Diet Selection and the Contribution of Detritus to the Diet of the Juvenile White Sucker (*Catostomus commersoni*)

Molly O. Ahlgren

Department of Biological Sciences, Michigan Technological University, Houghton, MI 49931, USA

Ahlgren, M. O. 1990. Diet selection and the contribution of detritus to the diet of the juvenile sucker (*Catostomus commersoni*). Can. J. Fish. Aquat. Sci. 47: 41–48.

The ash-free dry mass (AFDM) of detritus, invertebrates, and algae in the diet of juvenile white sucker (*Catostomus commersoni*) was determined by quantitative microscopy. Fish were collected from a northern Michigan pond from January through October 1986 and their seasonal diet was compared with benthc invertebrate abundance. The quantity of detritus in sucker foreguts was inversely related to benthic microcrustacean densities. In July, microcrustacean densities were high and they comprised 95% of the AFDM in foregut contents. By October, microcrustacean densities had declined to 13% of their maximum density and detritus comprised over 90% of the sucker's diet AFDM. In laboratory aquaria, sucker that were fed detritus mixed with four different densities of *Artemia* ingested significantly more detritus from diets that provided lower *Artemia* densities. In the presence of high *Artemia* densities, sucker completely rejected detritus and ingested only *Artemia*. The fact that juvenile sucker can separate detritus from invertebrates that they swallow demonstrates that detritus is not ingested incidentally. Both laboratory and field data support the hypothesis that detritus is ingested intentionally when preferred invertebrate prey are scarce.

La masse sèche sans cendre (AFDM) de détritus, le nombre d'invertébrés et le volume d'algues qui composent le régime alimentaire du jeune Meunier noir (*Catostomus commersoni*) ont été déterminés par microscopie quantitative. Les poissons ont été capturés dans un étang du nord du Michigan entre janvier et octobre 1986 et l'abondance de leur régime saisonnier en invertébrés benthiques a été comparée. La quantité de détritus trouvés dans les voies intestinales antérieures du Meunier était inversement reliée à la densité des microcrustacés benthiques. En juillet, la densité de ces microcrustacés était élevée et ceux-ci constituaient 95 % de la AFDM des contenus gastriques. En octobre, la densité des microcrustacés avait baissé à 13 % du maximum et les détritus formaient plus de 90 % de la AFDM du régime des poissons. Dans les aquariums de laboratoire, les Meuniers nourris de détritus mélangés à quatre densités différentes de *Artemia* ingéraient considérablement plus de détritus avec un régime à plus faible densité de *Artemia*. En présence de fortes densités de *Artemia* les Meuniers rejetaient complètement les détritus et n'ingéraient que *Artemia*. Le fait que les jeunes Meuniers peuvent séparer les détritus des invertébrés qu'ils avalent démontre que les détritus ne sont pas ingérés par hasard. Les données de laboratoire et les données de terrain viennent appuyer toutes deux l'hypothèse que les détritus sont ingérés intentionnellement lorsque les proies invertébrées préférées sont rares.

Received February 16, 1989
Accepted August 18, 1989
(JA060)

Reçu le 16 février 1989
Accepté le 18 août 1989

The white sucker (*Catostomus commersoni*) is one of the most widely distributed fishes in North America and can dominate fish community biomass (Keast 1966; Trippel and Harvey 1986). Despite observations that white sucker ingest amorphous detritus along with other identifiable plant and animal foods, the white sucker is generally considered to be a secondary consumer that feeds on benthic invertebrates and microcrustaceans (Eder and Carlson 1977; Lalancette 1977; Barton 1980). This apparent failure to consider detritus a potential food is not unique to studies of the white sucker. Many other presumed secondary consumer fish are known to ingest variable quantities of detritus, especially catostomids and cyprinids (Forbes 1888; Keast 1966; McNeely 1987).

Early views that detritus is indigestable, nutritionally insignificant to fish (Darnell 1967; Odum 1970) and ingested indiscriminately with invertebrates (Forbes 1888; Carl 1936; Macphee 1960) contributed to neglect of detritus as a food item. However, certain types of detritus have been shown to be 60–75% digested and assimilated by obligate detritivores and to be nutritionally adequate to support their growth (Bowen 1981; Lewis and Peters 1984). The role of detritus in the diet of omnivorous fish like the white sucker is poorly understood and needs to be assessed.

In this study I measured the ash-free dry mass (AFDM) of detritus, invertebrates, and algae present in the gut contents of juvenile white sucker throughout an annual cycle to assess whether enough detritus is present in the gut contents to be considered a potential food resource. I also examined the hypothesis that sucker ingest detritus intentionally and that the amount of detritus ingested varies inversely with the abundance of invertebrate prey.

Study Site

A 0.10-ha farm pond located in Houghton Co., MI (47°09′N, 88°40′W) served as the study site and source of fish and detritus for laboratory experiments. The pond is located at the edge of an old hay field and drains into an alder (*Alnus* sp.) marsh through tiles in an earthen dam constructed in 1971. The northeast shoreline is sheltered by a dense spruce (*Picea* sp.) grove. Groundwater discharges through a series of springs along the bottom and a small (<0.5 m^3/s low flow) permanent inlet stream that drains the field. This continuous flow prevents anoxic conditions and catastrophic fish mortality during periods of ice cover and during late summer when dense beds of *Potamogeton* sp. fill the water column. Substrate throughout the pond is sand and fine silt. Water temperatures from June through August range from 19 to 25°C throughout the water column. Four species of fish are abundant and reproduce in the pond or inlet stream: white sucker, golden shiner (*Notemigonus crysoleucas*), brook trout (*Salvelinus fontinalis*), and creek chub (*Semotilus atromaculatus*).

Materials and Methods

Fish Collection

Juvenile fish (35–70 mm standard length) were collected by seining at 3- to 4-wk intervals from May through October when the pond began to freeze and with minnow traps set under the ice in January and February. White sucker spawn in May. A length freqency distribution plotted from all fish captured in early May indicated that this size class represented the 1+ age class from May through June and 0+ fish from July through February. Hazardous ice conditions and low capture rates made sampling unsuccessful during other months. Fish were killed and iced immediately. The standard length of each fish was recorded and the entire gut was preserved in 10% formalin within 45 min. Only fish with full foreguts were analyzed. To assess diurnal variation in diet composition, a preliminary series of gut samples were collected over a 24-h period beginning at 0900 on July 30, 1982. Samples were collected at 2-h intervals from 1800 to 2400 and at 3-h intervals from 0000 to 1800.

Gut Content Analysis

Contents were removed from the anterior one fifth of the gut tract, up to the first bend, which delimits a recognizable foregut in this stomachless fish (Stewart 1926). To quantify invertebrates, foregut contents were agitated in 1 mL of distilled water in a test tube on a vortex mixer, diluted so that a 1-mL subsample contained 50–100 organisms (5–10 mL total volume), and suspended in a beaker with a magnetic stir bar. A 1-mL subsample was removed with a pipet and placed in a Sedgwick–Rafter counting cell (S-R cell). The entire S-R cell was scanned through a light microscope at 25×. A drawing tube calibrated against a stage micrometer was used to trace invertebrate outlines to scale on paper. The 1-mm depth of the S-R cell preserved the three-dimensional shape of food particles. In the case of foreguts containing fewer than 50 invertebrates, all foregut material was placed in the S-R cell.

The number of detritus particles in foregut contents greatly exceeds the number of invertebrates. Consequently, to quantify detritus, the first subsample was rinsed from the S-R cell back into the sample beaker and the entire sample was further diluted to 100–300 mL total volume with distilled water. A second 1-mL subsample was transferred to the S-R cell. Four or five transects, each comprising 5% of the S-R cell area, were scanned at 160× (phase contrast) until 50–100 detritus particles were counted and their outlines traced. Algae were similarly traced. Items recognized as inorganic matter, i.e. sand, were excluded from the analysis.

A single count of 50–100 items is an adequate sample of foregut contents, since the precision and accuracy associated with a single count can be estimated for randomly distributed particles that follow a Poisson distribution. Counts of 50–100 vary no more than 20–25% of the true value at the 95% significance level (Lund et al. 1958). Accuracy depends entirely on the size of the count and varies indirectly with the square root of the number counted (Lund et al. 1958). Consequently, counts 2–3 times greater than 100 do little to increase accuracy, but counts below 50 are subject to significantly greater statistical error. Analysis of counts of detritus particles and algae present in 1-mL subsamples of diluted gut contents indicated that particles were randomly distributed throughout both the sample beaker and the S-R cell (chi-square test for randomness, $p<0.05$; Lund et al. 1958).

Volumes of detritus, invertebrates, and algae were determined by measuring the length and width of each particle and calculating the volume of a similarly shaped geometric solid. Length was defined as the longest axis, and width was measured perpendicular to particle length at its midpoint. Preliminary measurements taken with a calibrated fine-focus adjustment on a light microscope confirmed that particle width closely approximated vertical height for detritus from a variety of sources. Detritus particles and diatoms shaped similarly to *Navicula* sp. were considered prolate spheroids, which slightly overestimated diatom volume. Diatoms were a small part of the diet, however, and overestimates were not expected to affect overall conclusions. Chironomid larvae and copepod volumes were calculated as cylinders and cladocerans as elliptical disks. Other invertebrate taxa were rarely encountered and could be classified as one of the previous geometric shapes or a sphere. The tracings were measured on a digitizer, and a microcomputer automatically calculated the appropriate volumes. The coefficient of variation associated with tracing and digitizing food items was <5% (M. O. Ahlgren, unpubl. masters thesis (1984)).

Estimates of the volume of detritus and invertebrates in the gut contents were converted into estimates of AFDM with conversion factors determined by direct measurement of detritus particles and invertebrates collected from the pond. The AFDM of detritus, invertebrates, and diatoms in the foregut samples was standardized relative to fish wet weight and expressed as milligrams of diet component per gram of fish. Seasonal differences in the quantity of diet components were analyzed by a Kruskal–Wallis ANOVA and nonparametric multiple comparisons (Conover 1980).

Conversion Factors

Weight/volume conversion factors were determined on 10 groups of chironomid larvae and 4 groups of cladocerans. The volume of invertebrates in each group was determined by microscopy. AFDM was calculated as dry mass lost after combustion at 550°C for 1 h. Each group of invertebrates was dried 24 h at 105°C in preashed aluminum pans, cooled in a desiccator, weighed to 0.01 mg on a Cahn microbalance, ashed in a muffle furnace, cooled, and reweighed. The average dry weights of 125.4 μg/chironomid and 1.5 μg/cladoceran were within the range of values for these taxa reported by others (Hall et al. 1970; Dumont et al. 1975). Chironomids and cladoceran AFDM was 80 and 90% of the dry mass, respectively. The resulting conversion factors were 0.1390 mg chironomid AFDM/mm^3 and 0.0514 mg cladoceran AFDM/mm^3.

The upper 2–4 mm of detritus from the sediment surface and from submerged macrophyte leaves was drawn by suction through a latex tube into an evacuated 1-L Erlenmeyer sidearm flask and preserved in 10% formalin. The volume of detritus in each sample was determined by quantitative microscopy. AFDM of the sample was calculated after ashing dried subsamples in a muffle furnace 1 h at 550°C. Detritus ranged from 31.8 to 35.6% AFDM. The resulting AFDM/volume conversion was 0.220 mg/mm^3 (SE = 0.0009, n = 5).

A diatom conversion of 0.2419 mg AFDM/mm^3 was derived from the average AFDM reported for 11 species of diatoms (Nalewajko 1966). To calculate AFDM of filamentous diatoms such as *Fragilaria* sp., *Tabellaria* sp., and *Melosira* sp., the number of cells per filament was conducted and converted to AFDM using AFDM/cell conversions derived from Nalewajko (1966).

Invertebrate Abundance

Benthic invertebrates were sampled every 3–4 wk from April through October 1986 from the inlet bay of the pond which consistently contained the highest densities of juvenile sucker. Samples from this habitat were considered to best reflect trends in the abundance of invertebates consumed by juvenile sucker. This section ranged in width from 5 to 25 m and had a maximum water depth of 130 cm.

Samples were collected along five transects, beginning 0.5 m from shore and extending toward the center of the bay. Transects were 10 m apart. Four samples were collected at 1.5-m intervals along each transect. Samples within each transect were pooled so that each sample represented the mean of four cores. Each transect incorporated the two main habitat types in the bay: sandy shoreline *Typha* sp. beds and central silty *Potamogeton* sp. beds.

The samples were collected with Plexiglas tubes (57-mm inner diameter, 33 cm high) inserted 10–20 cm into the sediment and immediately plugged at the top and bottom with a No. 12 solid rubber stopper. The upper 10–15 mm of the sediment core and all overlying water were removed with a syphon, collected on a 250-μm sieve, and rinsed into plastic bags with 80% ethanol. A small amount of rose bengal stain was added to the ethanol to facilitate invertebrate enumeration. Invertebrates <250 μm were not collected because they comprised <5% of the invertebrate AFDM observed in sucker foregut contents.

The sample was diluted with water to a total volume of 1 L and suspended in a magnetically stirred beaker. Five 10-mL subsamples were removed from the beaker with a wide-mouth pipet and transferred to a petri plate marked with a bottom grid. The entire plate was scanned at 35 × with a binocular dissecting scope and the invertebrates were identified to subclass, order, or family.

Intentional Ingestion

To evaluate the hypothesis that juvenile sucker ingest detritus intentionally and that the quantity ingested varies inversely with the abundance of invertebrate prey, I examined foregut contents of individuals offered diets of detritus combined with four densities of brine shrimp (*Artemia*). Each diet was fed to five groups of three sucker (average 45.6 mm SL and 1.29 g wet weight) contained in aerated, 2.5-L, 18-cm bottom diameter plastic pails. Two centimetres of washed sand covered the bottom of each pail. The depth of detritus over the sand substrate was approximately 5 mm, equal to half the height of the sucker's head. This quantity of detritus greatly exceeded the amount that sucker could ingest during the experimental feeding period.

TABLE 1. Mixtures of *Artemia* and detritus presented to juvenile white sucker in aquaria.

	Ration 1	Ration 2	Ration 3	Ration 4
Artemia as % dry mass	0.09	0.04	0.02	0.0
Artemia as % AFDM	0.5	0.2	0.1	0.0
Artemia, μg dry mass/cm^2	57.3	22.9	11.4	0.0
Artemia, μg dry mass/L	5819	2328	1164	0.0
Artemia, number/L	2530	1012	506	0.0
Artemia, number/cm^2	25	10	5	0.0
Detritus AFDM as % dry-mass	18.4	18.4	18.4	18.4

Detritus was collected from the littoral zone of the study site, sieved, and the <45-μm fraction allowed to settle into a dense layer. Excess water was decanted, the detritus sample was suspended as 900 mL total volume in a beaker with a magnetic stir bar, and 45-mL aliquots were removed with a volumetric pipet and placed in beakers.

Artemia were cultured from eggs in aerated salt water for 48 h at 22°C. Live *Artemia* were rinsed with tap water and added to 45-mL aliquots of concentrated detritus at the rations listed in Table 1. Ration composition was calculated from mean values of 2.3 μg dry mass/*Artemia* (SE = 0.03) and 1.7 μg AFDM/*Artemia* (SE = 0.03) determined from nine replicate groups of 160 – 250 rinsed *Artemia* according to the procedure described above for cladoceran and chironomid conversion factors. A detritus organic content of 18.4% was determined using a muffle furnace.

The fish fed 4 h, starting at 1400, and were then killed. The entire gut was removed and preserved in 10% formalin. The AFDM of detritus present in the foreguts was determined by microscopy as previously described. *Artemia* of a uniform size were the only invertebrates ingested. Thus, the number of *Artemia* in each foregut was estimated and multiplied by 1.7 μg ADFM/*Artemia* to determine ADFM.

Sucker were observed while they fed in laboratory aquaria and in the pond. Individual maneuvers, body position, and orientation to other fish were described.

Results

Diurnal Diet Composition

No diurnal changes in diet composition or feeding intensity were evident throughout the 24-h diet survey of July 30–31, 1982. Fish with full foreguts were always captured. All fish contained detritus, 97% contained invertebrates, and 63% contained algae, mainly diatoms and desmids. Detritus consisted of amorphous particles 20–80 μm long, with occasional recognizable plant fragments. Quantities of the three food types varied widely among individuals collected at the same time (Table 2) and did not differ between sample periods, or when sample periods were combined to correspond to periods of daylight, night, dawn, and dusk (Friedman test, $p > 0.75$) (Zar 1984). Diet composition in late July 1982 was similar to that in early August 1986 (Fig. 1; Table 2). Algae was a small part of the diet AFDM (3%), while detritus (43%) and invertebrates (54%) made similar contributions to diet AFDM.

TABLE 2. Diet composition for white sucker collected throughout a 24-h period beginning on July 30, 1982. Confidence limits (95%) for mean total AFDM are 23.2–31.6.

Time	Standard length (mm)	Foregut contents (mg AFDM/g fish)	% of AFDM		
			Detritus	invertebrates	Algae
0900	54	0.215	37.1	62.9	0.0
0900	57	0.138	39.6	57.7	2.7
0900	54	0.363	36.9	63.1	0.0
0900	60	0.183	58.2	41.8	0.0
1200	60	0.228	80.0	91.7	0.3
1200	62	0.146	72.2	26.8	0.4
1200	60	0.378	25.0	75.0	0.0
1200	66	0.646	65.8	34.2	0.0
1500	58	0.283	49.5	50.5	0.0
1500	64	0.246	68.9	31.1	0.0
1500	64	0.434	48.4	51.2	0.3
1500	66	0.525	97.2	00.0	2.8
1500	62	0.104	81.1	18.9	0.0
1800	65	0.114	47.2	47.9	4.8
1800	65	0.289	25.6	70.5	3.8
2000	62	0.130	47.7	52.3	0.0
2000	58	0.302	60.4	39.6	0.0
2000	58	0.222	33.4	66.6	0.0
2200	62	0.258	25.3	26.0	72.2
2200	62	0.261	11.9	87.4	0.6
2400	53	0.469	27.2	72.9	0.0
2400	58	0.106	36.0	96.4	0.0
2400	60	0.803	22.0	70.8	8.9
2400	62	0.237	51.4	48.6	0.0
0300	56	0.545	83.3	16.7	0.0
0300	62	0.391	54.0	94.5	0.2
0300	65	0.093	23.8	74.9	1.4
0600	65	0.091	10.9	89.1	0.0
0600	53	0.095	43.2	56.8	0.0
0600	57	0.263	83.2	16.8	0.0
Mean	60	0.274	43.1	53.6	3.3
Median	60	0.241	41.4	54.6	0.0
Range	(53–68)	(0.037–0.803)	(3.6–97.2)	(0.0–96.3)	(0.0–72.2)

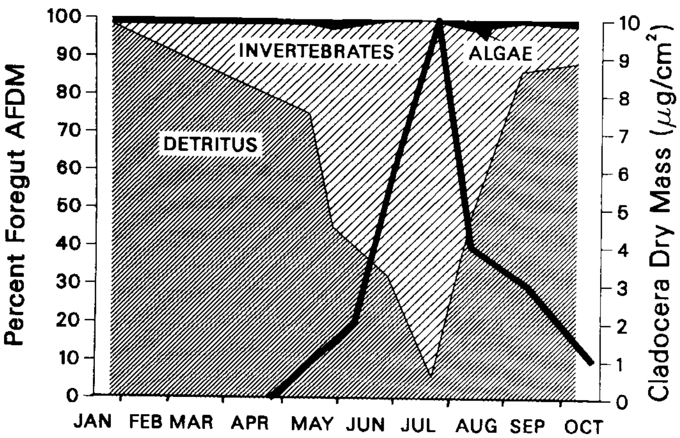

FIG. 1. Seasonal changes in diet composition of white sucker (shaded, median %AFDM, n = 15) and biomass of cladocerans in the sediment (solid line).

Seasonal Diet Composition

Diet composition varied significantly with season in 1986. The quantity of foregut detritus in September and October was greater than other nonwinter sample dates ($p < 0.05$, Table 3) and comprised 88 and 90% of the diet AFDM (Fig. 1). The quantity of foregut detritus in July was less than on all other sample dates ($p < 0.01$, Table 3) and accounted for only 5% of the diet AFDM (Fig. 1). Invertebrate AFDM increased consistently from January to a July peak when it comprised 95% of the diet AFDM (Fig. 1) and was greater than at all other sample dates ($p < 0.01$, Table 3). Invertebrate AFDM decreased steadily from August through October and was completely absent from the diet in January and February. Algae contributed less than 2% of diet AFDM in all seasons (Fig 1).

Benthic microcrustaceans, mainly cladocerans (Macrothricidae), comprised 100% of the invertebrate AFDM in September and October diets and varied between 80 and 90% of the invertebrate AFDM ingested at other times of the year. Similarly, benthic microcrustaceans made up 70% of the invertebrate AFDM ingested throughout the 24-h survey in 1982. Copepodite and nauplius stages of copepods accounted for <3% of the microcrustacean AFDM ingested. The remaining invertebrate AFDM consisted of chironomids and other dipteran larvae although occasional dipteran pupae, rotifers, and nematodes were observed. Several fish contained *Elodea* seeds in October but they were not a dominant diet component. Protozoan (Difflugiidae) casts were observed sporadically from July through October. It was impossible to detect naked protozoans or to distinguish empty and full casts; therefore, protozoan AFDM is included in detritus throughout this analysis.

TABLE 3. Diet composition for white sucker collected from January 29 to October 9, 1986. Data are mean standard length (SE) and median AFDM of detritus, invertebrates, and algae in sucker foreguts (range). Within each column, values followed by the same letter are not significantly different (Kruskal–Wallis ANOVA and multiple comparisons, p ⟨0.05).

Date	n	Length (mm)	mg AFDM/g fish wet weight			
			Detritus	Invertebrates	Algae	Total AFDW
Jan. 29 and 30, Feb. 24	10	42 (6.3)	0.201 c (0.06–1.74)	0.000 a (0.000–0.000)	0.002 b (0.000–0.008)	0.207 ab (0.057–1.74)
May 15	7	49 (2.8)	0.125 b 0.888–0.226)	0.016 b (0.006–0.279)	0.001 ab (0.000–0.006)	0.180 a (0.125–0.493)
May 28	15	48 (4.0)	0.154 b (0.002–0.382)	0.119 c (0.009–0.411)	0.008 ab (0.000–0.105)	0.323 abc (0.048–0.668)
June 30	10	70 (4.6)	0.103 b (0.004–0.450)	0.116 c (0.065–0.872)	0.000 ab (0.000–0.006)	0.282 abc (0.105–0.953)
July 22 and 23	15	39 (3.9)	0.020 a (0.003–0.044)	0.370 d (0.173–1.33)	0.000 a (0.000–0.004)	0.390 c (0.210–1.37)
Aug. 6 and 13	15	49 (6.4)	0.096 b (0.016–0.429)	0.093 c (0.000–0.028)	0.003 b (0.006–0.527)	0.212 ab (0.058–0.629)
Sept. 9	15	49 (6.7)	0.294 c (0.123–1.03)	0.034 b (0.003–0.178)	0.002 b (0.000–0.017)	0.357 bc (0.153–1.06)
Oct. 7 and 9	15	50 (4.0)	0.300 c (0.070–2.68)	0.033 b (0.000–0.164)	0.001 b (0.000–0.099)	0.340 abc (0.076–2.87)

TABLE 4. Availability of benthic invertebrates from April through October, 1986. Values are expressed as μg dry mass/cm^2 substrate (range) and represent the median of five replicates. Within each column, values followed by the same letter are not significantly different (Kruskal–Wallis ANOVA and multiple comparisons, p ⟨0.05).

Date	Chironomidae	Cladocera	Copepoda	Nauplii	Total invertebrates	Total benthic microcrustaceans
Apr. 26	99 b (50–182)	0 a (0–2)	0 a (0–8)	0 ab (0–0.1)	106 abc (51–184)	1 a (0–8)
June 9	165 b (99–198)	2 ab (1–4)	13 b (9–28)	0 c (0–0)	194 c (123–214)	16 c (10–20)
July 1	165 b (66–363)	6 d (3–9)	23 b (15–31)	0 c (0–0)	189 c (87–398)	26 c (21–37)
July 23	99 b (0–297)	10 d (3–19)	15 b (4–19)	0 bc (0–0)	118 abc (7–326)	26 c (7–26)
Aug. 12	66 a (33–66)	4 cd (3–6)	4 a (3–7)	0 a (0–0)	74 a (39–76)	9 b (6–11)
Sept. 12	165 b (66–363)	3 bc (1–4)	4 a (0–7)	0 a (0–1)	174 bc (77–368)	9 ab (1–11)
Oct. 17	99 b (33–165)	1 a (1–2)	0 a (0–0)	0 a (0–0)	106 ab (36–170)	4 ab (2–6)

Seasonal Availability of Benthic Invertebrates

The biomass of cladocerans present in the upper 10–15 mm of pond sediment peaked in late July. Throughout July, cladoceran abundance was significantly greater than during other sample dates except August (Table 4). Copepod densities appeared to peak by early July, dropped substantially after July, and remained low for the rest of the year. The biomass of chironomids greatly exceeded the biomass of benthic microcrustaceans and showed no significant seasonal variation (Table 4). Representatives of Nematoda, Oligochaeta, Ostracoda, and Rotatoria were abundant in the core samples, but were rarely ingested by sucker; therefore, they are not included in Table 4.

Selective Ingestion Experiments

Sucker ingested more detritus and less *Artemia* from experimental diets of mixed detritus/*Artemia* that provided lower *Artemia* densities (Newman–Keuls test, $p < 0.05$, Fig. 2). The AFDM of both *Artemia* and detritus ingested from diet 1 (highest *Artemia* density) differed from other diets ($p < 0.05$, Fig. 2) and comprised 99.5 and 0.5% of the ingested diet AFDM,

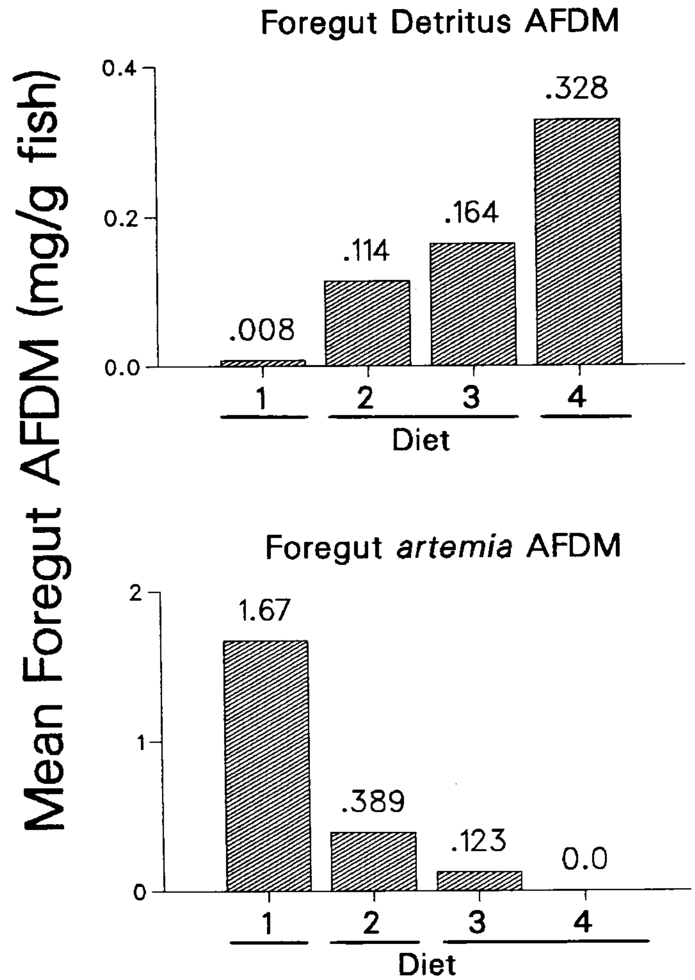

FIG. 2. Detritus, *Artemia*, and total AFDM present in the foreguts of white sucker fed detritus combined with the following rations of *Artemia* (μg dry mass/cm^2 substrate): diet 1 = 57, diet 2 = 22, diet 3 = 11, diet 4 = 0. Values connected by a line are not significantly different ($p > 0.05$).

respectively. Total AFDM ingested from diet 1 was higher than from diets 2–4 ($p < 0.05$) which did not differ. The AFDM of detritus consumed in the absence of *Artemia* was approximately 20% of the AFDM consumed by sucker fed the highest concentration of *Artemia*.

Feeding Behavior

Juvenile sucker exhibited two distinctive feeding behaviors: spitting and filtering. During the spitting maneuver, fish in the field and in laboratory aquaria aggressively bite into the sediment. This activity left distinct circular feeding marks 3–5 mm deep on the bottom of laboratory aquaria, a depth approximately half the height of the sucker's head. Sucker appeared to manipulate food inside their oral cavity before spitting debris out the mouth. Sucker in laboratory aquaria also skimmed sediment from the surface with a series of shallow bites and expelled debris from the opercular opening ("filtering").

Discussion

Detritus was a quantitatively important component of juvenile sucker foregut contents in all seasons sampled except midsummer. Seasonal variation in diet composition appears to be inversely correlated with variations in the abundance of invertebrate prey. Both laboratory and field results indicate that juvenile white sucker ingest more detritus as the availability of benthic microcrustaceans decreases. The proportion of detritus in the foreguts of sucker fed detritus mixed with different densities of *Artemia* was inversely proportional to the *Artemia* density of experimental diets. (Fig. 2). The spring shift from detritus to an invertebrate diet and the fall shift back to detritus corresponded to the summer increase and fall decrease in the abundance of benthic microcrustaceans (Fig. 1).

Changes in benthic cladoceran densities appeared to influence the sucker's diet composition more than changes in the abundance of other benthic invertebrates. Sucker consumed the greatest quantity of invertebrates during late July when cladoceran densities were greatest. Copepod abundance peaked 3–4 wk earlier at twice the cladoceran peak density. Chironomid densities did not appear to influence diet composition. Cladocera was the main invertebrate group ingested by juvenile sucker in all seasons. Others have stated that juvenile white sucker prefer cladocerans compared with copepods or benthic insect larvae (Lalancette 1977; Barton 1980). Sediment-dwelling cladocerans swim sluggishly at the water sediment interface (Brooks 1965) and are probably more vulnerable to sucker predation than strongly swimming copepods or burrowing, tube-building chrionomid larvae.

Juvenile sucker appear to ingest detritus intentionally. They entirely rejected detritus and consumed only *Artèmia* from an experimental diet that provided both *Artemia* and detritus ad libitum (Fig. 2). The fact that sucker can separate detritus from the invertebrates they swallow suggests that detritus ingested from the other diets was intentional, not incidental. Alternatively, sucker may not be able to efficiently separate invertebrate prey from detritus if the density of invertebrate prey is low. In a preliminary experiment, detritus used to make the experimental diets was accidentally allowed to go anoxic; sucker rejected detritus from all diets and consumed only *Artemia*. This observation supports the idea that detritus ingested from diets with low *Artemia* densities was not incidental and therefore was ingested intentionally. Other detritus-consuming omnivorous fish consume mainly invertebrates during periods of high invertebrate abundance (Persson 1983; Weisberg and Lotrich 1986; Prejs and Prejs 1987). The seasonal absence of detritus in the diet of these fish suggests that they can also exclude detritus from invertebrates that are swallowed and that detritus is ingested by choice during periods of low invertebrate prey availability.

The spitting and filtering behaviors suggest that sucker sort food in their bucal cavity. This region appears highly adapted to discriminante and sort food items. Dense rows of sensory papillae and taste buds line the lips, mouth, gill arches, and thick fleshy palatal organ which forms the roof of the pharynx (Stewart 1926). External morphology of the brain reflects greater development of taste and touch within the oral cavity relative to the lips and skin (Miller and Evans 1965). Rows of fleshy, papillose, plate-shaped gill rakers interdigitate forming a variable meshed sieve similar to other catostomids (Weisel 1962; Dunham et al. 1979.)

Sucker appear to glean invertebrates from detritus by spitting. In response to gustatory and tactile stimuli, the gill rakers and palatal organ probably maneuver invertebrates until pinned between the palatal organ and comblike pharyngeal teeth (Eastman 1977). When the palatal organ contracts, the pharynx constricts and gill rakers, interdigitate tightly, blocking external gill openings. Unwanted debris is ejected out the mouth and invertebrates swallowed whole. Sucker appear to filter detritus through gill rakers. Filtering may enable sucker to discard large particulate debris or heavy inorganic material. Detritus particles as large as the invertebrates and sand grains were rare in gut contents.

Short-term individual variation characterizes all aspects of fish foraging behavior (Ringler 1983) and was evident in the diet composition of this sucker population over diurnal (Table 2) and seasonal cycles as evidenced by the standard error associated with diet composition of individuals collected on the same date (Table 3). Variation among individuals was greatest when invertebrate densities in the pond were intermediate and sucker ingested substantial quantities of both detritus and invertebrates. Individual variation decreased when sucker ingested primarily detritus or invertebrates (Table 3) which corresponded to periods of low and high invertebrate abundance. This pattern of variability may reflect the patchy distribution of preferred foods and opportunistic feeding by omnivorous fish. The ability to use many different foods effectively is an important characteristic of ubiquitous species (Lowe-McConnell 1975, p. 210) and has probably contributed to the white sucker's widespread distribution.

Juvenile sucker appear to gorge themselves on unlimited invertebrates but not on detritus. They ingested 5 times more AFDM from experimental diet 1 (ad libitum *Artemia* and detritus) than sucker fed diet 4 (ad libitum detritus alone). The total AFDM consumed by sucker in the pond was similar to the AFDM ingested from diets 2–4 but much lower than that ingested from diet 1 (Fig. 2; Table 3). The *Artemia* biomass provided by diet 1 may have been unnaturally high and could explain the apparent discrepancy between the maximum AFDM consumed by fish fed diet 1 and fish in the pond. The *Artemia* biomass provided by diet 1 was approximately 2 times greater than the highest microcrustacean biomass value measured in the pond. However, the *Artemia* biomass in diets 2–4 was similar to the microcrustacean biomass measured in the pond (Tables 1 and 4). The limited availability of invertebrate prey in the pond may have prevented sucker from gorging on invertebrates. Alternatively, *Artemia* provide approximately 4 times more AFDM per unit dry weight than detritus. A foregut filled with *Artemia* would be expected to contain much more AFDM than one filled with detritus.

There are several reasons why sucker may not gorge on detritus. Specific amino acids are known to stimulate short-term appetite in fish (Fletcher 1984). Detritus typically contains low concentrations of amino acids (Bowen 1987) and may not strongly stimulate appetite. Many gustatory and olfactory stimuli inhibit fish feeding (Fletcher 1984). The fraction of fine particulate detritus derived from fragmentated plant debris retains secondary metabolites such as phenolic acids which may deter feeding through changes in acidity or noxious flavors they give detritus (Valiela and Rietsma 1984). Although copious quantities of detritus are always present, the quantity of palatable detritus may be limited.

Detritus typically contains much less protein and energy per unit AFDM than invertebrates and is less digestible (Bowen 1987). Assimilation efficiencies determined for a variety of aquatic detritivores averaged 0–40% whereas invertebrates are usually assimilated with 80–100% efficiency (Valiela 1984). Although the efficiency with which sucker assimilate nutrients from detritus relative to invertebrates has not been well studied, invertebrates appear to be a higher quality food than detritus. The fact that sucker clearly prefer invertebrates is not surprising; however, the fact that they choose to ingest detritus at certain times of the year suggests that detritus is nutritionally valuable. The exact nature of this nutritional benefit is unknown.

Most energy and materials in freshwater and marine ecosystems enter food webs as detritus rather than as living plant material (Mann 1988). Studies of the trophic basis of fish production have often overlooked the potential direct contribution of detritus to fish production and have focused on benthic invertebrates as necessary intermediates in the conversion of detritus to fish biomass (Lotrich 1973; Horwitz 1978; Eggers et al. 1978; Boisclair and Leggett 1985). Results presented here show that juvenile white sucker ingest detritus intentionally and that detritus can comprise a large part of the diet when invertebrate prey are the least abundant. Future studies that assess the nutritional contribution of detritus to the diet and its ability to support the growth of white sucker as well as other fish species are necessary for a more complete understanding of the trophic basis of fish production.

Acknowledgements

I am grateful to Dr. Stephen H. Bowen for many helpful suggestions throughout this study. N. Auer and R. Creed, N. H. Ringler, and one anonymous referee provided helpful comments on the manuscript.

References

BARTON, B. A. 1980. Spawning migration, age, growth, and summer feeding of white and long nose suckers in an irrigation reservoir. Can. Field-Nat. 94: 300–304.

BOISCLAIR, D., AND W. C. LEGGETT. 1985. Rates of food exploitation by littoral fishes in a mestrophic north-temperate lake. Can. J. Fish. Aquat. Sci. 42: 556–566.

BOWEN, S. H. 1981. Digestion and assimilation of periphytic detritial aggregate by *Tilapia mossambica*. Trans. Am. Fish. Soc. 110: 239–245.

1987. Composition and nutritional value of detritus, p. 192–216. *In* D. J. W. Moriarity and R. S. V. Pullin [ed.] Detritus and microbial ecology in aquaculture. ICLARM Conference Proceedings 14. 420 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

BROOKS, J. L. 1965. Cladocera, p. 587–656. *In* W. T. Edmondson [ed.] Freshwater biology. John Wiley & Sons, Inc., New York, NY.

CARL, G. C. 1936. Food of the coarse-scaled sucker (*Catostomus commersoni* Girard). J. Biol. Board Can. 3: 20–25.

CONOVER, W. J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley & Sons, Inc., New York, NY. 493 p.

DARNELL, R. M. 1967. The organic detritus problem, p. 397–407. *In* G. H. Lauff [ed.] Estuaries. American Association for the Advancement of Science. Publication 83, Washington, DC.

DUMONT, H. J., I. VAN DE VELDE, AND S. DUMONT. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19: 75–97.

DUNHAM, A. E., G. R. SMITH, AND J. N. TAYLOR. 1979. Evidence for ecological character displacement in Western American catostomid fishes. Evolution 33: 877–896.

EASTMAN, J. T. 1977. The pharyngeal bones and teeth of catostomid fishes. Am. Midl. Nat. 97: 68–88.

EDER, S., AND C. A. CARLSON. 1977. Food habits of carp and white suckers in the South Platte and St. Vrain Rivers and Goosequill Pond, Weld County, Colorado. Trans. Am. Fish. Soc. 106: 339–346.

EGGERS, D. M., N. W. BARTOO, N. A. RICKARD, R. E. NELSON, R. C. WISSMAR, R. L. BURGNER, AND A. H. DEVOL. 1978. The Lake Washington ecosystem: the perspective from the fish community production and forage base. J. Fish. Res. Board Can. 35: 1553–1571.

FLETCHER, D. J. 1984. The physiological control of appetite in fish. Comp. Biochem. Physiol. Vol. 78A: 617–628.

FORBES, S. A. 1888. On the food relations of fresh-water fishes. *In* F. N. Egerton [ed.] History of ecology. Vol. II. Arno Press, New York, NY. 437 p.

HALL, D. J., W. E. COOPER, AND E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839–928.

HORWITZ, R. J. 1978. Temporal variability patterns and the distribution patterns of stream fishes. Ecol. Monogr. 48: 307–321.

KEAST, A. 1966. Trophic interrelationships in the fish fauna of a small stream. Univ. Mich. Great Lakes Res. Div. Publ. 15: 51–79.

LALANCETTE, L. M. 1977. Feeding in white suckers (*Catostomus commersoni*) from Gamelin Lake, Quebec, over a 12 month period. Nat. Can. 104: 369–376.

LEWIS, V. P., AND D. S. PETERS. 1984. Menhaden — a single step from vascular plant to fishery harvest. J. Exp. Mar. Biol. Ecol. 84: 95–100.

LOTRICH, V. A. 1973. Growth, production, and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. Ecol. Monogr. 43: 377–397.

LOWE-MCCONNELL, R. H. 1975. Fish communities in tropical freshwaters. Longman, Edinburgh, Scotland. 337 p.

LUND, J. W. G., C. KIPLING, AND E. D. LE CREN. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143–170.

MACPHEE, C. 1960. Postlarval development and diet of the largescale sucker, *Catostomus macrocheilus*, in Idaho. Copeia 1960: 119–125.

MANN, K. H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. Limnol. Oceanogr. 33: 910–930.

MCNEELY, D. L. 1987. Niche relations within an Ozark stream crypinid assemblage. Environ. Biol. Fishes 3: 195–208.

MILLER, R. J., AND H. E. EVANS. 1965. External morphology of the brain and lips in catostomid fishes. Copeia 1965: 467–487.

NALEWAJKO, C. 1966. Dry weight, ash, and volume data for some freshwater planktonic algae. J. Fish. Res. Board Can. 23: 1285–1288.

ODUM, W. E. 1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*, p. 397–407. *In* J. H. Steele [ed.] Marine food chains. University of California Press, Berkley, CA.

PERSSON, L. 1983. Food consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake. Oikos 41: 118–125.

PREJS, A., AND K. PREJS. 1987. Feeding of tropical freshwater fishes: seasonality in resource availability and resource use. Oecologia 71: 397–404.

RINGLER, N. H. 1983. Variation in foraging tactics of fishes, p. 159–171. *In* D. L. G. Noakes et al. [ed.] Predators and prey in fishes. Dr. W. Junk Publishers, The Hague, The Netherlands.

STEWART, N. H. 1926. Development, growth and food habits of the white sucker, *Catostomus commersonii* Lesueur. U.S. Bur. Fish. Bull. 42: 147–184.

TRIPPEL, E. A., AND H. H. HARVEY. 1986. Abundance, growth, and food supply of white suckers (*Catostomus commersoni*) in relation to lake morphometry and pH. Can. J. Zool. 65: 558–564.

VALIELA, I. 1984. Marine ecological processes. Springer-Verlag, New York, NY.

VALIELA, I., AND C. S. RIETSMA. 1984. Nitrogen, phenolic acids, and other feeding cues for salt marsh detritivores. Oecologia 63: 350–356.

WEISBERG, S. B., AND V. A. LOTRICH. 1986. Food limitation of a Delaware salt marsh population of the mummichog, *Fundulus heteroclitus* (L.). Oecologia 68: 168–173.

WEISEL, G. F. 1962. Comparative study of the digestive tract of a sucker, *Catostomus catostomus*, and a predaceous minnow, *Ptychocheilus oregonense*. Am. Midl. Nat. 68: 334–346.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 p.