

Selection and Digestive Efficiencies of Gizzard Shad Feeding on Natural Detritus and Two Laboratory Diets

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Abstract.—Selective feeding on and digestion of detritus in surface sediments (organic matter < 10%, nitrogen < 0.4%) by age-0 and adult (ages 3 and 4) gizzard shad *Dorosoma cepedianum* in Acton Lake, Ohio (water temperature = 15–18°C) were compared with those of age-0 fish fed two particulate diets (low-quality diet: organic matter = 10%, nitrogen = 0.3%; high-quality diet: organic matter = 89%, nitrogen = 6.7%) at 18°C in the laboratory. Fish feeding on natural detritus and the low-quality diet exhibited mean selection efficiencies, ratios of nutrient weight percentages in the gizzard to those in the sediment or food, of 1.8–2.9 for total organic matter, 2.4–4.4 for total carbon, and 3.2–13.2 for total nitrogen. Fish fed the high-quality diet exhibited no selective feeding. Mean digestive efficiencies, $100 [1 - (\text{feces value} \div \text{gizzard value})]$, for total organic matter, total carbon, and total nitrogen in the diets had ranges of 50–66, 51–64, and 62–84%, respectively. Age-0 fish feeding on natural detritus and the two laboratory diets exhibited similar digestive efficiencies. In addition, age-0 and adult gizzard shad were equally efficient at digesting the components of natural detritus. Gizzard shad apparently can ingest selectively the more nutritious portions of low-quality particulate diets in the field and laboratory and digest a substantial proportion of the nutrients present.

Organic detritus is consumed by many fish species to meet part or all of their nutritional needs (Odum 1970; Bowen 1979, 1983; Persson 1983; Bowen et al. 1984; Mundahl and Wissing 1987). However, fish that feed on this material face two problems (Bowen 1983): (1) detritus is often mixed with large quantities of undigestible inorganic sediments (e.g., sand, silt, clay), and (2) much of the organic matter in detritus may be enclosed within plant cell walls resistant to digestive enzymes, or may be in the form of refractory compounds that are difficult to digest. Many detritivorous fishes have various morphological and physiological adaptations, however, that enable them to select or sort organic detritus from inorganic particles and then to digest this material efficiently (e.g., Bowen 1976, 1981, 1983; Payne 1978; Marais 1980).

Although detritivory has been studied extensively for several tropical and subtropical fishes, little information is available on the many temperate species (e.g., cyprinids, freshwater clupeids, and catostomids) that eat detritus (Bowen 1983; Persson 1983). It is not known whether the adaptations that allow many tropical and subtropical fishes to exploit detritus as a food source are also characteristic of temperate forms with the same mode of feeding. Morphological and histological analyses indicate that the gizzard shad *Dorosoma*

cepedianum, an important prey fish in many North American waters, is similar in many respects to the neotropical detritivores. For example, gizzard shad have a mouth cavity with a ventral keel that may allow it to function as a settling chamber, long, finely spaced gill rakers that retain small particles, and intestinal modifications that increase the surface area for absorption and increase food retention time (Lagler and Kraatz 1944; Bodola 1965; Dalquest and Peters 1966; Schmitz and Baker 1969). Thus, gizzard shad may be well equipped to feed on and digest detritus.

Gizzard shad are omnivorous, feeding on zooplankton, phytoplankton, and other live foods when these are available and abundant (Jester and Jensen 1972; Jude 1973; Drenner et al. 1982, 1984). In many systems, however, gizzard shad depend heavily on detritus grazed from bottom sediments and submerged objects (Dalquest and Peters 1966; Baker and Schmitz 1971; Mundahl and Wissing 1987). In Acton Lake, a small reservoir in southwestern Ohio, gizzard shad ingest detritus throughout the growing season (Pierce et al. 1981; Mundahl and Wissing 1987). The present study was designed to examine the abilities of gizzard shad to select detritus from inorganic sediments and to digest the nutrients contained in this food material.

Methods

Selection efficiency.—Field experiments were conducted to examine the selection efficiencies of young-of-the-year (age 0) and adult (ages 3 and 4) gizzard shad feeding on natural detritus in surface sediments. Fish were collected monthly (age-0: August–November 1982, July–November 1983; adult: July–November 1982, July and September 1983, May 1986) from Acton Lake by electrofishing during midday. The fish were killed, immediately placed on ice, and then frozen until processed. Later, the food materials were removed from the gizzard (muscular stomach) of each fish and oven-dried at 60°C. Because of the small amounts of material in each gizzard, the gizzard contents of three adult or five age-0 fish were combined to produce a sample adequate for the analyses.

Potential foods (i.e., surface sediments) were collected monthly with sediment traps within 2 d of the fish collections and then oven-dried. The cylindrical, Plexiglas sediment traps (70-cm² opening) rested on the lake bottom and collected sediments that settled from the water column over a period of 18–20 h. Because gizzard shad in Acton Lake feed almost exclusively by grazing on freshly deposited surface sediments (Pierce et al. 1981; Mundahl and Wissing 1987), the materials collected by the sediment traps were assumed to be representative of the foods available to the fish (see Discussion for rationale).

Gizzard contents and surface sediments were analyzed for total organic, carbon, and nitrogen contents. Total organic matter was determined by weight loss after combustion of subsamples at 550°C for 3 h (Cummins and Wuycheck 1971). Combusted samples were rehydrated with distilled water and oven-dried before final weights were taken in order to reintroduce the water of hydration of clay and other minerals driven off by combustion (Weber 1973). The carbon and nitrogen contents of ingested foods and sediments were determined with an elemental analyzer (Carlo-Erba model 1106) coupled to a data processor (Adams-Smith model 2000C). The analyzer was calibrated with a standard of cyclohexanone (51.59% carbon and 20.14% nitrogen by weight). Selection efficiencies of gizzard shad feeding on surface sediments were calculated by comparing the total organic, carbon, and nitrogen contents (percent of dry weight) of gizzard materials with those of the sediments (ratio of gizzard materials value to sediment value; Marais 1980). Ratios that greatly ex-

ceed 1.0 indicate selective rejection of inorganic particles during feeding.

Selection efficiencies of age-0 gizzard shad were also examined in laboratory feeding experiments. Fish were collected from Acton Lake in October and November 1985, returned to the laboratory, and placed immediately in a 492-L Living Stream (Frigid Units) at 18°C. Fish were acclimated to laboratory conditions (constant temperature, natural lighting through laboratory windows) for 2 weeks and fed a high-quality diet (pulverized Zeigler trout pellets) ad libitum. Although this diet did not have the bacterial or fungal coating of natural detritus, microscopic examination (25 and 100× magnification) revealed that the food particles were within the general size range (20–100 μm) of those ingested by age-0 gizzard shad in Acton Lake (Mundahl 1984). After the acclimation period, four groups ($N = 25$ –50) of fish were fed either the high-quality diet or a low-quality diet (quality similar to that of natural detritus) made from a 5:1 mixture, by weight of dried Acton Lake surface sediments and dried aufwuchs. (Aufwuchs was scraped gently with a knife from submerged logs in Acton Lake and placed in polyethylene bags filled with lake water. Samples were returned immediately to the laboratory and oven-dried at 60°C.) The particulate food sank within minutes of introduction into the Living Stream and formed a thin layer on the bottom, where it was fed on readily by the fish. After feeding on these materials for 4 h, the fish were killed and frozen. Their gizzard contents were later removed and analyzed as described previously.

Digestive efficiency.—Age-0 fish were collected by electrofishing in October 1985 (water temperature, 18°C). Twenty-five individuals were placed immediately on ice for later analyses of the natural detritus in their gizzards; the remainder were transported alive to the laboratory and placed immediately in the Living Stream (water temperature, 18°C). Feces were collected from one group ($N = 40$) for a 30-min period immediately after their placement in the Living Stream. The feces were assumed to be representative of those egested by fish in the lake.

Fecal pellets were siphoned from the tank immediately upon egestion; approximately 10 pellets were combined to form one sample. No attempt was made to separate feces from different fish. Earlier attempts to collect feces produced by individual fish proved unsuccessful because fish placed individually in 10-L aquaria produced no feces during a 4-h period.

Adult (ages 3 and 4) gizzard shad were collected from Acton Lake in May 1986 (water temperature, 15°C) and handled in a manner similar to that described for younger fish. However, individual fecal pellets produced by adult fish were large enough for each to comprise a single sample.

Four groups ($N = 15-30$) of age-0 gizzard shad were acclimated in the laboratory and, after a 48-h starvation period (sufficient to empty digestive tracts; Salvatore 1984), offered either the high- or low-quality diet. Feces egested by these fish were collected in the manner described previously. Several fishes in each group were killed for analysis of gizzard contents.

Both the foods removed from gizzards and the feces from field- and laboratory-fed fish were oven-dried at 60°C and analyzed for total organic, carbon, and nitrogen contents. Digestive efficiencies (amount digested as a percentage of amount ingested) for each of the three food components were calculated for each group of gizzard shad by the method of Conover (1966); mineral ash was an undigested reference compound. Although some species of fish are known to absorb a small fraction of the ash in their diets (Buddington 1980), it is doubtful that this would have a significant effect on the calculation of gizzard shad digestive efficiencies when the diet contains large amounts of inorganic sediments. Food samples from gizzards, rather than the foods offered, were used to calculate digestive efficiencies because little or no chemical digestion of food materials is believed to occur in this organ (Dalquest and Peters 1966). Furthermore, calculations may be biased if fish select for or against one or more of the components of the food available.

Statistical analyses.—Selection efficiencies for each of the three food components were calculated monthly for age-0 and adult gizzard shad that fed on Acton Lake detritus and for each experimental group of fish that were fed the laboratory diets. Within each fish group and food component, *t*-tests were performed to determine whether mean selection efficiencies differed significantly from 1.0, which would indicate selective feeding. Values for field-fed fish were compared statistically between age groups with *t*-tests and among food components within each age group with paired *t*-tests. Selection efficiencies were compared among field- and laboratory-fed age-0 fish by single-factor analyses of variance and Duncan's new multiple-range tests (SAS 1982).

Digestive efficiencies for each food component were calculated for each of the four test groups by

pairing each individual gizzard content value with a single, randomly selected feces value from the same data set for food component and test group. This was done to facilitate statistical comparisons among food components and test groups and to provide a conservative estimate of digestive efficiency. Mean digestive efficiencies were compared among food components within each test group with single-factor analyses of variance and Duncan's new multiple-range tests. Intergroup comparisons were made by *t*-tests (between age groups fed Acton Lake sediments) and single-factor analyses of variance (among test groups of age-0 fish).

Transformations of the data were made to meet the normality assumptions of the analysis of variance and *t*-test models (Sokal and Rohlf 1981). The level of significance for statistical tests was set at 0.05 unless otherwise noted.

Results

Sizes of Experimental Fish

During the 1982 and 1983 growing seasons, wet weights of age-0 gizzard shad in Acton Lake ranged from 2.5 to 11.1 g; standard lengths ranged from 47 to 80 mm. The 3- and 4-year-old fish had wet weights of 40.5–252.3 g and standard lengths of 122–207 mm. Mean (\pm SD) wet weight and standard length of age-0 gizzard shad used in the laboratory experiments were 1.4 ± 0.3 g and 42 ± 3 mm, respectively. The 3- and 4-year-old fish used in the laboratory averaged 173.1 ± 56.1 g wet weight and 200 ± 17 mm standard length.

Sediment Trap Samples and Gizzard Contents

Microscopic examination (25 and 100 \times magnification) of sediment trap samples from Acton Lake and the gizzard contents of age-0 and adult gizzard shad revealed the presence of detritus, inorganic particles, filamentous green (*Cladophora* sp., *Spirogyra* sp.) and blue-green (*Oscillatoria* sp.) algae, diatoms, ciliates, and rotifers. Green algae, diatoms, ciliates, and rotifers were observed only rarely in gizzards. Detrital particles and algal filaments from age-0 fish were generally smaller than those in gizzards of adult fish.

Selection Efficiency

Gizzard contents of fish that fed on natural detritus generally contained higher percentages of organic matter, carbon, and nitrogen than those observed in surface sediments (Figure 1). Mean monthly selection efficiencies for these fish ranged from 1.8 to 6.1 for the various food components

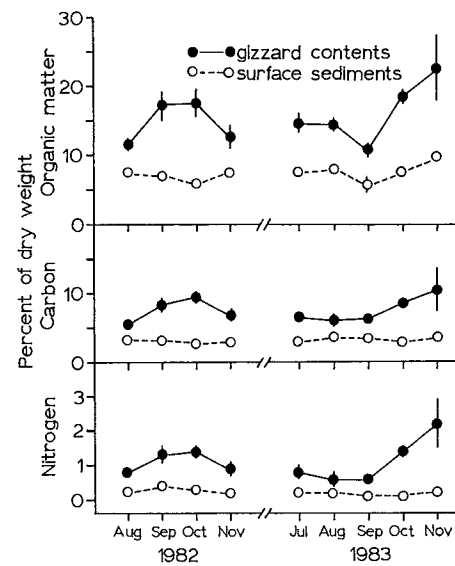


FIGURE 1.—Organic, carbon, and nitrogen contents (percent of dry weight) of surface sediments and gizzard contents of age-0 gizzard shad from Acton Lake during summer and autumn, 1982 and 1983. Values are means \pm 1 SE. Monthly $N = 3$ (1983) or 4 (1982) for sediments and 5 for gizzard contents.

(Table 1). Significant selective feeding (mean selection efficiencies greater than 1.0; $P < 0.05$) was evident for all three food components in both age

groups of fish. The mean selection efficiency for nitrogen (6.1) was significantly higher ($P < 0.05$) than those for carbon (2.4) or total organic matter (2.1) for age-0 fish, but not for adult fish. There were no significant differences ($P > 0.1$) in selection efficiencies between age-0 and adult fish for any of the three food components.

Age-0 fish fed the low-quality diet exhibited mean selection efficiencies for the three food components that were similar to those of fish feeding on natural detritus (Table 1). However, no selective feeding occurred among fish fed the high-quality diet ($P > 0.5$); these fish had mean selection efficiencies for organic matter (0.9) and carbon (1.0) that were significantly lower than those (2.1 and 2.4, respectively) of age-0 fish feeding on natural detritus. No significant differences in mean selection efficiencies were detected between fish fed the low- or high-quality diets in the laboratory, owing primarily to the low number of replicates.

Digestive Efficiency

Gizzard shad in Acton Lake digested 50.2–79.0% of the food materials contained in natural detritus (Table 2). Nitrogen was digested more readily than either carbon or total organic matter by age-0 fish ($P < 0.07$) but not by adult fish. There were no significant differences ($P > 0.1$) in mean digestive

TABLE 1.—Selection efficiencies (ratio of gizzard contents value—% organic matter, carbon, or nitrogen—to sediment or food value; mean \pm 1 SE, sample size in parentheses) of adult (ages 3 and 4) and age-0 gizzard shad that fed on detritus in Acton Lake and of age-0 fish fed two laboratory diets. Selection efficiencies that differ greatly from 1.0 are evidence of selective feeding. Values for sediments and gizzard contents of fish from Acton Lake are ranges of monthly mean values; those for food and gizzard contents from laboratory experiments are ranges of replicate trials. For age-0 fish, mean selection efficiencies (within each column only) not followed by a common letter are significantly different from one another.

Measure	Food component (% of dry weight)		
	Total organic matter	Total carbon	Total nitrogen
Adult fish, Acton Lake sediments			
Sediments	5.8–7.8	2.8–3.4	0.1–0.4
Gizzard contents	7.1–19.1	5.6–12.8	0.2–1.9
Selection efficiency	1.8 \pm 0.2 (8)	2.6 \pm 0.3 (7)	3.2 \pm 1.1 (7)
Age-0 fish, Acton Lake sediments			
Sediments	5.9–9.7	2.8–3.6	0.1–0.4
Gizzard contents	10.8–22.6	5.6–10.5	0.6–2.2
Selection efficiency	2.1 \pm 0.1 (9) z	2.4 \pm 0.2 (9) z	6.1 \pm 1.3 (9) z
Age-0 fish, low-quality laboratory diet			
Food	9.8–10.0	4.3–4.4	0.2–0.4
Gizzard contents	21.6–36.1	9.9–28.3	0.9–7.0
Selection efficiency	2.9 \pm 0.7 (2) yz	4.4 \pm 2.1 (2) yz	13.2 \pm 10.1 (2) z
Age-0 fish, high-quality laboratory diet			
Food	89.2–89.4	44.6–45.3	6.5–6.8
Gizzard contents	83.7–84.1	43.4–46.0	7.4–8.1
Selection efficiency	0.9 \pm 0.0 (2) y	1.0 \pm 0.0 (2) y	1.2 \pm 0.1 (2) z

TABLE 2.—Amounts digested and digestive efficiencies (amount digested as percentage of amount ingested) of adult (ages 3 and 4) and age-0 gizzard shad that fed on detritus in Acton Lake and of age-0 fish fed two laboratory diets. Values for gizzard contents and feces are means \pm 1 SE; sample sizes are in parentheses. For digestive efficiencies, the first (nonparenthetical) value in each row (used to determine weight of food digested per weight of food ingested) was calculated from mean gizzard contents and feces values. Digestive efficiencies in parentheses (means \pm 1 SE) were calculated by pairing individual gizzard contents values with single, randomly selected feces values and were used in statistical comparisons.

Food component	Milligrams of food component per milligram of ash		Milligrams digested per gram food ingested	Digestive efficiency (%) ^a
	In gizzard contents	In feces		
Adult fish, Acton Lake sediments (May 1986)				
Organic	0.292 \pm 0.062 (7)	0.145 \pm 0.014 (7)	96	50.2 (39.1 \pm 11.7)
Carbon	0.178 \pm 0.028 (7)	0.083 \pm 0.009 (7)	72	53.4 (42.8 \pm 14.1)
Nitrogen	0.030 \pm 0.005 (7)	0.007 \pm 0.001 (7)	17	76.7 (68.6 \pm 10.5)
Age-0 fish, Acton Lake sediments (Oct 1985)				
Organic	0.242 \pm 0.034 (5)	0.089 \pm 0.004 (15)	122	63.3 (58.6 \pm 5.0)
Carbon	0.116 \pm 0.012 (5)	0.057 \pm 0.001 (15)	48	51.1 (49.2 \pm 5.1)
Nitrogen	0.018 \pm 0.003 (5)	0.004 \pm 0.000 (15)	11	79.0 (75.8 \pm 6.2)
Age-0 fish, low-quality laboratory diet				
Organic	0.376 \pm 0.073 (6)	0.130 \pm 0.004 (9)	173	65.6 (60.3 \pm 6.6)
Carbon	0.205 \pm 0.081 (4)	0.074 \pm 0.003 (9)	97	64.2 (50.9 \pm 15.4)
Nitrogen	0.036 \pm 0.024 (4)	0.006 \pm 0.000 (9)	22	84.3 (64.1 \pm 11.2)
Age-0 fish, high-quality laboratory diet				
Organic	5.254 \pm 0.162 (8)	2.436 \pm 0.307 (11)	450	53.6 (55.7 \pm 7.2)
Carbon	2.780 \pm 0.072 (8)	1.282 \pm 0.140 (11)	241	53.9 (50.3 \pm 6.5)
Nitrogen	0.477 \pm 0.014 (8)	0.181 \pm 0.017 (11)	48	62.0 (62.8 \pm 3.5)

^a Digestive efficiency = 100 [1 - (feces value \div gizzard contents value)].

efficiencies between the age groups for any of the three food components.

Age-0 gizzard shad also digested large fractions of the two laboratory diets (Table 2). Mean digestive efficiencies of fish fed either diet did not differ ($P > 0.1$) from those of age-0 fish that fed on natural detritus. However, fish fed the high-quality diet digested two to four times more total food per gram of food ingested than fish fed the other diets (Table 2).

Discussion

The assumption that gizzard shad in Acton Lake feed almost exclusively on freshly deposited surface sediments is based on several observations. First, a common feeding behavior exhibited by this species in this system is a grazinglike movement along sediments or submerged objects (Mundahl and Wissing 1987). Dalquest and Peters (1966) reported that gizzard shad in Lake Diversion, Texas, fed in a similar fashion and ingested only the surface layer of bottom sediments. The detritivorous striped mullet *Mugil cephalus* also has been reported to feed in a similar manner (Odum 1970). Secondly, microscopic analyses of gizzard contents have revealed that food materials not present in the sediments seldom appear in the diets of Acton Lake gizzard shad (Garland 1972;

King et al. 1977; Mundahl and Wissing 1987). Zooplankton is not usually present in numbers sufficient to provide gizzard shad with a reliable food source (Mundahl and Wissing 1987), and phytoplankton generally makes up an insignificant (<5% of total volume) portion of the diet (Garland 1972). Finally, "older" sediments that may have been colonized by bacteria were always similar to, or lower in organic and nitrogen contents than, the materials collected by the sediment traps (Mundahl 1984; Mundahl and Wissing 1987). Although the diets of gizzard shad in Acton Lake occasionally may include "older" detritus and plankton, the evidence suggests that recently deposited sediments are a major source of food materials during summer and autumn, and that the detrital particles collected by the traps should have been representative of those available to the fish during those seasons.

Previous investigators have noted that when live foods such as zooplankton and phytoplankton are not abundant or are available only seasonally, the diet of the gizzard shad will contain large amounts of detritus grazed from sediments or other surfaces (Dalquest and Peters 1966; Baker and Schmitz 1971; Pierce et al. 1981; Mundahl and Wissing 1987). However, this mode of feeding has been assumed to be largely unselective (Dalquest

and Peters 1966). The results of our study suggest some degree of selectivity in the detritivory exhibited by this species. Surface sediments were collected within a major gizzard shad feeding area, and when the nutritional quality of these was compared with that of ingested food materials, significant differences were observed. In some months, gizzard shad selected or concentrated certain food components up to 14-fold over their abundances in typical surface sediments. There was no evidence that the fish actively sought out feeding areas with high-quality detritus, although this behavior has been reported for other detritivorous fishes (Bowen 1979, 1983).

Although our results only suggest selective feeding on freshly deposited detritus by gizzard shad, they do complement what is known about the anatomy and presumed function of the feeding apparatus of this and other detritivorous species. The gizzard shad is well equipped for removing particles from the water or from surfaces. The sub-terminal mouth lacks teeth (Dalquest and Peters 1966), but a ventral keel in the posterior pharynx directs incoming water and food particles away from the esophageal entrance and into the gill rakers and epibranchial organs (Schmitz and Baker 1969). The gill rakers are numerous, elongated, and finely spaced, permitting young fish to filter particles as small as 20 μm efficiently (Drenner et al. 1984; Mummert and Drenner 1986). Large, heavy particles (e.g., sand grains) ingested along with detritus may settle out on the floor of the pharynx on either side of the ventral keel from where they may be expelled. Such anatomical settling chambers are present in the oral cavities of other detritivorous fishes (Bowen 1983). The pouchlike epibranchial organs also are richly innervated and have been hypothesized to function in food accumulation and consolidation, as well as in acceptance or rejection of materials already accumulated (Lagler and Kraatz 1944; Schmitz and Baker 1969).

It is not known whether the ability of gizzard shad to feed selectively results from mechanical selection in the oral cavity for small particles that are often richer in organic matter than are large materials (e.g., Odum 1968; Marais 1980), or from a chemical selection by gustatory receptors bordering the epibranchial organs (Schmitz and Baker 1969), or both. Observations of gizzard shad feeding behavior in the field and laboratory revealed what appeared to be the expulsion of unwanted materials through the mouth a few seconds after food ingestion (Mundahl 1984), an action suggestive of some type of selectivity. Feeding selectivity

by other detritivorous fishes commonly involves some type of release of unwanted materials through the mouth or the opercular openings (Odum 1968; Bowen 1979). In our study, gizzard shad confronted with a food source low in organic matter apparently exhibited such selective feeding; those fish offered particulate food high in organic matter showed no selection. More investigations are needed to determine whether selective feeding begins when the food value of bottom sediments reaches some lower threshold.

After ingesting detritus, gizzard shad digested a significant proportion of this material, especially the nitrogen fraction. Very few studies have examined the digestion of detritus by fish. Bowen (1981) observed digestive efficiencies ranging from 62 to 77% for the Mozambique tilapia *Tilapia mossambica*; Gneri and Angelescu (1951) reported values of 30–60% for *Prochilodus platensis*. In general, digestive efficiencies of gizzard shad feeding on natural detritus and the particulate laboratory diets in our study were similar to those reported for subtropical detritivorous fishes.

Digestive efficiencies of gizzard shad remained remarkably consistent despite the wide ranges in fish size and food quality used in our study. Adult gizzard shad ingested larger food particles than age-0 fish (Mundahl and Wissing 1987); the older fish also had relatively longer intestines than the young fish (Mundahl 1984). Both of these factors potentially could cause differences in digestive efficiencies between the age groups. In addition, no differences in digestibility were detected between the pulverized trout pellets and the natural detritus, even though many of the nutrients in natural detritus may be highly resistant to digestion (Bowen 1983). The ability of gizzard shad to digest detritus is undoubtedly related directly to its highly modified digestive tract. The stomach is modified as a muscular gizzard capable of rapid mixing and grinding movements (Schmitz and Baker 1969). The intestine is relatively short (2–5 times the standard length; Mundahl 1984), but hundreds of branched ceca arise from the lateral surface of the duodenum, and large longitudinal and smaller transverse mucosal folds occur throughout the intestine (Bodola 1965; Schmitz and Baker 1969). These modifications increase the surface area for absorption and increase food retention time (Kapoor et al. 1975). Foods move slowly through the digestive tract of a gizzard shad, requiring 4 h or more for complete passage (Salvatore et al. 1987). This time period is apparently sufficient for gizzard shad to digest a major portion of the detritus ingested.

At least two factors may have influenced, to varying degrees, our determinations of digestive efficiencies for gizzard shad. First, efficiencies may have been underestimated if the fish absorbed some of the ash from the diets (Buddington 1980). Most of the ash in the natural detritus consisted of unabsorbable inorganic particles such as sand, silt, and clay. Thus it is doubtful that digestive efficiencies of gizzard shad feeding on natural detritus were significantly underestimated. However, ash from the high-quality diet (pulverized trout pellets) may have been more easily absorbed (Buddington 1980), possibly resulting in greater underestimation of the digestion of this diet. Second, the digestive efficiencies determined in the laboratory after a 48-h period of starvation may not have been truly representative of the digestive process that occurs in the field. Food passage rates, and consequently digestive efficiencies, may be altered by lack of food in the digestive tract. However, given that digestive efficiencies did not differ significantly between field- and laboratory-fed fish, food deprivation apparently had little effect on determinations of gizzard shad digestive efficiencies in the laboratory.

Because digestion of detritus by gizzard shad was examined over only a narrow water temperature range (15–18°C), it is not known whether fish feeding on detritus at higher or lower temperatures may exhibit different digestive efficiencies from those reported here. Gizzard shad feed heavily on detritus at temperatures from 10 to 30°C (Mundahl 1984), and processes such as gut motility, digestive enzyme secretion and activity, and intestinal absorption are temperature-dependent (Kapoor et al. 1975). Changes in water temperature have been shown to alter digestive efficiencies of other fishes (Elliott 1979), and they also may affect the efficiency of detritus digestion by gizzard shad.

In summary, gizzard shad in Acton Lake appear to selectively ingest certain components of detritus grazed from surface sediments and to digest these efficiently. This ability allows the gizzard shad to take advantage of an extremely abundant food resource. However, given the overall poor quality of detritus in this and other similar systems, gizzard shad still must process large amounts of these materials to insure adequate nutrition for normal growth and maintenance.

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