard shad of more than 35-mm standard length (SL) derived most of their C from sediment detritus. When gizzard shad biomass was low (<15 kg/ha), zooplankton biomass increased and all sizes of gizzard shad derived most of their C from zooplankton. Conventional gut analyses corroborated these findings. Zooplanktivorous age-0 gizzard shad grew at three or more times the rate of those that were detritivorous. Rapid age-0 growth led to high gizzard shad biomass, a decrease in large zooplankton, and a subsequent shift to detritivory. Therefore, diet quality and growth rates are strongly linked to gizzard shad biomass, and these biomass-dependent feedbacks tend to keep gizzard shad biomass high in this system during most years. Because zooplanktivorous gizzard shad recycle nutrients within the water column, whereas detritivorous gizzard shad transport nutrients from sediments to the water column, biomass-induced diet shifts modify the impact of this species on phytoplankton through both top-down and bottom-up mechanisms.

Knowledge of an organism's diet is central to understanding its interactions with other species, including direct and indirect effects on food webs. Despite this importance and the prevalence of omnivory (Darnell 1961; Polis and Strong 1996), the diets of many omnivores are poorly understood, especially concerning the nutritional significance of detritus (Lemke and Bowen 1998). Detritivorous fishes and invertebrates are common in many aquatic communities, such as tropical rivers and streams (Bowen 1983), estuaries (Deegan et al. 1990), temperate streams (Cummins 1974), shallow lakes (Meijer et al. 1990), and reservoirs (Miranda 1984). Yet despite studies indicating that many species of fish ingest detritus in a facultative or obligate manner (Darnell 1961; Bowen 1983), little is known about its contribution to the nutrition of many omnivorous fishes (Ahlgren 1990; Lemke and Bowen 1998)—probably because of the difficulty in assessing its value to the long-term nutrition of an organism.

Much of the energy flux and nutrient cycling within a variety of ecosystems occurs through the

detritus food chain (e.g., Cummins 1974; Gosz et al. 1978; Polis and Hurd 1996; Polis and Strong 1996). Recent studies in aquatic systems have demonstrated that benthic-feeding omnivorous and detritivorous fish may have large impacts on ecosystem processes such as internal nutrient loading (Lamarra 1975; Brabrand et al. 1990), sediment resuspension (Meijer et al. 1990; Havens 1991) and maintaining high levels of fish productivity (Adams et al. 1983). The effects of omnivorous fishes on these processes depend highly on diet. For example, omnivorous fish feeding on benthic food sources (i.e., detritus, benthic invertebrates) may impact the benthos directly but also can transport nutrients into the water column via their excretions, serving as a net source of nutrients to pelagic phytoplankton, and potentially increasing total water column nutrients (Lamarra 1975; Shapiro and Carlson 1982; Persson 1997a). However, if these omnivores feed on plankton, they may have direct impacts through their planktivory but would not serve as a net source of nutrients to phytoplankton (Shapiro and Carlson 1982).

This study examined the linkage between the diet and ecosystemic role of an omnivorous fish, the gizzard shad *Dorosoma cepedianum*, in a reservoir system to determine when this species functioned as a net source of nutrients to phytoplankton. By combining dietary data with information

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on nutrient excretion rates (Schaus et al. 1997) and their effects on phytoplankton and zooplankton (Schaus and Vanni 2000), we could assess the functional importance of this species in a reservoir ecosystem. To determine this value, we needed to quantify (1) contributions of benthic detritus versus zooplankton to the diet; (2) environmental or population characteristics that favor a particular mode of feeding; and (3) dietary consequences for the fish population (e.g., growth, reproduction). We used the gizzard shad as our model omnivore because it is abundant, has a wide distribution, and often dominates the fish biomass in Midwestern and southern reservoirs (e.g., Miranda 1984; Stein et al. 1995), especially those that are eutrophic (Bachmann et al. 1996; DiCenzo et al. 1996). Much is known about the food habits of gizzard shad. In some systems, adult gizzard shad consume zooplankton extensively (Drenner et al. 1982; Mundahl 1988); in others, however, they feed extensively on organic detritus associated with sediments (e.g., Mundahl and Wissing 1987; Buynak and Mitchell 1993). Previous studies have demonstrated that gizzard shad can transport substantial quantities of nutrients into the water column when they feed on detritus (Schaus et al. 1997) and can have substantial effects on zooplankton (e.g., Drenner et al. 1982; Dettmers and Stein 1992; Schaus and Vanni 2000). Thus, diet quantification is critical to understanding the role of this species in food web and ecosystem processes.

We used a multiple stable isotope technique to assess the contribution of detritus and zooplankton to the diet of gizzard shad. Stable isotope analyses have been used in food web studies to quantify carbon sources (e.g., Peterson et al. 1985; Keough et al. 1996), trophic structure (e.g., Kling et al. 1992; Hobson and Welch 1995), and migration between habitats (reviewed in Hobson 1999) to better quantify material transport and energy flow in food webs (e.g., Anderson and Polis 1998; Schindler and Lubetkin, in press). They also have been successfully used to quantify the importance of detritus to the diets of omnivorous fishes in other systems (Araujo-Lima et al. 1986; Deegan et al. 1990; Forsberg et al. 1993). This technique integrates feeding history over the time scale of tissue turnover and quantifies the importance of potential food sources (Peterson and Fry 1987). Whereas conventional gut samples provide only a "snapshot" of items in the gut over a very short time interval, isotopes measure actual assimilation of various food sources and thus account for selective digestion of particular food items (Peterson and

Fry 1987). In this study, we coupled isotopic analyses with conventional gut analyses, estimation of gizzard shad biomass, and environmental sampling (zooplankton and seston abundance) to predict the conditions that facilitate a particular mode of feeding.

Methods

Diet analyses.—We used a multiple stable isotope technique in 1995–1997 to quantify the contribution of zooplankton and detritus to the diet of gizzard shad in Acton Lake, Ohio, a 253-ha eutrophic reservoir where gizzard shad are abundant (Mundahl and Wissing 1987; Schaus et al. 1997). Samples were collected in two periods during each of the 3 years: early to midsummer (June 4–July 23) and late summer to early fall (August 25–October 5). Zooplankton and seston samples were generally analyzed from several dates to better quantify the range of isotopic signatures present for these potential food sources, given that $\delta^{13}\text{C}$ signals exhibit large seasonal variance (Yoshioka et al. 1994; Zohary et al. 1994).

We collected samples from a range of sizes of gizzard shad (from 25-mm standard length [SL] larvae to 297-g age-5 gizzard shad) as well as their potential food sources (sediments, zooplankton, and seston). Gizzard shad were collected by electrofishing (>1 g wet mass) or using an ichthyoplankton net (<1 g wet mass) and immediately placed on ice. In the laboratory, they were weighed, measured, and frozen until further processing. For gizzard shad larger than 2 g wet mass, dorsal muscle samples were removed by dissection, oven-dried at 60°C, ground with a mortar and pestle, and frozen until analyzed. For gizzard shad smaller than 2 g wet mass, the entire body was oven-dried at 60°C, ground with a mortar and pestle, and frozen until analyzed.

Sediment samples were collected by using a K-B sediment corer. The top 1 cm was removed, oven-dried at 60°C, ground with a mortar and pestle, and frozen until analyzed. Zooplankton were collected either by a plankton net or a Schindler–Patalas trap, both of which had a 63- μm mesh. Zooplankton samples were washed on a 63- μm -mesh screen, either rinsed into vials or filtered onto a 25-mm diameter Gelman A/E glass fiber filter (1- μm pore size), oven-dried at 60°C, and frozen until analyzed. Seston samples were collected from the epilimnion by using an integrated tube sampler. Samples were passed through a 63- μm -mesh screen to remove any zooplankton, filtered onto a 25-mm diameter Gelman A/E glass fiber

filter (1- μm pore size), oven-dried at 60°C, and frozen until analyzed.

The samples were sent to the Institute of Marine Science, University of Alaska, Fairbanks, where they were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with a Europa 20–20 continuous-flow isotope ratio mass spectrometer. Stable isotope ratios were expressed in conventional δ notation, which is the difference (in parts per thousand [‰]) from the conventional isotopic standards: Peedee Belemnite Limestone for $^{13}\text{C}/^{12}\text{C}$ and atmospheric nitrogen for $^{15}\text{N}/^{14}\text{N}$. Larger values indicate relative enrichment in the heavier isotope. Analytical precision of the analyzer during the runs was plus or minus 0.2 ‰ (N. Haubenstock, University of Alaska, Fairbanks, personal communication).

To determine the proportions of diet resulting from zooplankton C (% C_{ZP}) and sediment detrital C, we constructed the following mixing model (Forsberg et al. 1993):

$$\%C_{\text{ZP}} = \left\{ \frac{1 - [(\delta^{13}\text{C}_{\text{GS}} - \text{TF}) - \delta^{13}\text{C}_{\text{ZP}}]}{(\delta^{13}\text{C}_{\text{SD}} - \delta^{13}\text{C}_{\text{ZP}})} \right\} \cdot 100,$$

where $\delta^{13}\text{C}_{\text{GS}}$ is the $\delta^{13}\text{C}$ value of gizzard shad, TF is the trophic fractionation, $\delta^{13}\text{C}_{\text{ZP}}$ is the $\delta^{13}\text{C}$ value of zooplankton, and $\delta^{13}\text{C}_{\text{SD}}$ is the $\delta^{13}\text{C}$ value of sediment detritus. We set TF = 0.2‰, the value reported as the average trophic fractionation of C for freshwater ecosystems (France and Peters 1997). Because $\delta^{13}\text{C}$ of zooplankton varied over time, we calculated % C_{ZP} for each gizzard shad by using the mean isotopic signatures for zooplankton and sediment detritus measured during the periods when gizzard shad were collected. However, when $\delta^{13}\text{C}$ of zooplankton and sediment detritus were indistinct during a season (fall 1995 and summer 1997), we used their mean isotopic signatures over the duration of our study.

To check the validity of the isotopic diet analysis, we analyzed gut contents of gizzard shad from a subset of the sampling periods. Fish were collected by electrofishing and placed on ice. In the laboratory, they were weighed, measured, and frozen until later gut analysis by a modification of the weight difference determination method (Bowen 1979; Ahlgren and Bowen 1992). We used this method instead of the volume determination method (Wallace 1975) because the large quantities of silt and clay present could have been misidentified as detrital particles (Ahlgren and Bowen 1992). Gut contents anterior to the gizzard were removed by dissection and dispersed in water in a Sedgewick–Rafter counting cell. Zooplankton were iden-

tified to the lowest taxonomic unit and counted. A subset of individuals from each taxon were measured for determination of dry mass from their length according to published regressions and standardized geometric:dry mass relationships (Dumont et al. 1975; Bottrell et al. 1976; Ruttner-Kolisko 1977; Rosen 1981; Culver et al. 1985). Gut samples were then rinsed into aluminum pans and oven-dried at 60°C. Samples were weighed (to the nearest 0.1 mg), ashed at 550°C for 8 h, and reweighed to determine the total ash-free dry mass (AFDM) of each sample. Estimates of zooplankton biomass were then divided by the AFDM to determine what percent of AFDM consisted of zooplankton (Yako et al. 1996). Detrital contribution to the diet was considered to be the remaining proportion of AFDM (Yako et al. 1996) because phytoplankton were rarely observed in gut samples.

Population and environmental monitoring.—To determine the characteristics of the gizzard shad population that may be linked to diet, we conducted monthly population surveys during 1993–1997 by electrofishing and determined population biomass with quadrat rotenone surveys (Johnson et al. 1988; Schaus et al. 1997) in midsummer 1994 and seasonally during 1996 and 1997. Quadrat rotenone sampling provided estimates of gizzard shad biomass in nearshore quadrats. We then extrapolated these measurements over the whole lake on the basis of relative catch per unit effort (CPUE) data obtained from lakewide electrofishing surveys. A detailed description of our modification of the technique developed by Johnson et al. (1988), and the results for the 1994 sampling period ($N = 8$ quadrats), are given by Schaus et al. (1997). Sampling and lakewide extrapolations during 1996 and 1997 were carried out using the same methods except that lakewide extrapolations were based on total fish CPUE (g/min) rather than CPUE within an age-group. Because age-0 gizzard shad had high variance on one sampling date, comparing mean age-0 CPUE from different areas of the lake probably would have overestimated total lakewide biomass on that date; comparing total gizzard shad CPUE greatly reduced this bias. Because biomass estimates were similar within a season (early to midsummer and late summer to fall), we combined all biomass estimates within a season for a sample size of $N = 6$ quadrats for each season in 1996 and 1997. Population age distribution was determined by using scale annuli (DeVries and Frie 1996) to age a subset of the individuals collected during monthly electrofishing surveys.

An estimate of biomass during 1995 was obtained by comparing electrofishing during 1995 with that during 1996 and 1997, when quadrat rotenone measurements of biomass were conducted. Lakewide electrofishing CPUE data for age-0 and adult gizzard shad during 1996 and 1997 were regressed against total lakewide gizzard shad biomass during the same periods ($N = 6$ sampling periods). The resulting regressions were used to predict 1995 lakewide gizzard shad biomass from the mean electrofishing CPUE during 1995. Electrofishing CPUE data from 1994 were not included for this comparison because we modified our electrofishing equipment substantially between the 1994 and 1995 field seasons. Thus, CPUE data from 1995 are most directly comparable with 1996 and 1997 CPUE estimates.

The monthly electrofishing surveys and our estimates of age distributions were used to determine growth rates for age-groups that did not overlap in size with other age-groups. The quadrat rotenone data and age distributions allowed us to examine the abundance of year-classes over long intervals (seasons and years) without the size bias generally associated with electrofishing (Reynolds 1983).

To determine the biomass of zooplankton and seston prey items, we sampled zooplankton and epilimnetic seston with a Schindler-Patalas trap and an integrated tube sampler, respectively. Previous reports of Acton Lake zooplankton counts and Secchi depths for 1993–1996 by Pollard et al. (1998) allowed us to make inferences about zooplankton and seston abundance throughout the duration of this study. Particulate carbon samples for zooplankton (1995–1997) and seston (1994–1997) samples were collected, filtered onto glass fiber filters as previously described, and analyzed for C (as a rapid surrogate for the estimation of total zooplankton biomass) with a Perkin-Elmer 2400 Elemental Analyzer.

Results

Lakewide gizzard shad biomass varied over two orders of magnitude during the duration of our study. Gizzard shad abundance in 1994 was very high (Figure 1) and was dominated by the 1992 cohort. By May 1996, this cohort had decreased in abundance and overall gizzard shad biomass declined to approximately 4 kg/ha lakewide (Figure 1). Production and recruitment of a relatively strong 1996 cohort allowed substantial increases in biomass during summer 1996 (Figure 1). The

1996 year-class was dominant in late 1996 and throughout 1997, with biomass remaining at around 35–65 kg/ha during August 1996 through September 1997 (Figure 1).

Large changes in the abundance of zooplankton and seston were concurrent with the changes in gizzard shad biomass (Figure 2; Pollard et al. 1998). These changes are consistent with expectations of increased zooplanktivory by gizzard shad and subsequent declines in zooplankton grazing on seston. Zooplankton biomass (measured as concentration of C in particles more than 63 μm in diameter) during June–July 1996 was about three times the maximum observed during May–August 1995 and about four times the maximum abundance observed during 1997. Mean seston biomass (measured as concentration of C in particles 1–63 μm in diameter) during 1996 was 43–50% less than the means observed during other years. These observations are consistent with shifts in zooplankton and Secchi depth reported in Acton Lake during 1993–1996 by Pollard et al. (1998). Those authors observed that increases in zooplankton during 1996 reflected increases in both *Daphnia parvula* (which were very rare in other years) and rotifers. They also observed that water transparency (Secchi depth) was low (typically 0.3–0.7 m) during 1993–1995 but greater (up to 1.3 m) at the same time that gizzard shad biomass was extremely low and *Daphnia* biomass peaked (June–July 1996; Pollard et al. 1998).

Stable isotope samples from 1995 clearly showed a strong shift in gizzard shad diet from zooplanktivory as larvae to detritivory as larger juveniles and adults (Table 1; Figure 3). Age-0 gizzard shad obtained the majority of their C from zooplankton, the smallest fish showing 100% reliance on zooplankton. As fish size increased, the juveniles showed increased enrichment in ^{13}C , indicating an ontogenetic shift from zooplankton to sediment detritus. Adult gizzard shad obtained most of the C in their tissues from sediment detritus (Table 1).

In July 1996, all sizes of gizzard shad showed a strong reliance on zooplankton (Table 1; Figure 3). By October 1996, the $\delta^{13}\text{C}$ signal of age-0 fish had become enriched somewhat in ^{13}C , indicating a shift back toward detrital foods (Figure 3; Table 1). Because isotopic signals integrate feeding over the time scale of tissue turnover, it was not possible to determine whether the signal indicated an intermediate diet during late summer and fall or a nearly complete shift to sediment-feeding at that time, which diluted the previously assimilated iso-

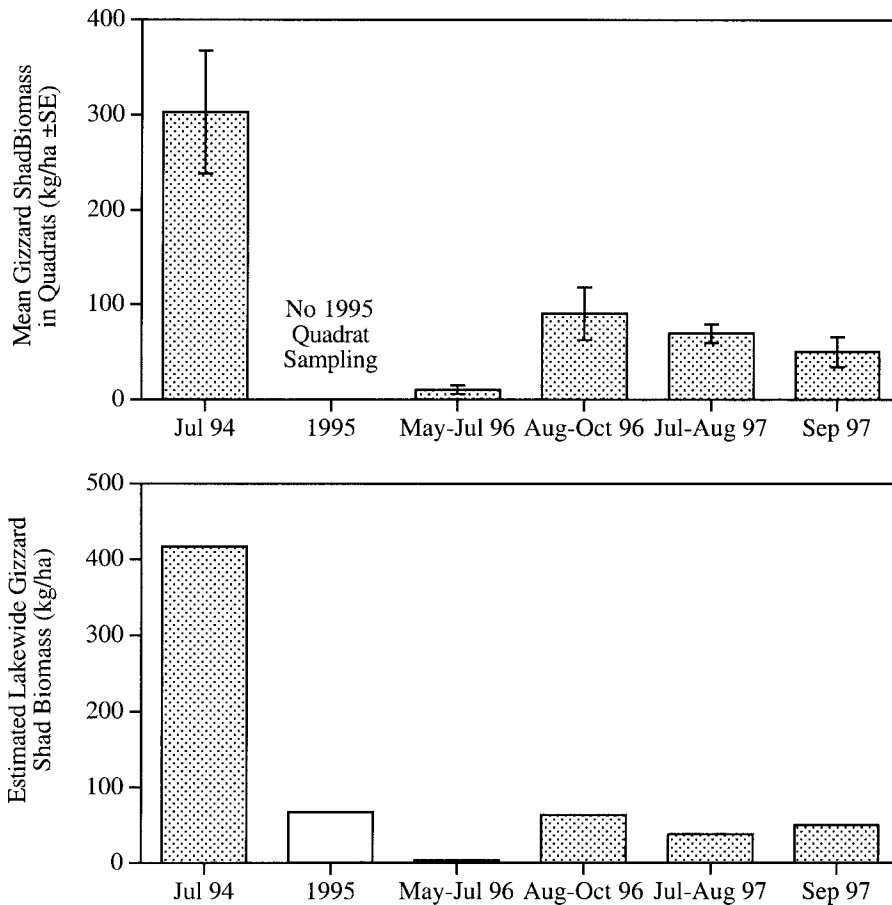


FIGURE 1.—Gizzard shad biomass estimates from rotenone quadrats (top panel) and lakewide extrapolations of the mean during 1994–1997. The lakewide biomass estimate for 1995 is depicted as an open bar because it is the only estimate based solely on electrofishing CPUE data (see Methods). All other biomass estimates (stippled) are based on nearshore quadrat rotenone measurements that were then extrapolated lakewide by using electrofishing data (see Methods). No quadrat biomass measurement is given for 1995 because no rotenone quadrats were sampled during 1995. Error bars indicate ± 1 SE.

topically lighter C. In either case, the signal obtained from age-0 fish indicated that an average of ~40% of the C in their muscle tissues came from zooplankton and the remainder from detritus. Adult gizzard shad also exhibited a shift in $\delta^{13}\text{C}$ from -30‰ (July) to -29‰ (October), however, this value is still within the range of zooplankton analyzed from that period, indicating that 100% of the C in their tissues came from zooplankton (Table 1). In June and July 1997, gizzard shad C became further enriched in ^{13}C , indicating greater reliance on sediment detritus (Table 1). Samples from October 1997 indicated that most gizzard shad obtained virtually all of their C from sediment detritus.

In all gizzard shad (across all years) that showed evidence of zooplanktivory, $\delta^{15}\text{N}$ signals were enriched by about 4‰, indicating an enrichment by one trophic level over zooplankton prey. Fish that showed isotopically enriched $\delta^{13}\text{C}$ signals (i.e., those that relied more heavily on C from sediment detritus) had $\delta^{15}\text{N}$ signals that were typically enriched 8–10‰ over the signal of the sediments, suggesting an enrichment by two trophic levels over bulk sediment organic material.

Conventional gut analyses followed the same general pattern as the results of the stable isotope analyses. During July 1996, zooplankton accounted for 6.75% of AFDM in gut samples (Table 2). During August–October 1996, zooplankton aver-

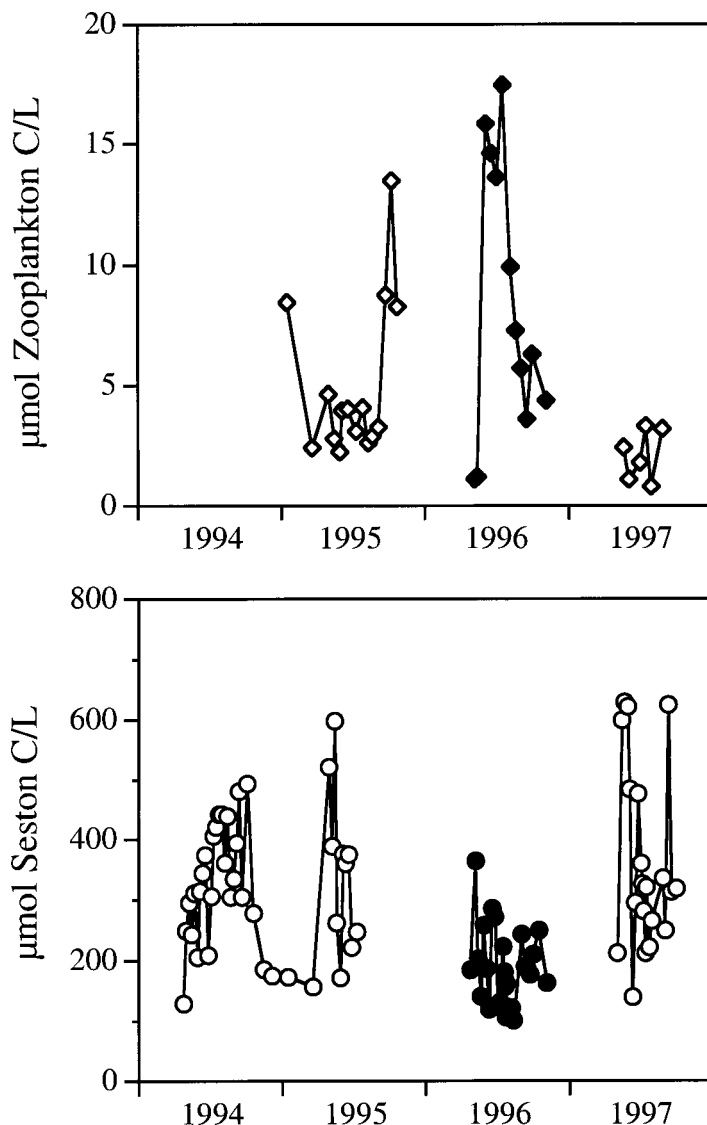


FIGURE 2.—Biomass (given as particulate C concentrations) of zooplankton (top panel) and seston (bottom panel) across years. Plot symbols are darkened during 1996 (lakewide gizzard shad biomass <15 kg/ha before August) and open during all other years (lakewide gizzard shad biomass >35 kg/ha). Zooplankton refers to particles more than 63 μm in diameter; seston refers to particles 1–63 μm in diameter. Note different y-axis scales.

aged 0.71–0.61% of AFDM in gut samples (Table 2). On all other dates, very little of the AFDM in gut samples consisted of zooplankton (Table 2). In general, whether using stable isotope results or gut contents, gizzard shad relied much more heavily on sediment detritus during their periods of larger biomass (>35 kg/ha). When gizzard shad biomass was low (<15 kg/ha), fish relied extensively on zooplankton, which became abundant at that time.

During June–July 1996, when zooplankton

abundance was greatest (Figure 2), as was zooplanktivory (Table 1; Figure 3), growth rates of age-0 gizzard shad increased dramatically. During 1996, age-0 gizzard shad reached a mean wet mass at least threefold that observed for age-0 gizzard shad during all other years of the study (Figure 4). Growth rates of age-0 gizzard shad for all other years of this study were similar to one another (Figure 4), despite an order of magnitude difference in lakewide biomass (Figure 1).

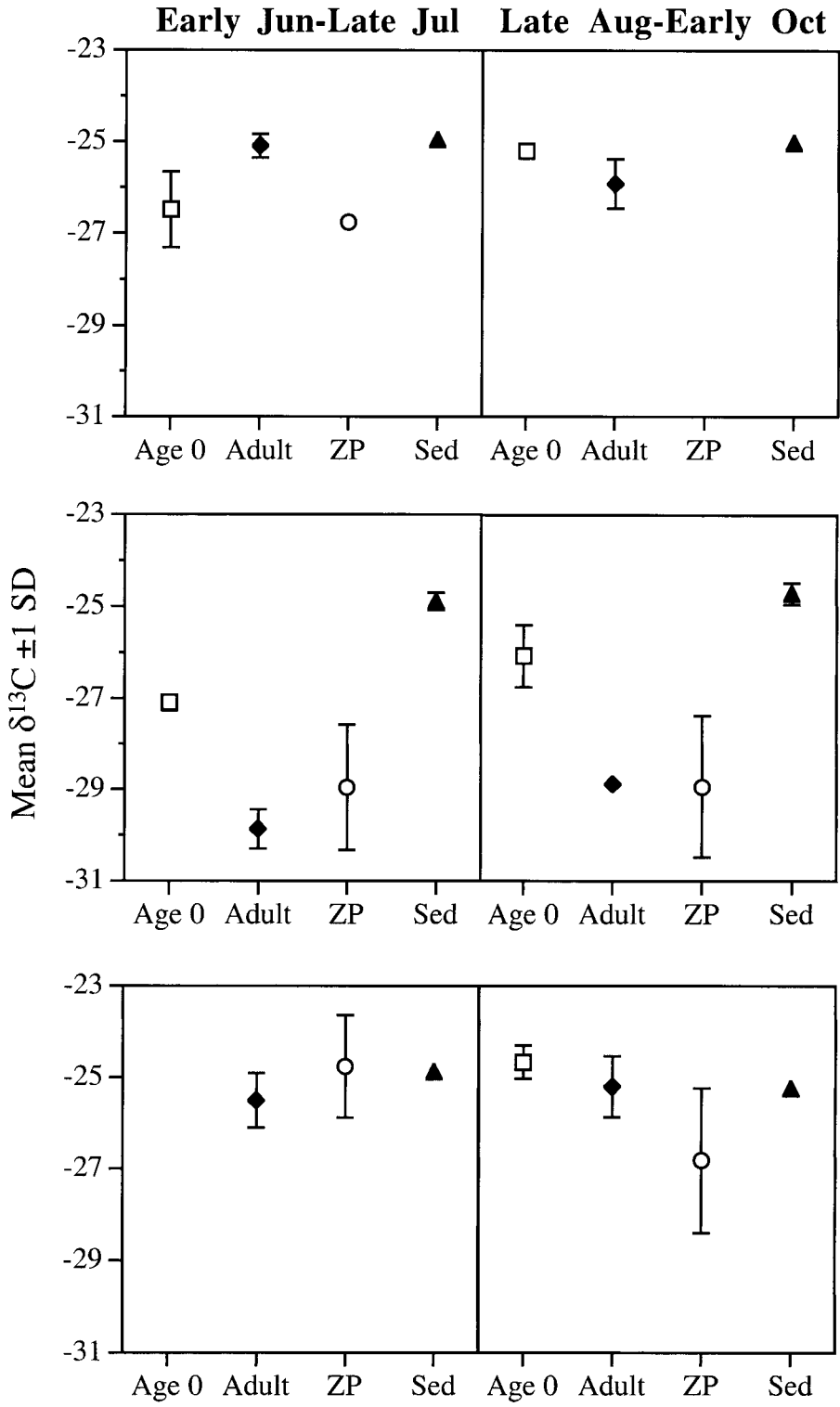


TABLE 1.—Results of a mixing model to estimate the proportion of gizzard shad C that is derived from zooplankton and sediment detritus based on $\delta^{13}\text{C}$ values. Values are given for the percentage of tissue C that is derived from zooplankton; the remainder is derived from sediment detritus. Comparisons were made between fish tissue and the mean zooplankton and sediment detritus isotopic signatures, except where indicated below; in these cases, comparisons were made between seasonal sediment isotopic composition and the mean isotopic composition of zooplankton across years. The sample size was 2–6 fish per age group reported during each season ($N = 40$).

Date	Age-group	% of C from zooplankton	
		Mean	Range
Jul 1995	Age 0	80.6	57.2–100.0
	Adults	19.2	0.0–34.0
Sep 1995 ^a	Age 0	13.6	10.4–16.8
	Adults	39.9	20.3–64.7
Jul 1996	Age 0	59.2	54.9–65.2
	Adults	100.0	
Oct 1996	Age 0	36.9	19.5–51.2
	Adults	100.0	
Jul 1997 ^a	Adults	28.6	0.0–50.4
Oct 1997	Age 0	0.0	
	Adults	20.5	0.0–66.2

^a Comparisons were made between the mean isotopic composition of zooplankton across years and seasonal sediment and gizzard shad values because the seasonal zooplankton values either were unreliable (fall 1995) or overlapped with the sediment isotopic signal (June–July 1997).

Discussion

Diet and Population Dynamics

Gizzard shad biomass and zooplankton abundance varied substantially across years; our results show that the fish diets were strongly dependent on density. When gizzard shad biomass dropped below a threshold of about 20–30 kg/ha, zooplankton (especially *Daphnia*) became very abundant (Pollard et al. 1998; this study) and gizzard shad fed extensively on them. Above this threshold, zooplankton were much less abundant (Pollard et al. 1998; this study), and gizzard shad generally relied on benthic detritus as their major food source. These biomass-dependent diet shifts have important implications for gizzard shad growth,

reproduction, and potential role in ecosystem processes.

TABLE 2.—Results of the conventional gut analyses. The percent of ash-free dry mass (AFDM) from zooplankton was determined by the mass difference determination method (Bowen 1987; Ahlgren and Bowen 1992). The percent of organic C from zooplankton was estimated assuming mean percent organic C values for zooplankton and sediments of 48% (Andersen and Hessen 1991) and 8.5% (Vanni et al., unpublished data), respectively. The sample size was 5–15 fish for all dates.

Date	% of AFDM from zooplankton		Mean % of organic C from zooplankton
	Mean	Range	
4 Sep 1995	0.32	0.00–1.55	1.8
17 May 1996	0.03	0.01–0.07	0.2
3 Jun 1996	0.19	0.01–0.50	1.1
19 Jul 1996	6.75	0.58–14.01	29.0
21 Aug 1996	0.61	0.20–1.84	3.3
5 Oct 1996	0.71	0.00–6.94	3.9
21 May 1997	0.15	0.02–0.54	0.8

reproduction, and potential role in ecosystem processes.

Yako et al. (1996) examined gizzard shad diets by gut content analysis and obtained results similar to those of the present study. They observed that nonlarval gizzard shad were zooplanktivorous only when zooplankton were abundant; in such cases, zooplankton constituted as much as 3% of dry mass in the diet. They also observed that smaller gizzard shad were more zooplanktivorous than larger fish. In the present study, we observed extensive zooplanktivory in both small and large gizzard shad in early 1996, probably because of the abundant zooplankton at that time. Although determining what proportion of AFDM consists of zooplankton is fairly straightforward, calculating the nutritional contribution of zooplankton and benthic detritus to gizzard shad growth and metabolism is much more difficult. Zooplankton are a higher-quality food (~48% organic C [Andersen and Hessen 1991]) than sediments are (~8.5% of AFDM is organic C in Acton Lake [Vanni et al., unpublished data]). Thus, when 6.75% of the diet consisted of zooplankton (i.e., at the end of the

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FIGURE 3.—Stable isotope analyses for 1995 (top panel), 1996 (middle panel), and 1997 (bottom panel). Each year's samples are divided into early summer (left half) and late summer to fall (right half) to show seasonal trends. Age-0 gizzard shad are indicated by open squares. Adult gizzard shad are indicated by black diamonds. Zooplankton are identified as ZP and indicated by open circles. Sediment detritus is identified as Sed and indicated by black triangles. Zooplankton samples during fall 1995 showed too much variability within a sample for inclusion. Age-0 gizzard shad were not analyzed during June–July 1997. Error bars indicate ± 1 SD; where they are omitted, the SD was smaller than the size of the symbol. More-negative $\delta^{13}\text{C}$ values indicate relative depletion in ^{13}C ; less-negative values indicate relative enrichment in ^{13}C .

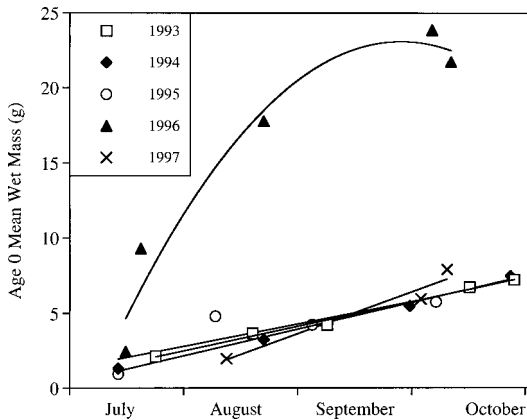


FIGURE 4.—Seasonal (July–October) growth of age-0 gizzard shad during 1993–1997. Plot symbols represent the mean wet mass for all age-0 gizzard shad collected on each sampling date. Lakewide gizzard shad biomass was low (<15 kg/ha) in May–July 1996 but was estimated to be greater (>35 kg/ha) at all other times.

large zooplankton peak), this food source composed about 29% of the organic C in gut samples (Table 2). However, the importance of zooplankton could be much greater in this case, because zooplankton are probably assimilated much more easily than detritus (Bowen 1987), underscoring the difficulty of determining the importance of benthic detritus to the diet directly from gut analyses.

Stable isotope analyses provide better quantification of nutrition over long periods (e.g., over the time scale of tissue turnover; Peterson and Fry 1987) than conventional gut analyses. As a result, stable isotope analyses showed stronger evidence of the dietary importance of zooplanktivory in 1996, possibly because our July 1996 gizzard shad sampling occurred after the peak in *Daphnia*, as the zooplankton were declining and rotifers were becoming abundant (Pollard et al. 1998). In this case, stable isotopes reflected the high zooplanktivory and rapid growth that had occurred during the previous month, whereas the gut analyses reflected zooplanktivory from the previous hour or so. One advantage of isotopes is that they integrate short-term opportunistic shifts in diet that might otherwise be overlooked. However, gut analyses did clearly show the decline in zooplanktivory during August–October 1996. This comparison of measurements indicates that stable isotopes are more suitable for quantifying feeding history integrated over longer time scales, whereas a fine-scale series of gut analyses may provide a better assessment of the timing of diet shifts over short time intervals (Beaudoin et al. 1999).

During most sampling periods, zooplankton and sediment detritus yielded distinct isotopic signals that allowed determination of the degree to which each food item contributed to the diet of gizzard shad. However, variability in planktonic $\delta^{13}\text{C}$, potentially caused by shifts in phytoplankton C sources (atmosphere, bacterial respiration, dissolved organic C) or differences in physiology of the dominant phytoplankters (Yoshioka et al. 1994; Zohary et al. 1994), must be taken into account by repeated sampling. Our seston isotopic signals suggested that detrital materials contributed somewhat to the seston $\delta^{13}\text{C}$ signal, because zooplankton are somewhat depleted in ^{13}C relative to seston (del Giorgio and France 1996; France and Peters 1997).

The ^{15}N enrichment with each trophic level can be influenced by the C:N ratio of food items (Adams and Sterner 2000), nutritional stress (Hobson et al. 1993), selective feeding or assimilation (Mundahl and Wissing 1988; Smoot 1999), or the deriving of C primarily from one food source and N primarily from another (Lopez et al. 1989; Bowen et al. 1995). Any of these mechanisms could account for the observed 8–10‰ enrichment of ^{15}N when gizzard shad feed on sediments. However, Mundahl and Wissing (1988) have presented evidence for selective feeding by gizzard shad in Acton Lake. Building on this information, Smoot (1999) separated Acton Lake sediments into two density fractions and found that the low-density fraction contained a much greater organic content and was preferentially consumed by gizzard shad. In addition, the light-sediment fraction was enriched in ^{15}N relative to the heavier fraction, so selective consumption of the lighter fraction could explain the greater $\delta^{15}\text{N}$ values of gizzard shad in this system (Smoot 1999). In general, interpretation of stable isotope results should be done cautiously (Hobson et al. 1993); an understanding of food web interactions is enhanced by combining stable isotope data with conventional diet data (Beaudoin et al. 1999).

Few other studies have examined the diet of gizzard shad by using stable isotopes. Mitchell et al. (1996) observed that the $\delta^{13}\text{C}$ of age-0 gizzard shad in Oneida Lake, New York, was intermediate between that of *Daphnia* and sediments but was closer to the signal of *Daphnia*. Gizzard shad appeared to rely more heavily on planktonic prey items, although the $\delta^{13}\text{C}$ was somewhat enriched relative to what would be expected if gizzard shad fed exclusively on *Daphnia* (Mitchell et al. 1996). Gu et al. (1996) estimated that gizzard shad in

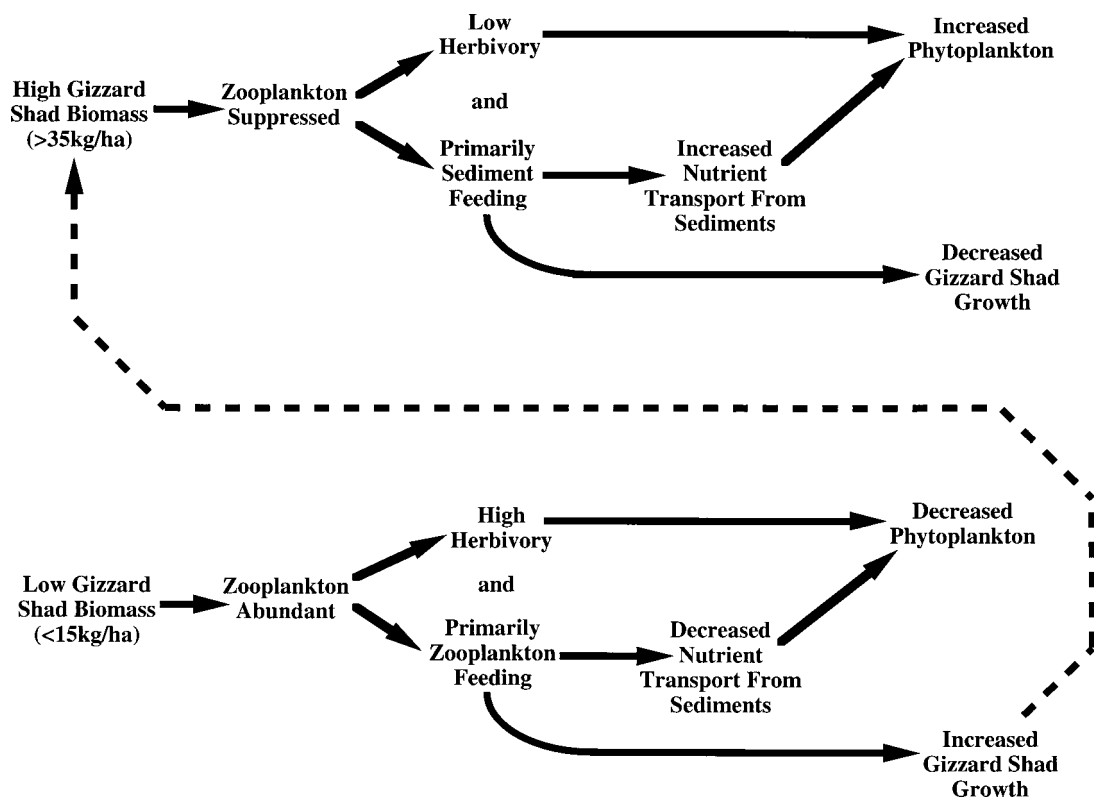


FIGURE 5.—Schematic representations of the two types of effects of gizzard shad in this system, both of which depend on population biomass. These effects occur via alteration of both herbivory by zooplankton and the rate of nutrient transport from sediments. Increased gizzard shad growth can lead to high gizzard shad biomass (dashed line). However, many factors (for example, aging of a dominant year-class, winterkill) may reduce population biomass. We are unable to predict the effects of gizzard shad biomass between 15 and 35 kg/ha because we did not observe biomasses in this range during our study and because other investigators (e.g., Mills et al. 1987; Post and McQueen 1987) have observed some degree of variation in the threshold fish biomass that suppresses *Daphnia* and other large zooplankton.

hypereutrophic Lake Apopka, Florida, obtained about 40% of their C from zooplankton. However, their study did not explicitly examine the isotopic composition of sediments but merely observed that gizzard shad $\delta^{13}\text{C}$ was intermediate to that of zooplankton and *Microcystis*. Thorp et al. (1998) found that gizzard shad in the Ohio River displayed $\delta^{15}\text{N}$ signals greater than expected on the basis of sediment or zooplankton $\delta^{15}\text{N}$, as in our study. They also found that gizzard shad displayed a relatively high variance in $\delta^{13}\text{C}$ compared with most other consumers and attributed this to their omnivorous nature (Thorp et al. 1998).

In this study, growth of gizzard shad was strongly linked to diet. When gizzard shad fed extensively on high-quality zooplankton prey, they exhibited growth rates much greater than when they fed primarily on the low-quality detritus associated

with sediments. Therefore, it appears that gizzard shad growth is highly dependent on diet quality (Mundahl and Wissing 1987; Buynak and Mitchell 1993), which in turn is influenced by gizzard shad abundance (Figure 5). When gizzard shad are abundant (>35 kg/ha), they probably suppress zooplankton and then switch to an abundant but low-quality detrital food source. Growth of age-0 fish was similar above the threshold biomass of about 20–30 kg/ha regardless of whether the gizzard shad biomass was 40 or 400 kg/ha. Below this threshold, however, their growth was much greater. Growth may serve therefore as a useful predictor of diet and to some extent of gizzard shad biomass. Because growth was depressed in 1993 (Figure 4), we infer that gizzard shad were primarily detritivorous during that year and that their biomass probably exceeded 35 kg/ha. Although we

are less confident of our biomass estimates derived from the 1995 CPUE data, growth rates of age-0 gizzard shad in that year also suggest that 1995 biomass was greater than 35 kg/ha.

The effect of diet on growth can impact overwinter survival, age at maturity, size—structure, and population biomass. The larger size attained by zooplanktivorous gizzard shad probably improves the survival rate during their first winter (Cargnelli and Gross 1997). In 1996, high growth and survival of age-0 fish led to dramatic increases in gizzard shad biomass between early summer and the fall. The 1996 year-class was even large enough to spawn after its first winter, unlike other year-classes in Acton Lake (Wissing et al. 1984; this study) and other systems, in which this species typically requires 2 years to reach maturity (Kilambi and Baglin 1969; Jester and Jensen 1972; but see Bodola 1965). Rapid growth and early reproduction can allow populations to recover rapidly from severe declines in biomass. Since 1997, gizzard shad biomass in Acton Lake has continued to increase (Vanni et al., unpublished data). Thus, the low biomass observed in 1996 may be a relatively rare occurrence in this system, partly because the shift to zooplanktivory allows rapid growth and ultimately high biomass. These factors, coupled with the high fecundity of gizzard shad (Kilambi and Baglin 1969; Jester and Jensen 1972) may favor the success of dominant year-classes after periods where biomass is depressed.

In general, many fish species feed opportunistically on preferred resources when they are abundant but rely on less preferred resources at other times (Ahlgren 1990; Beaudoin et al. 1999). Even organisms that are generally thought to be exclusively piscivorous have been shown to supplement their diet with invertebrate prey when suitable fish prey are not available (Vander Zanden et al. 1997; Beaudoin et al. 1999). Many fish species supplement their diet with detritus or rely heavily on it (e.g., Darnell 1961; Jester and Jensen 1972; Bowen 1983). Facultative detritivory may serve to provide fish with a source of energy when high-quality prey items are scarce and may reduce the degree of nutritional stress experienced during these times (Ahlgren 1990; Lemke and Bowen 1998).

Implications of Diet Shifts for Food Web and Ecosystem Processes

Biomass-dependent diet shifts in gizzard shad can greatly affect the role of this species in lake food webs (Figure 5). Gizzard shad in Midwestern reservoirs generally are not regulated by their

predators; hence, they are thought to regulate reservoir food webs from the “middle out” (Stein et al. 1995) through several mechanisms. In this study, the collapse in gizzard shad biomass during 1996 caused zooplankton to increase greatly, thereby decreasing seston abundance and greatly increasing water transparency (Pollard et al. 1998). The strong reduction in phytoplankton during 1996 occurred despite a greater loading of soluble and total N and P than in the other years of the study, because of more precipitation in that year (Vanni et al. 2001). This association suggests that phytoplankton were predominantly limited by grazing during the peak in *Daphnia* and rotifer abundance during that year, unlike other years, when grazing by zooplankton was probably much lower (Pollard et al. 1998). Other systems have also exhibited similar decreases in phytoplankton after decreases in planktivores (e.g., Carpenter and Kitchell 1988; Vanni et al. 1990; Brett and Goldman 1996); in some cases these occurred despite greater nutrient loading from the watershed (Vanni et al. 1990).

In contrast, when gizzard shad are abundant, they suppress zooplankton and switch to benthic detritus as their primary food source. In doing so, they transport substantial quantities of N and P from sediments into the water column (Schaus et al. 1997), thereby stimulating phytoplankton and increasing total water column nutrients (Schaus and Vanni 2000). Hence, detritivorous gizzard shad can maintain high phytoplankton productivity even when external nutrient loading is reduced (Vanni 1996). Because the magnitude of this effect is proportional to the biomass of the population, a larger biomass would have a much larger nutrient-mediated effect. In 1994, when gizzard shad biomass was greatest, phytoplankton were abundant despite the lowest watershed nutrient loading during the study period (Vanni et al. 2001).

The mechanisms behind these “top-down” and “bottom-up” processes have been examined previously (Schaus and Vanni 2000). Lake mesocosms containing gizzard shad exhibited suppressed zooplankton abundance and increased phytoplankton abundance. In contrast, mesocosms without gizzard shad exhibited high zooplankton abundance and decreased phytoplankton, despite increased concentrations of dissolved nutrients. In addition, enclosures in which gizzard shad could feed directly on sediments had a greater concentration of phytoplankton than those in which gizzard shad were prevented from feeding on sediments—indicating that transport of nutrients from sediments to the water column is an important

mechanism behind the increase in phytoplankton (Schaus and Vanni 2000). Thus, gizzard shad impact phytoplankton by way of an interaction between "top-down" and "bottom-up" effects.

Similar effects have been observed for planktivorous fishes (e.g., Vanni and Findlay 1990; Persson 1997b; Vanni and Layne 1997), in which the increase in phytoplankton in the presence of planktivorous fish resulted from both grazer suppression and increased nutrient recycling. Other investigators (e.g., Mills et al. 1987; Post and McQueen 1987) have noted that planktivore biomass of about 20–50 kg/ha is sufficient to suppress large *Daphnia*, thus greatly reducing grazing by zooplankton. This threshold abundance of fish appears to be important in shifting the phytoplankton between predominant control by grazers and predominant control by nutrients (e.g., Hairston et al. 1960; Wootton and Power 1993).

Benthic-feeding omnivores presumably would have a greater impact on phytoplankton than would planktivores because the nutrients transported from the benthos to the water column by omnivores represent a net source of "new" nutrients to phytoplankton (Shapiro and Carlson 1982), in addition to any top-down effects of planktivory by these omnivores. This source of nutrients is fundamentally different from the nutrients recycled within the water column by planktivores because it can increase the total nutrient concentration of the water column rather than simply recycling nutrients already present within the water column. Our mesocosm experiments exhibited increased concentrations of total P in the presence of gizzard shad that fed on sediment detritus (Schaus and Vanni 2000).

By virtue of their diet flexibility, omnivorous species such as the gizzard shad potentially can impact aquatic systems through a variety of different mechanisms, including consumptive effects at multiple trophic levels, nutrient release, and bio-turbation (Lamarra 1975; Scheffer et al. 1993; Drenner et al. 1996). Benthic omnivores are theorized to increase ecosystem resilience, especially in productive systems, by providing a detrital subsidy that can stabilize or enhance productivity (DeAngelis et al. 1989; Polis and Strong 1996). Omnivores can dominate fish assemblages, especially in eutrophic systems (e.g., Miranda 1984; Meijer et al. 1990; Bachmann et al. 1996), increasing the potential for strong effects on ecosystem processes. Moreover, omnivorous fish can have stronger effects in eutrophic systems than in oligotrophic systems (Drenner et al. 1996). Thus,

it appears that omnivorous fish can maintain lakes in a highly productive state (Adams et al. 1983; Scheffer et al. 1993; Drenner et al. 1996), with benthic feeding and subsequent excretion being important mechanisms behind this process.

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