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Nutritional importance of detritivory in the growth and condition of gizzard shad in an Ohio reservoir

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Synopsis

Gizzard shad, *Dorosoma cepedianum,* in Acton Lake, Ohio, ingested foods of varying nutritional quality during the 1981–1983 growing seasons. Adult (ages 2–4) fish fed on a mixed diet (ORG>30%; C:N<7:1) of zooplankton and organic detritus in early summer, and on detrital materials (ORG<16%; C:N>11:1) during the remainder of the growing season. Age 0 (<35 mm standard length) fish ingested only detrital materials. The nutritional quality (ORG = 10 – 20%; C:N<11:1) of these foods displayed little seasonal variation, but was higher than that of organic detritus taken by adult fish in late summer and autumn. Growth and condition of gizzard shad were poor when the diet consisted of detrital materials; however, age 4 fish (1983) grew rapidly and condition improved when zooplankton were consumed. These results suggest that ingestion of poor-quality detritus can reduce the growth and condition of gizzard shad in Acton Lake, whereas the seasonal inclusion of high-quality zooplankton in the diet can result in rapid growth and improved condition.

Introduction

Detritivory is common in many freshwater fishes in the tropical areas of the world (Lowe-McConnell 1975, Bowen 1983). It is observed also in temperate freshwater species such as the gizzard shad, *Dorosoma cepedianum,* an important forage fish (e.g. Dendy 1946, Kutkuhn 1958, Dalquest & Peters 1966) in waters of the midwestern and southern portions of the United States. In systems where plankton standing crops are too low to provide an adequate food supply, gizzard shad will ingest large quantities of detrital aggregates which are obtained by filter-feeding or grazed from sediments or other substrates (Bodola 1965, Baker & Schmitz 1971, Pierce et al. 1981).

Gizzard shad constitute the main forage base for large game fishes in Acton Lake, an impoundment in southwestern Ohio (Carline et al. 1984). In this system, gizzard shad greater than 35 mm (standard length, SL) consume detrital particles and aggregates during much of the growing season (Garland 1972, Pierce 1977), and exhibit growth rates that are considerably lower than those reported for this species in other lakes and reservoirs at similar latitudes (Lagler & Applegate 1942, Lagler & Van Meter 1951, Lewis 1953, Turner 1953, Bodola 1965). As other investigators have concluded that the ingestion of low-quality detrital aggregates can contribute to the poor condition and lower growth rates of detritivorous fishes (Lowe-McConnell 1975, Bowen 1979, Persson 1983), we became interested in analyzing the effects of food quality on the growth and condition of young and adult gizzard shad in Acton Lake.

The present study was designed to address the following questions. (1) Does food quality influence the growth or condition of gizzard shad in

Acton Lake? (2) Is there a difference in the quality of foods ingested by gizzard shad of different ages in this system?

Methods

Study site

Acton Lake is a shallow (mean depth <4 m), 253-hectare reservoir on Four Mile Creek in Butler and Preble Counties (39° 30′ N), Ohio, U.S.A. It receives runoff from a predominantly agricultural, 270-km² watershed. A long-term dredging program to facilitate boat traffic began in 1983 in the very shallow (<1 m) upper end of the lake.

Gizzard shad dominate (numbers and biomass) the fish community of Acton Lake, especially in the upper reaches (N.D. Mundahl, unpublished data). Bluegill, *Lepomis macrochirus,* green sunfish, *L. cyanellus,* golden redhorse, *Moxostoma erythrurum,* golden shiner, *Notemigonus crysoleucas,* carp, *Cyprinus carpio,* and yellow bullhead, *Ictaluras natalis,* are also abundant. Major piscivores include largemouth bass, *Micropterus salmoides,* white crappie, *Pomoxis annularis,* channel catfish, *Ictalurus punctatus,* and muskellunge, *Esox masquinongy.*

Field collections

Gizzard shad were collected monthly by electrofishing from July–October, 1981, and May–November, 1982 and 1983. Collections were made in early afternoon (1200–1500 h), when maximum amounts of food are present in gizzard shad digestive tracts (Pierce et al. 1981), and were restricted to the shallow, upper end of the lake. Adult gizzard shad were collected in most months; however, age 0 fish were not collected in large numbers until September, 1981, and July, 1982 and 1983. After capture, the fish were placed on ice and later frozen in the laboratory.

To assess the nutritional value of potential food materials, Acton Lake surface sediments and Aufwuchs were collected monthly from May–November, 1982, and April–November, 1983. Samples were taken within two days of each gizzard shad collection date. To minimize variability owing to sample site, collections were restricted to the upper end of the lake. Three sediment samples were taken from similar depths (<1 m) on each date with a K.B. gravity-type core sampler. Only the upper 0.5-cm layer of each sample was retained for analysis. Beginning in July, 1982, sediments were also collected monthly with three (1982) or four (1983) sediment traps positioned across the mouth of a shallow bay. The traps collected materials settling from the water column over a period of 18 to 20 h. Each trap was equipped with a messenger-activated, spring-closure mechanism to prevent loss of sediments during retrieval.

Aufwuchs was collected from Acton Lake on the same dates as sediments. Three Aufwuchs samples were collected from concrete retaining walls, and three from submerged logs located in the major feeding areas of the fish. Samples were gently scraped from the submerged surfaces with a knife and placed in polyethylene bags filled with lake water.

Collection of zooplankton, also a potential food of gizzard shad in Acton Lake, was not included in the experimental design. However, zooplankton were collected from Acton Lake during other studies (Lewis 1984, L. Kissick & G. Walsh, Miami University, unpublished data) in the summers of 1982, 1983, and 1985. These data on zooplankton abundance and community composition served as a measure of the living animal foods available to gizzard shad in the lake during these periods.

Growth and condition

Standard lengths (SL) of gizzard shad were measured to the nearest 1 mm. Wet body weights (W) were determined to the nearest 0.1 g with an analytical balance (fish <160 g) or a triple beam balance (fish >160 g). Scales were removed from individuals in each size category for age determinations. Growth was determined from changes in SL during the 1981–1983 growing seasons. Condition factors (K) of gizzard shad before and after removal of the digestive tract were calculated with the equation, $K = 10^5 WSL^{-3}$ (W in g, SL in mm).

Growth and changes in condition of gizzard shad are not limited to changes in body morphometry. During the growing season, gizzard shad store large amounts of lipids in the viscera and muscle tissues (Fagan & Fitzpatrick 1978, Pierce et al. 1980). Lipids stored in the muscles of fish change the chemical composition of these tissues (Lagler et al. 1977). To assess seasonal changes in the chemical composition of muscle tissue resulting from lipid storage, muscle tissue samples were removed from the dorsolateral area of each fish collected during 1982 and 1983. Samples were oven-dried to constant weight at 60° C, and ground to a fine powder with mortar and pestle. Dried tissue samples (approximately 1 mg) were weighed to the nearest 0.1 μg with a Cahn automatic electrobalance (Model 25). Total organic carbon (% dry weight), total organic nitrogen (% dry weight), and a carbon to nitrogen (C:N) ratio were determined for each sample with a Carlo-Erba Elemental Analyzer (Model 1106) coupled to an Adams-Smith Data Processor (Model 2000C). Cyclohexanone (51.59% carbon and 20.14% nitrogen by weight) was used to calibrate the analyzer and data processor.

Food quality

Three Aufwuchs samples each from retaining walls and submerged logs, three sediment samples each from the traps and corer (four trap samples per month in 1982), and five food samples from gizzards of each age group of gizzard shad were analyzed monthly. Samples from gizzards were selected as representative of foods ingested by gizzard shad because, even though some enzyme activity has been detected in gizzards (Bodola 1965, King et al. 1977), little or no digestion of food materials is believed to occur in this organ (Dalquest & Peters 1966). The detritivorous South American fish, *Prochilodus platensis,* retains sand in its gizzard to grind food (S.H. Bowen, personal communication). However, food apparently is not pulverized in the gizzards of gizzard shad (Dalquest & Peters 1966, Schmitz & Baker 1969), and sand particles in the gizzard are passed into the intestine along with the food materials.

The organic contents and C:N ratios of Aufwuchs, surface sediments, and gizzard materials were used as indicators of nutritional quality. These or similar measures are commonly used to quantify the nutritional quality of foods ingested by detritivorous fishes and invertebrates (Odum 1968, Bowen 1979, 1984, Cummins 1979, Zimmerman & Wissing 1980, Mattingly et al. 1981, Lawson et al. 1984, Rasmussen 1984, Roman 1984, Valiela & Rietsma 1984). Samples were oven-dried to constant weight at 60° C and ground to a fine powder with mortar and pestle. The gizzard contents of three (>age 0) or five (age 0) fish of similar length were combined to form one food sample.

The organic contents of Aufwuchs, surface sediments, and food samples were determined by weight difference after combustion of these materials in a muffle furnace at 550° C for 3 hours (Cummins & Wuycheck 1971). Because combustion drives off the water of hydration of clay and other minerals (Weber 1973), ashed materials were moistened with distilled water and dried again to reintroduce the lost water before final weights were taken.

The carbon and nitrogen contents of Aufwuchs, surface sediments, and food samples were determined with the procedure described for muscle tissue. A C:N ratio was calculated for each sample.

Aufwuchs, surface sediments, and gizzard contents of fish in each age group were also analyzed for seasonal changes in fatty acid content. These analyses provided an additional measure of food quality and helped to identify the source of materials ingested by gizzard shad. Dried samples (5.4–537.6 mg) were weighed to the nearest 0.1 mg and placed in screw-top test tubes. Total lipids were extracted with a modification (Pierce et al. 1980) of the technique of Bligh & Dyer (1959). Lipids were hydrolyzed at 60° C for 30 minutes in 2 ml of 1.0 M potassium hydroxide:methanol (1:1). Following acidification with 2 drops of 12 N hydrochloric acid, the free fatty acids were extracted in chloroform and evaporated to dryness under a stream of nitrogen. Fatty acids were converted to their methyl esters by heating at 60° C for 30 minutes in 2 ml of 14% (weight per volume) boron trifluoride in methanol. Fatty acid methyl esters were extracted in chloroform, evaporated to dryness under a stream of nitrogen, and dissolved in 0.5 ml of analytical grade pentane. Samples (2.4–5.4 μl) were analyzed at 175° C with a Becker gas chromatograph (Model 427) on a 1.83-m (6-mm ID) glass column packed with 3% SE-30 on Gas Chrom Q. A flame ionization detector was employed to detect mass peaks. Peak areas were integrated electronically and converted to mg per g dry weight by using response factors for known standards (methyl oleate, methyl palmitate, methyl stearate).

Representative samples of Aufwuchs, surface sediments, and gizzard contents were examined with a light microscope at 25 and 100 × magnification. Organisms were identified, but no attempt was made to quantify the plant, animal, or detrital portions of these materials. However, general observations were made on the size and abundance of some items.

Statistical analyses

Statistical analyses were carried out with the Statistical Analysis System (SAS Institute, Incorporated 1982). Standard length-weight relationships were determined by regression analysis. Single-factor analysis of variance (ANOVA) and Duncan's new multiple range test were used to compare mean monthly values for each variable. Two-factor ANOVA and Newman-Keuls multiple range test (Zar 1974) were used to compare mean monthly organic contents and C:N ratios of Aufwuchs, surface sediment, and gizzard contents. Log (variables expressed as ratios) and arcsine (variables expressed as percentages) transformations of the data were made accordingly to meet the normality assumptions of the ANOVA models (Sokal & Rohlf 1981). The level of significance for all statistical tests was set at 0.05.

Results

Age and growth

Ages 0–4 gizzard shad were collected during the 1981–1983 study period. However, no more than three age groups were collected during any one year (Fig. 1). Ages 1 and 2 fish suffered major die-offs in April, 1982 and 1983, resulting in the virtual absence of these age groups in samples taken during those years. The sex ratios for ages 0–2 gizzard shad were not determined because gonads were undeveloped in most individuals. Male to female ratios of ages 3 (1982, N = 105) and 4 (1983, N = 39) fish were 1.76:1 and 2.55:1, respectively.

Growth of gizzard shad was poor throughout the study periods. Age 0 gizzard shad displayed significant increases in standard length during each collecting season, but older fish displayed significant growth only in 1983 (Fig. 1). Even when only two age groups of gizzard shad were present (much of the 1982 growing season), adult fish exhibited little growth.

The C:N ratios of muscle tissue of age 0 fish exhibited significant seasonal variation during 1982 and 1983, although the pattern and magnitude of change were identical for both years (Fig. 2). The mean muscle C:N ratio (3.2:1; SE = 0.0; N = 25) of dying age 1 gizzard shad collected in April, 1983 was significantly lower than that (3.4:1) for age 0 gizzard shad in November, 1982 (Fig. 2).

Muscle C:N ratios for age 4 fish increased more dramatically in 1983 than those for age 3 fish in 1982 (Fig. 2). Muscle tissue samples from age 4 fish collected in July and September, 1983 were saturated with lipids after oven-drying. Few tissue samples from age 3 gizzard shad in 1982 contained noticeable quantities of lipids.

Potential foods and gizzard contents

Surface sediments and Aufwuchs collected from Acton Lake contained detrital aggregates, inorganic particles, filamentous green (*Cladophora* sp., *Spirogyra* sp.) and blue-green (*Oscillatoria*

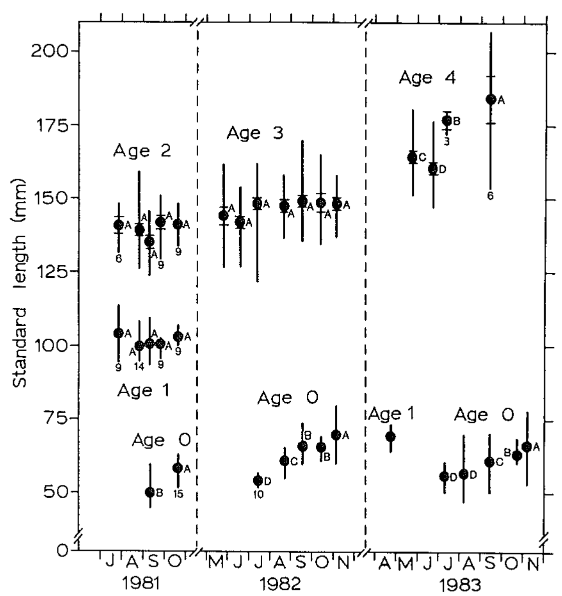

Fig. 1. Change in standard length of Acton Lake gizzard shad during the 1981–1983 growing seasons. Points are means of 15 (ages 1–4) or 25 (age 0) observations, unless otherwise indicated by numbers. Vertical lines are ranges and horizontal lines are ±1 SE. Within each age group and year, means followed by a common letter are not significantly different from each other.

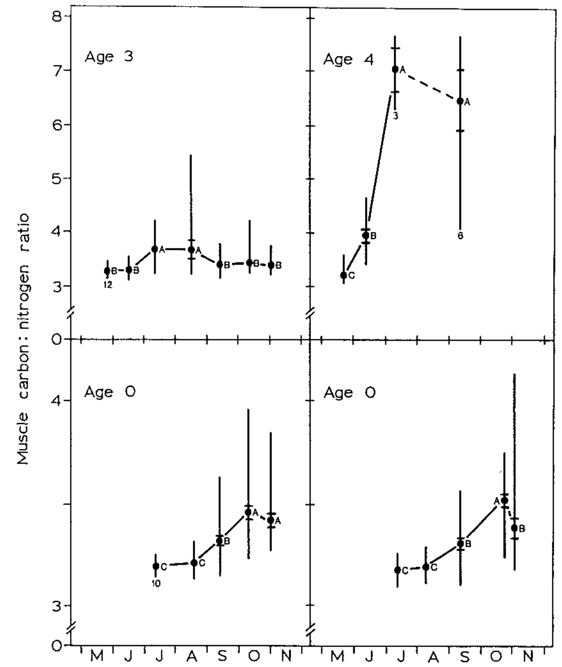

Fig. 2. Seasonal change in muscle C:N ratios of ages 0, 3, and 4 gizzard shad, 1982 and 1983. Points are means of 15 (age 3 or 4) or 25 (age 0) observations, unless otherwise indicated by numbers. Vertical lines are ranges and horizontal lines are ±1 SE. Within each age group and year, means followed by a common letter are not significantly different from one another.

sp.) algae, chironomid larvae, diatoms, ciliates, and rotifers. Sediments contained a greater proportion of inorganic particles, whereas Aufwuchs contained more algae.

Gizzards of age 0 and adult gizzard shad usually contained detrital aggregates, inorganic particles, and blue-green algae (*Oscillatoria* sp.). Detrital aggregates and algal filaments from age 0 fish (Fig. 3A) were generally smaller than those in gizzards of adult fish (Fig. 3B). In addition, gizzards of adult fish collected in early summer often contained zooplankton (Fig. 3C). Zooplankton (cyclopoid copepods and cladocerans) were usually mixed with large numbers of detrital aggregates and algal filaments. However, in June 1983, gizzards of some adult fish contained mainly crustacean zooplankton. No zooplankton were observed in the gizzards of post-larval (<35 mm SL) age 0 fish.

Surface sediments usually contained less organic matter (Table 1) and had higher C:N ratios (Table 2) than Aufwuchs. In addition, Aufwuchs contained larger quantities of the three most abundant fatty acids than did the surface sediments (Fig. 4). These data suggest that surface sediments had lower potential food value than Aufwuchs.

Juvenile and adult gizzard shad ingested materials that differed in food value. Gizzard contents of juvenile fish had C:N ratios and fatty acid contents similar to those of Aufwuchs (Table 2, Fig. 4). The organic contents of juvenile foods were lower than those of Aufwuchs, but higher than those of the surface sediments and adult foods (Table 1). Adult fish ingested foods with C:N ratios and fatty acid contents similar to those of the sediments in most months (Table 2, Fig. 4). The nutritional value of adult foods was superior to that of juvenile foods or Aufwuchs only in early summer (Tables 1, 2, Fig. 4), when adult fish ingested zooplankton.

Condition versus measures of food quality

Condition factors of age 0 gizzard shad exhibited

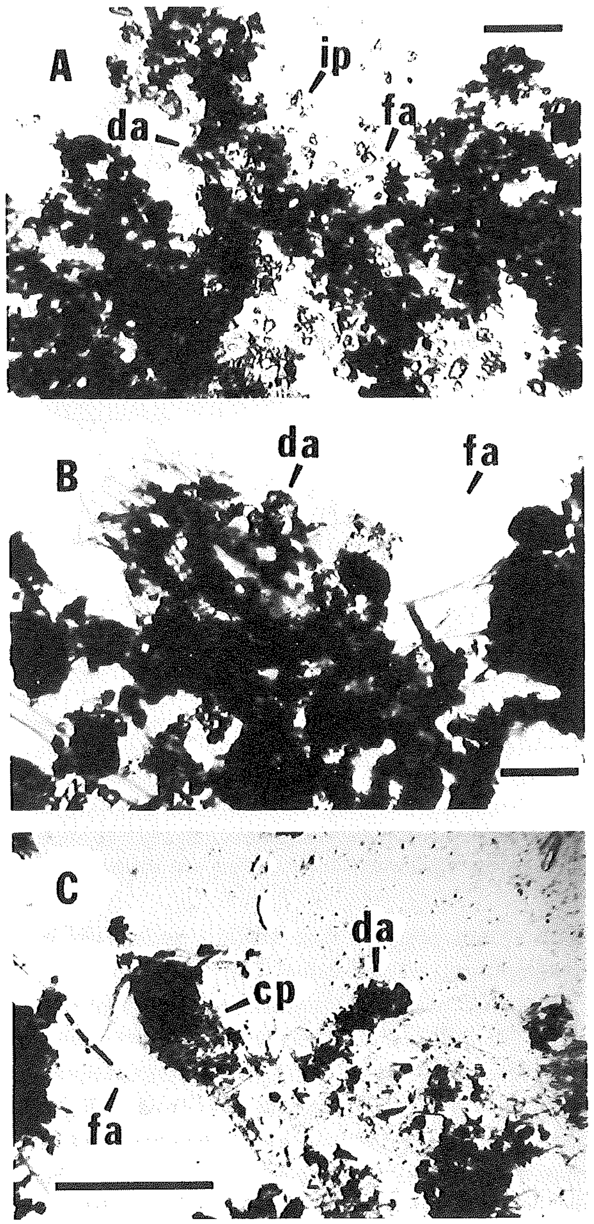

Fig. 3. Light micrographs of gizzard contents of Acton Lake gizzard shad. Scale bar = 0.1 mm (A, B) or 0.5 mm (C). A – gizzard contents of age 0 fish in August, 1982; B – gizzard contents of age 4 fish in August, 1983; C – gizzard contents of age 4 fish in June, 1983 (cp = copepod; da = detrital aggregate; fa = filamentous alga; ip = inorganic particle).

the same seasonal trends (highest in late summer, gradual decline through late autumn) in each of the three years (Fig. 5). However, no consistent seasonal patterns were observed in the quality of food taken from the gizzards of these fish. Mean food organic contents ranged from 10.8 to 27.4% of dry weight and mean C:N ratios from 5.2 to 11.7:1.

Condition factors and the quality of food materials in the gizzards of ages 1 and 2 fish did not vary significantly during 1981 (Fig. 6). The mean C:N ratios for food from ages 1 (10.6:1, Fig. 6) and 2 (11.8:1, Fig. 6) fish were significantly higher than the value (6.8:1, Fig. 5) for age 0 individuals in 1981.

Condition factors of adult (ages 3 and 4) gizzard shad increased significantly between spring and summer in 1982 and 1983, but changed little thereafter (Fig. 6). The quality of food in the gizzards of these fish changed greatly during the growing seasons. Mean food organic content decreased from spring-early summer values >30% of dry weight to late summer-autumn values <15% of dry weight. Mean C:N ratios of the food of age 3 fish in 1982 increased from <5:1 in May and June to >16:1 in August, and remained at high levels through November. Mean ratios for age 4 fish in 1983 were highly variable, ranging from <5:1 in June to >30:1 in July.

Condition factors of ages 0 (Fig. 5) and 4 (Fig. 6) gizzard shad in 1983 were significantly ($P<0.01$) positively correlated with standardized digestive tract weights (digestive tract wet weight (g) cm SL^{-1}). However, when condition factors were recalculated after subtracting digestive tract weight from wet body weight, significant seasonal trends similar to those based on total wet body weights were still evident.

As condition factors of ages 3 and 4 gizzard shad improved in mid-summer (Fig. 6), muscle C:N ratios of these fish also increased (Fig. 2), suggesting a direct relationship between condition and lipid deposition in muscles of adult shad. A similar relationship was not evident in age 0 fish. The muscle C:N ratios of these individuals increased in autumn (Fig. 2) as condition factors declined (Fig. 5).

Discussion

Effect of food quality on growth and condition

Growth rates and condition factors of gizzard shad in Acton Lake are low in comparison to values reported for the species in other systems at similar latitudes (37–43° N) (Table 3). Poor growth and condition may partly reflect the quality and quantity of foods available to the species. In systems where gizzard shad feed heavily on live foods, the species grows rapidly and has high condition factors. However, populations of gizzard shad that depend heavily on detritus (amorphous material, mud, debris, silt) often grow slowly and have low condition factors. These observations suggest that the degree to which gizzard shad feed on organic detritus, as well as the nutritional value of this material, exert some influence on the growth and condition of this species throughout its range.

Gizzard shad in Acton Lake seldom take live prey in large quantities. Previous studies of the food habits of this species in this system have shown that zooplankton are largely absent from the diets of fish larger than 35 mm SL (Garland 1972, Pierce et al. 1981). King et al. (1977) reported, however, that insect remains (exuviae and body fragments) were present in the digestive tracts of age 2 gizzard shad taken during the summer of 1975. Diatoms, phytoplankton, and filamentous green and blue-green algae are also ingested by gizzard shad in Acton Lake, but these materials generally comprise an insignificant (<5% of total volume) portion of the diet (Garland 1972, present study).

The unimportance of crustacean zooplankton in the diets of early juvenile and adult gizzard shad in Acton Lake is probably related to the low standing

Table 1. Mean (±SE) organic contents (% dry weight) of sediments from traps and corer, Aufwuchs from retaining walls and submerged logs, and gizzard contents of ages 0, 3, and 4 gizzard shad, 1982 and 1983. Monthly N = 3 (walls, logs, traps 1983, corer), 4 (traps 1982), or 5 (age 0, 3, or 4 shad), unless otherwise indicated. Values within each month followed by a common letter are not significantly different (P>0.05) from one another.

Date	Sediments		Aufwuchs		Gizzard contents	
	Traps	Corer	Walls	Logs	Age 0	Age 3 or 4
1982						
May	–	6.3(0.4)c	15.2(0.7)b	21.1(4.2)b	–	39.3(12.0)a[1]
Jun	–	4.5(0.3)c	15.8(0.8)b	22.7(2.0)ab	–	32.6(3.1)a
Jul	7.8(0.3)c	5.3(0.3)c	22.5(0.2)b	39.6(3.5)a	–	14.1(3.0)b[2]
Aug	7.4(0.6)bc	5.4(0.1)c	28.8(0.6)a	24.3(0.9)a	11.6(0.7)b	9.8(0.6)b
Sep	7.1(0.2)c	5.4(0.0)c	30.0(0.1)a	30.8(5.2)a	17.2(2.2)b	9.9(0.5)c
Oct	5.9(0.6)d	5.2(0.1)d	37.0(1.8)a	22.4(0.1)b	17.7(2.1)b	12.2(0.6)c
Nov	7.7(0.3)c	5.5(0.1)c	34.5(2.5)a	18.4(4.6)b	12.8(1.7)b	14.5(0.7)b
1983						
Apr	7.1(0.1)b	6.9(0.2)b	16.2(0.5)a	15.0(3.2)a	–	–
May	6.8(0.3)c	6.1(0.3)c	14.7(0.2)b	15.2(3.1)b	–	29.5(2.8)a
Jun	6.8(0.2)c	5.7(0.6)c	13.2(0.2)b	26.3(4.2)b	–	66.9(10.7)a
Jul	7.6(0.3)cd	6.6(0.3)d	18.7(0.9)ab	30.2(2.0)a	14.8(1.5)bc	7.1d[3]
Aug	8.0(0.2)bc	6.4(0.1)d	26.9(0.3)a	26.7(2.1)a	14.6(0.8)b	–
Sep	5.8(1.1)c	6.3(0.4)c	28.1(0.2)a	18.8(2.0)ab	10.8(0.9)bc	13.6b[4]
Oct	7.7(0.1)c	6.4(0.3)c	25.2(0.8)ab	34.8(11.2)a	18.4(0.9)b	–
Nov	9.7(0.3)b	6.2(0.3)b	24.5(0.8)a	20.9(1.7)a	22.6(5.0)a	

[1] N = 3
[2] N = 4
[3] N = 1
[4] N = 2

crops of these prey organisms during most of the summer. During the summers of 1982, 1983, and 1985, total zooplankton densities ranged generally from 400 to 1200 per liter (Lewis 1984, L. Kissick & G. Walsh, Miami University, unpublished data). The zooplankton community in the lake during these years was usually dominated (>80% by number) by small rotifers. In June 1983, however, cladocerans (*Daphnia parvula, Bosmina longirostris,* and *Diaphanosoma leuchtenbergianum*) and adult cyclopoid copepods increased dramatically and comprised 70 to 90% (by number) of the zooplankton community for a period of approximately two weeks (G. Walsh, unpublished data). Gizzard shad can capture these small crustaceans in large numbers by filter-feeding (Cramer & Marzolf 1970, Drenner et al. 1982). Thus, their appearance in the gizzards of age 4 fish in June, 1983 probably reflected the unusually high abundance of these forms in the lake at that time.

Although blue-green algae and diatoms are also abundant in Acton Lake (Lewis 1984, N.D. Mundahl, personal observation), gizzard shad in this reservoir consume these forms in low quantities (Garland 1972, present study). It is not known why the fish fail to take advantage of this abundant food source, as gizzard shad in other systems ingest large numbers of blue-green algae and diatoms (Kutkuhn 1957, Dalquest & Peters 1966). It was reported previously that gizzard shad were unable to digest blue-green algae (Valasquez 1939); however, more recent evidence (Payne 1978) suggests that fish with muscular, gizzard-like stomachs can effectively rupture and assimilate the contents of blue-green algal cells.

Because living plant or animal foods can vary seasonally in abundance, gizzard shad may often shift to organic detritus as a food source for a large portion of the growing season. Organic detritus is generally abundant and available in the reservoir

Table 2. Mean (±SE) C:N ratios of sediments from traps and corer, Aufwuchs from retaining walls and submerged logs, and gizzard contents of ages 0, 3, and 4 gizzard shad, 1982 and 1983. Monthly N = 3 (walls, logs, traps 1983, corer), 4 (traps 1982), or 5 (age 0, 3, or 4 shad), unless otherwise indicated. Values within each month followed by a common letter are not significantly different from each other.

Date	Sediments		Aufwuchs		Gizzard contents	
	Traps	Corer	Walls	Logs	Age 0	Age 3 or 4
1982						
May	–	44.1(7.7)a	12.6(1.5)b	12.5(2.3)b	–	5.5(0.7)c[1]
Jun	–	8.8(1.3)a	10.8(0.2)a	9.1(0.4)a	–	4.7(0.1)b
Jul	8.2(0.6)c	20.0(6.8)a	10.6(0.3)b	10.8(0.2)b	–	9.7(2.4)bc
Aug	13.7(0.9)a	19.7(1.5)a	7.3(0.2)b	8.9(0.3)b	7.6(0.2)b	16.3(0.9)a
Sep	8.4(0.3)b	23.7(7.0)a	7.4(1.1)b	7.6(0.3)b	6.8(0.7)b	15.5(1.2)a
Oct	10.8(0.6)ab	11.5(0.6)ab	6.3(0.4)c	7.0(0.6)bc	7.2(0.5)bc	15.1(2.0)a
Nov	20.6(2.1)b	32.2(7.9)a	7.1(0.3)c	8.7(0.6)c	8.1(1.0)c	15.3(1.6)b
1983						
Apr	27.4(4.2)a	24.2(2.2)a	13.9(0.6)b	11.8(1.3)b	–	–
May	27.1(3.1)a	35.6(9.1)a	14.3(0.1)b	14.0(0.9)b	–	7.9(0.5)c
Jun	49.0(7.8)a	37.7(6.4)a	16.2(1.4)b	10.4(1.8)b	–	4.7(0.3)c
Jul	20.3(0.8)b	39.2(11.5)a	14.1(0.3)bc	9.0(1.2)c	8.4(0.5)c	30.9a[2]
Aug	15.1(0.8)b	33.2(4.3)a	9.1(0.3)b	10.2(0.5)b	11.1(1.5)b	–
Sep	32.5(8.5)a	46.3(14.2)a	6.9(0.4)b	8.0(0.4)b	11.7(0.9)b	8.6b[3]
Oct	24.0(3.5)b	68.8(23.2)a	11.7(0.3)c	7.8(0.7)c	6.6(0.4)c	–
Nov	18.5(1.6)b	29.0(1.4)a	9.8(0.3)c	8.8(0.6)c	5.2(0.3)c	–

[1] N = 3
[2] N = 1
[3] N = 2

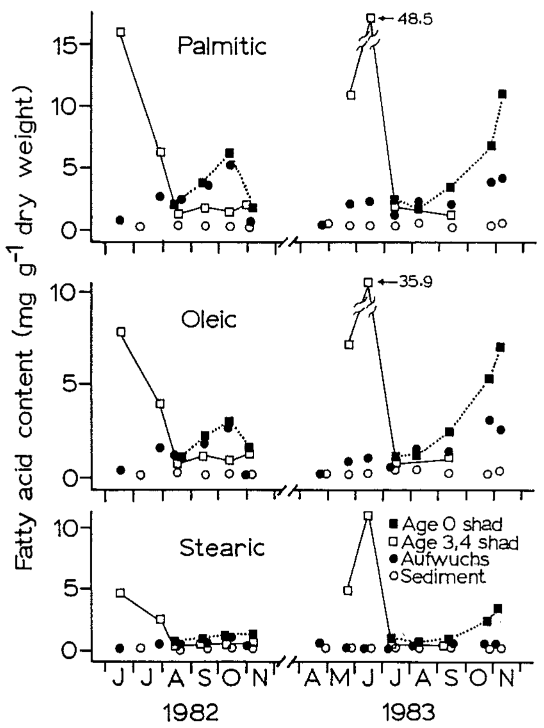

Fig. 4. Seasonal changes in the major fatty acids in Aufwuchs from retaining walls, sediment from traps, and food from gizzards of ages 0, 3, and 4 gizzard shad, 1982 and 1983.

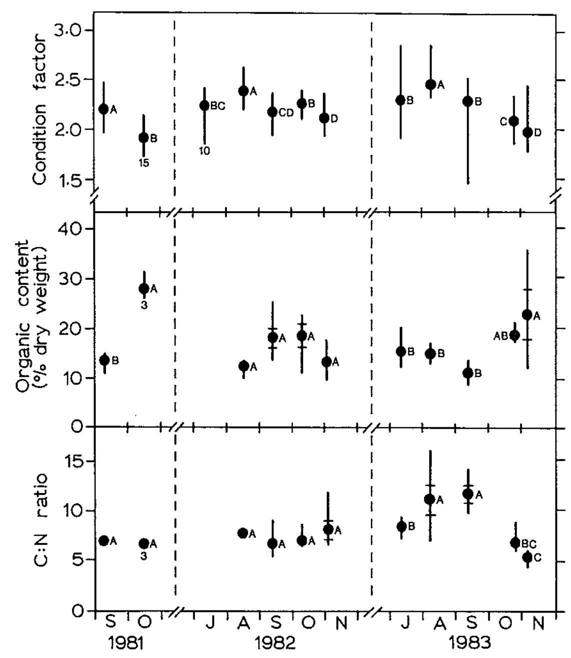

Fig. 5. Seasonal change in condition factor, and in organic content and C:N ratios of food from gizzards of age 0 gizzard shad, 1981–1983. Points are means of 25 (condition factor) or 5 (organic content, C:N ratio) observations, unless otherwise indicated by numbers. Vertical lines are ranges and horizontal lines are ±1 SE. Within each year, means followed by a common letter are not significantly different from each other.

Table 3. Mean total length at first annulus, mean condition, and diets of gizzard shad in waters of the east-central and midwestern United States.

Location	Mean total length (mm) at first annulus	Mean condition (K_{SL})	Major diet components (in order of importance)	Reference
North Twin Lake, Iowa	85	–	amorphous material, phyto-, zooplankton	Kutkuhn (1957, 1958)
Acton Lake, Ohio	95	2.15	detrital aggregates	Garland (1972), Pierce (1977), present study
Herrington Lake, Kentucky	110	2.26	–	Turner (1953)
Norris Reservoir, Tennessee	130	–	mud, debris, zoo-, phytoplankton	Dendy (1946)
Smith Mountain Reservoir, Virginia	145	2.20	silt, phyto-, zooplankton	Schneider (1969), Smith (1971)
Beaver Dam Lake, Illinois	157	2.38	–	Lagler & Van Meter (1951)
Foots Pond, Indiana	190	2.36	–	Lagler & Applegate (1942)
Lake Erie, Ohio	259	2.58	zoo-, phytoplankton, debris	Price (1963), Bodola (1965)
Mississippi River, Iowa	–	2.62	sphaeriid clams, sand, unidentified material	Jude (1973)

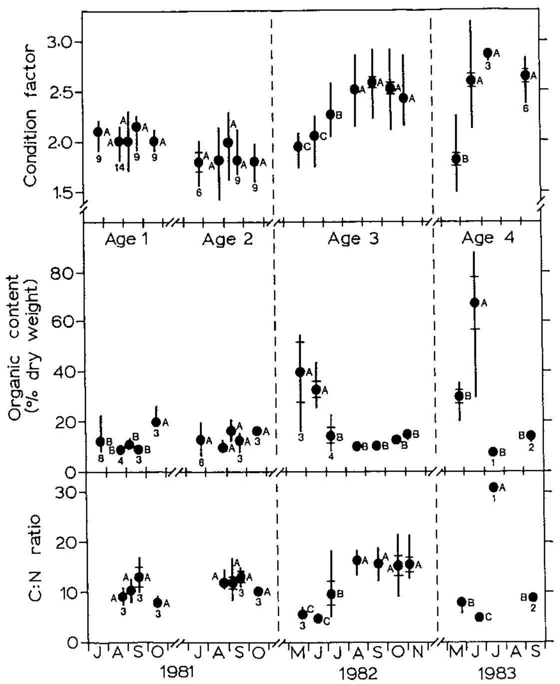

Fig. 6. Seasonal change in condition factor, and in organic content and C:N ratios of food from gizzards of ages 1–4 gizzard shad, 1981–1983. Points are means of 15 (condition factor) or 5 (organic content, C:N ratio) observations, unless otherwise indicated by numbers. Vertical lines are ranges and horizontal lines are ±1 SE. Within each year, means followed by a common letter are not significantly different from each other.

environment, but its actual nutritional value is likely to be the critical factor regulating the growth and condition of the fish. Ingestion of poor-quality detrital materials reduced growth and produced stunting in other fishes (Bowen 1979, Persson 1983), and may have a similar effect on the gizzard shad.

The nutritional quality of organic detritus ingested by the fish is determined in part by its organic (Mattingly et al. 1981) and protein or nitrogen (Bowen 1979, 1980) contents. The organic content of the detritus determines the total amount of food available for assimilation, but detritus must also contain sufficient assimilable nitrogen (C:N ratios <17:1, Russell-Hunter 1970) to support fish growth. Much of the organic nitrogen in detrital aggregates may be present in polypeptides, non-protein amino acids, or other non-protein nitrogen compounds (Parsons & Strickland 1962, Harrison & Mann 1975, Odum et al. 1979, Bowen 1980), and may not be available for assimilation by detritivores. When these measures are used as indicators of nutritional quality, it seems clear that the organic detritus ingested by gizzard shad in the present study was of poor quality. The organic contents (<20%) of the detrital foods were much lower than those (25–95%) of organic detritus consumed by gizzard shad in other systems (Dalquest & Peters 1966, Baker & Schmitz 1971, L. Knerli, John Carroll University, unpublished data), and C:N ratios frequently exceeded 16:1. The poor growth and condition of Acton Lake gizzard shad, when feeding heavily on organic detritus, suggest that the nutritional quality of this material is too low to support normal growth.

The key to rapid growth and good condition in Acton Lake gizzard shad is apparently the seasonal, if not regular, inclusion of plant or animal matter in the diet. Foods such as plankton, molluscs, leeches, insect larvae and exuviae, and fish have a much higher caloric content than organic detritus (Cummins & Wuycheck 1971, Wissing & Hasler 1971, Garland 1972, Pierce et al. 1981), and, when available and abundant, can constitute an energy-rich food source for gizzard shad. In the present study, growth was rapid, and condition and muscle C:N ratios (fat stores) improved after adult fish consumed large quantities of zooplankton. However, little growth or change in condition occurred during periods when poor-quality detrital materials dominated the diets of age 0 and adult gizzard shad. Because Acton Lake gizzard shad rely predominantly on poor-quality detritus for food, and only occasionally ingest large quantities of high-quality living foods, the fish generally exhibit poor condition and slow growth.

Relationships between fish age and food quality

Gizzard shad of ages 1–4 fed mainly on organic detritus during the summer and autumn of 1981–1983, and there was no apparent difference in the quality of the detrital materials consumed by these age groups. L. Knerli (John Carroll University, unpublished data) noted a rise with increasing age

(1–3) in the organic content of detrital food materials consumed by gizzard shad in Lake Erie; however, other data suggest no difference in the quality (organic content, C:N ratio) of foods ingested by ages 1–5 gizzard shad in this lake (Mundahl 1984). There are no quantitative data available on the quality of detritus ingested by adult gizzard shad in other reservoirs.

Comparisons of food quality suggested that age 0 gizzard shad in Acton Lake fed on Aufwuchs, whereas adult fish were highly dependent on surface sediments. Gizzards of age 0 fish consistently contained food material of better quality than that taken from yearling and adult fish. The Aufwuchs had higher organic and fatty acid contents and lower C:N ratios than the surface sediments and, hence, was a much better food source.

Despite the biochemical similarities between Aufwuchs and the food of age 0 gizzard shad, there was a major physical difference between these materials. The Aufwuchs usually contained large quantities of filamentous algae; however, these algae were rarely ingested by the age 0 fish. In fact, greater quantities of filamentous algae were generally observed in the poor-quality gizzard contents of adult fish than in the gizzards of age 0 fish.

Despite the observed differences among the ingested materials, it is possible that age 0 and adult gizzard shad obtained their food from the same source. Selective feeding or differences in feeding behavior among the age groups may have been partly responsible for the observed differences in diet quality. Some detritivorous mullets (*Mugil* spp. and *Liza* spp.) (Odum 1968, Ching 1977, Marais 1980) and the detritivorous cichlid, *Oreochromis mossambicus* (Bowen 1979), select actively for organically-rich food particles. These species use various structures in the oral cavity to sort and retain organic detritus (Odum 1968, Bowen 1979). Some investigators have suggested that the gizzard shad is also equipped anatomically for size-selective feeding. It has numerous, elongated, finely-spaced gill rakers (Schmitz & Baker 1969), that permit the fish to filter particles 70 μm or larger from the water (Drenner 1977). Gizzard shad may use these gill rakers to filter plankton from the water column (Tiffany 1921, Kutkuhn 1957, Jude 1973, Drenner et al. 1982), or to retain fine particles collected from the bottom sediments (Dalquest & Peters 1966). This species also possesses pouch-like pharyngeal organs, that may function in food accumulation and consolidation, as well as the acceptance or rejection of materials already accumulated (Lagler & Kraatz 1954, Schmitz & Baker 1969). Because interraker distances generally become greater with increased age of gizzard shad (Mummert & Drenner 1986), it is possible that the various age groups of fish select food particles of differing size and quality, even when feeding on the same material.

Feeding behavior may also influence the quality of food materials ingested by gizzard shad of all ages. In the present study, age 0 and adult gizzard shad were observed feeding on surface sediments and Aufwuchs in a manner similar to that described previously for this species (Dalquest & Peters 1966, Smith 1971) and for the detritivorous striped mullet, *Mugil cephalus* (Odum 1968, 1970). Small turbid areas were created, and suspended particles were apparently ingested, when fish contacted the submerged surfaces. Feeding movements by adult fish were more rapid and produced more turbidity than those of age 0 fish. The more vigorous feeding activity of adult fish probably disturbed coarser materials than did the activity of age 0 fish, and thus made these available as food for the older fish. Although no measurements were made, microscopic examination of adult gizzard contents revealed larger detrital aggregates and algal filaments than were observed in the gizzards of age 0 fish. Fine sediments or detrital particles provide a greater surface area for microbial growth per unit volume than large particles, and are often richer in adsorbed organic materials than coarser sediments (Newell 1965, Odum 1968, Thomas 1969, Kemp 1971, Marais & Erasmus 1977, Marais 1980). Thus, it is possible that the organic detritus ingested by age 0 gizzard shad in Acton Lake is nutritionally superior to that consumed by adult fish because it consists of smaller particles and is more heavily colonized by microbiota. Marais (1980) reported that small mullet, *Liza dumerili,* ingest smaller detrital particles than larger individuals, and that their diet is higher in fat, carbohydrate, and energy than that of larger fish.

In the present study, the quality of the organic detritus consumed by age 0 gizzard shad was higher than that ingested by adult fish. However, this higher-quality detritus did not promote rapid growth in the juvenile fish. Age 0 gizzard shad in other lakes and reservoirs feed predominantly on zooplankton and phytoplankton (Tiffany 1921, Dendy 1946, Kutkuhn 1957, Mundahl 1984), which appear to support rapid growth in this age group. In Acton Lake, age 0 fish >35 mm SL rely heavily on organic detritus as a food source during the first growing season (Garland 1972, Pierce 1977, present study). This lack of high-quality plant or animal matter in the diet appears to contribute to the slower growth of age 0 gizzard shad in Acton Lake than in other lakes and reservoirs.

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