Food Habits and Feeding Periodicity in Two Sympatric Stonerollers (Cyprinidae)

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ABSTRACT: Food habit comparisons between two sibling species of minnows, the large-scale stoneroller *Campostoma oligolepis* and the central stoneroller *C. anomalum pullum*, suggest a microhabitat separation in syntopic populations in SW Missouri. The measurable food habit differences between species with respect to inorganic matter and species composition of diatoms consumed indicated that *C. a. pullum* feeds in slower flowing sections of the riffle habitat than *C. oligolepis*. Both species showed selection of nonmotile over motile diatoms. Young-of-the-year stonerollers (species combined) had a mean consumption rate of 0.0144 ml/g body wt/hr during daylight with maximum intestinal volume occurring at dusk. Daily ration, measured in September, was 27% of body weight and was completely digested overnight.

INTRODUCTION

Large compact schools of stonerollers are characteristic of Ozark streams (Pflieger, 1975). Two sympatric species, *Campostoma anomalum pullum* (Agassiz), the central stoneroller, and *C. oligolepis* Hubbs and Greene, the large-scale stoneroller, occur in most of the Ozark region except for the Arkansas River system (Pflieger, 1975). The central stoneroller occurs alone in the Arkansas River system except for the Illinois River of Oklahoma (Burr *et al.*, 1979). Both species occur in and around riffles where they graze over the gravel and rock substrate.

The taxonomic relationship of the central stoneroller and the large-scale stoneroller has been the subject of many recent investigations (Pflieger, 1971; Burr and Smith, 1976; Buth and Burr, 1978; Rakocinski, 1977, 1980; Cloutman, 1976). These workers indicate that the two forms of stonerollers are closely related, and Cloutman (1976) labeled them sibling species. Pflieger (1971) first assigned specific rank to the large-scale stoneroller and stated that it generally preferred large riffles.

Kraatz (1923), in his classic study, described *Campostoma anomalum* food habits in Ohio. Other major studies on *C. anomalum* food habits were conducted in Iowa (Starrett, 1950), Alabama (Mathur, 1972) and Kentucky (Burkhead, 1980). In Oklahoma, grazing central stonerollers influenced the distribution of attached algae (Power and Matthews, 1983). Food habits of *C. oligolepis* have not been studied, but Pflieger (1975) indicated that its food habits should be similar to *C. anomalum.* The basic purpose of this investigation was to compare the food habits of these sympatric species of *Campostoma* to determine if an ecological separation of feeding niches exists.

The James River in Greene Co., Missouri, and Pomme de Terre River in Polk Co., Mo., were chosen for study of the food habits of sympatric central and large-scale stonerollers. The population ratio of large-scale to central stonerollers was 1.5:1 in the Pomme de Terre River and 1:2:1 in the James River. An allopatric population of central stonerollers in Spring River, Lawrence Co., Mo., was concurrently studied. These rivers represent the major drainages of the Ozark uplift of SW Missouri; the White, Osage and Arkansas river systems, respectively. Daily feeding periodicity was determined in Flat Creek (a James River tributary) in Barry Co., Mo. These are all relatively clear, high-gradient streams with alternating pool and riffle habitats over a gravel and rock substrate.

METHODS

Collections. — Samples of 10-20 stonerollers were taken with seines at or just before dusk from all three streams within a 3-8 day period in April, June, August, October and February. These collection times encompassed major seasonal differences in water temperature and flow. Fish were usually found over riffles or in swift runs, but in February they were primarily found in pools. Composite periphyton samples were taken from submerged rocks for comparison with diatom genera in stoneroller diets. Captured stonerollers were placed in an ice bath to prevent regurgitation (Doxtater, 1963). The sample was then frozen until food habit analysis.

Stonerollers were measured to the nearest 1.0 mm standard length and weighed to the nearest 0.01 g. Taxonomically useful scale counts followed the methods of Trautman (1957). Because of thermal lability of lateral line scales (LLS) in the central stoneroller (Carmichael, 1983), and because both lateral line and circumferential scale (CS) counts vary by drainage and region (Pflieger, 1971; Burr and Smith, 1976), a character index, sum of LLS and CS (Pflieger, 1971, 1975), was used to separate species. A frequency distribution of this index indicated a bimodal break point at 90-91 (Table 1) in the James and Pomme de Terre rivers.

Food habits. — Food habits were analyzed by comparing the average volume percentages of food types in the gut as recommended by Wallace (1981). To facilitate identification, only contents of the foregut (to the point where the intestinal tract makes its first bend) were pressed out and analyzed, following the method of Lotrich (1973). The food of each fish was washed into a test tube and diluted to ca. 1:100 with water before

TABLE 1. — Frequency distribution for the character index, sum of lateral line and circumferential scales (LLS & CS), in SW Missouri: syntopic *C. A. pullum* and *C. oligolepis* in Pomme de Terre and James rivers, allopatric *C. a. pullum* in Spring River. (SE = standard error)

LLS & CS	Pomme de Terre River		James River		Spring River	
78	5					
79	4					
80	5		1			
81	4		0			
82	18		3			
83	10	$\bar{x} = 83.7$	3			
84	13	N = 94	15			
85	12	SE = 0.31	13	$\bar{x} = 86.0$		
86	7		11	N = 80		
87	2		13	SE = 0.23		
88	6		12		1	
89	7		7		4	
90	1		2		4	
91	1		1		7	
92	3		4		3	
93	2		1		4	$\bar{x} = 93.8$
94	3		6		8	N = 50
95	7		3	$\bar{x} = 95.8$	6	SE = 0.45
96	9		3	N = 30	4	
97	7	$\bar{x} = 97.6$	7	SE = 0.41	0	
98	8	N = 62	2		2	
99	6	SE = 0.41	2		4	
100	3		1		2	
101	7				1	
102	0					
103	3					
104	2					
105	0					
106	1					

mixing with a vortex mixer. One ml was withdrawn and placed in a Sedgewick-Rafter cell. The volume of four food categories was estimated at 200X (using a Whipple disc in one ocular of an Olympus BH-2 microscope) for five random fields across the counting chamber. Assigned categories of diet were inorganic, detritus, diatoms and green-bluegreen algae. Green algae and bluegreen algae were combined due to the small amount of each present. Dietary detritus included partially decomposed plant remains, bacteria, fungi, unidentifiable eggs and other undefined organic matter. Inorganic material consisted of individual mineral particles larger than 2μ (sand and silt) and were usually in the size range of diatom frustules. Dominant genera of diatoms were ranked by volume from periphyton samples and foreguts of individual fish. Up to five fish of each species were analyzed when available in a sample.

Feeding periodicity.—Diel feeding periodicity and consumption rates were determined by periodic sampling in Flat Creek on 17-18 September 1982. Thirty to 40 young-of-the-year *Campostoma*, 30-74 mm SL, were collected at 3-hr intervals (except 0300 hr). One-half of each collection was preserved immediately in 10% formalin, and remaining fish were starved before preservation for 3 hr in an open-mesh, food-free minnow trap located in a shallow run. The intestine was removed from five specimens of each starved group and five from each nonstarved group. It was uncoiled, cut into short sections and placed in the bottom of a petri dish containing a small amount of water. Contents were pressed from each section with a 2-cm-sq wooden block with rounded corners. Food was flushed into a 6.5-ml packed-cell-volume, graduated centrifuge tube and spun at 550 rpm for 20 min. Food volume was then measured to the nearest 0.01 ml.

An index of fullness as suggested by Windell (1971) was calculated for each fish by dividing food volume in milliliters by grams of body weight. Daily feeding periodicity was determined according to the method of Keast and Welsh (1968) by comparing the average of the fullness index for five nonstarved fish for each sampling period. The amount digested (total amount of food passage) for each 3-hr period was determined by subtracting the mean fullness of the starved group from the mean of the nonstarved group collected at the beginning of the period (Windell, 1978). The amount consumed during each 3-hr period was determined by adding the change in mean fullness index of the nonstarved fish from one collection to the next, to the mean amount digested during the same period.

Statistical analysis.—Since the data from food habits and feeding periodicity were in the form of percentages and ratios, all data were arcsine-transformed (Zar, 1974) prior to tests for significance by analysis of variance. Within each food category, two-way ANOVAs compared volumetric data for each species for the five seasonal collections from James and Pomme de Terre rivers. Since only the central stoneroller was present in Spring River, one-way ANOVAs were used to test for significant seasonal variation in diet within each food category. The indexes of fullness from starved and nonstarved *Campostoma* were tested by two-way ANOVA for differences in periodic consumption and amounts digested. Rankings of dominant genera of diatoms from intestines for each season and location were compared to analogous rankings from the periphyton samples along the nonparametric Kolmogorov-Smirnov test (Zar, 1974)

RESULTS

Food habits.— Central stonerollers in Spring River did not exhibit significant seasonal variation in diet by percent volume within the four food groups (Table 2). Green algae were an important part of the summer diet only. Individuals which consumed large amounts of green algae tended to consume fewer diatoms, which were an important diet component throughout the year. Dominant diatom forms ranged from 20-190 micrometers in length and included *Gomphonema*, *Cymbella*, *Navicula* and *Synedra*.

Central stonerollers in James River ingested significantly more inorganic material than large-scale stonerollers ($F = 9.11$, $P < 0.01$; Table 2). There was no significant seasonal variation in inorganic diet percentages in either species. The percent volume of green-bluegreen algae in their diets did not differ significantly between the species and neither exhibited significant seasonal variation in consumption of these algae. The diet also did not differ significantly between the species in diatom or detritus consumption in James River. In February, foreguts of both species contained a significantly lower volume of detritus ($F = 6.29$, $P < 0.001$) and a higher volume of diatoms ($F = 11.83$, $P < 0.0005$). The dominant genus of diatom ingested by both species was *Cymbella*, but in February the large-scale stoneroller also ate equal amounts of *Meridion*. *Navicula*, *Synedra* and *Gomphonema* were other diatoms frequently found in the diet of James River stonerollers.

Central stonerollers from Pomme de Terre River, as in James River, had significantly more inorganic matter in the foregut ($F = 11.42$, $P < 0.0025$) than large-scale stonerollers and both exhibited significant seasonal variation for this dietary component ($F = 6.5$, $P < 0.001$; Table 2). There was no significant volumetric difference between seasons or species within the detritus food category for Pomme de Terre River stonerollers. There was significant seasonal variation in the quantity of green-bluegreen algae in the foregut ($F = 14.97$, $P < 0.0005$) but not between species. There was no significant difference in the quantity of diatoms consumed by the two species, but in February stonerollers had significantly higher volumes of diatoms ($F = 3.10$, $P < 0.05$). There was more seasonal variation in diatom genera found in the diet of Pomme de Terre River *Campostoma* than in the other rivers. *Cymbella* and *Synedra* dominated in February, April and June. *Gomphonema* was also important in February. *Navicula* and *Melosira* were most important in August and October, respectively.

A measurement of diatom selection by *Campostoma* (species combined) was made using the Kolmogorov-Smirnov (Zar, 1974) goodness-of-fit test. The rankings of

TABLE 2.—Food habits of *C. a. pullum* and *C. oligolepis* by mean percent volume of foregut contents. Data for both species were pooled when no significant difference was found between them. (SE = standard error)

	Apr		Jun		Aug		Oct		Feb	
	%	± SE	%	± SE	%	± SE	%	± SE	%	± SE
Spring River										
Detritus	70	13	53	9	69	5	61	6	54	4
Diatoms	24	11	25	8	9	4	27	5	36	3
Inorganic	6	2	7	4	14	4	11	2	11	2
G-bg algae[1,2]	-	-	15	14	7	3	-	-	-	-
James River										
Detritus	64	4	58	2	66	3	64	3	41	3
Diatoms	17	3	24	2	14	3	16	3	45	3
Inorganic										
C. anomalum	18	2	22	3	18	4	17	3	12	0
C. oligolepis	18	4	13	2	18	4	11	2	8	2
G-bg algae[3]	1	1	-	-	2	1	6	2	3	2
Pomme de Terre River										
Detritus	57	7	61	3	63	2	59	5	59	6
Diatoms	29	5	22	4	11	1	13	1	34	7
Inorganic										
C. anomalum	13	4	25	4	26	1	16	4	7	1
C. oligolepis	10	4	10	2	22	4	6	1	7	3
G-bg algae[4]	3	1	-	-	2	1	17	6	-	-

[1]Green-bluegreen
[2]*Microspora, Oedogonium, Ulothrix, Oscillatoria*
[3]*Microspora, Oedogonium, Ulothrix, Cosmarium, Scenedesmus, Oscillatoria, Calothrix*
[4]*Cladophora, Mougotia, Spirogyra, Ulothrix, Cosmarium*

diatoms found in the foregut of *Campostoma* from James and Pomme de Terre rivers deviated significantly (D = 0.514, P < 0.001 and D = 0.425, P < 0.001, respectively) from the rankings of available benthic diatoms pedicted by periphyton samples. Similar results were found for Spring River central stonerollers (D = 0.400, P = 0.002). The selection was for nonmotile attached diatoms such as *Gomphonema* and against motile forms such as *Navicula*.

Feeding periodicity. —Underwater observations of smaller (age groups 0 and 1) stonerollers in August indicated that they fed diurnally with little change in intensity throughout the daylight hours. Measured food volume in the intestine (Table 3) gradually increased to a maximum in those taken at 2100 hr; however, the actual maximum was probably between sample periods near dusk (2000 hr). Feeding did not occur between 2100 and 0600 hr on a night which was partly cloudy to rainy with no moonlight. The fullness index at 3-hr intervals showed significant variation (F = 57.03, P < 0.0005). Stoneroller guts decreased in fullness from 2100 to 0600 hr. Intestines from fish collected at 0600 hr contained only yellow/white mucous clumps and fragments of green algae. Thus the food consumed during the day was completely digested by dawn the next day.

A significant amount of food was digested during the 3-hr starvation periods (F = 104.4, P < 0.0005). Interaction between collection time and starvation treatment was slight (F = 2.20, 0.10 > P > 0.05), probably due to the 0600 hr sample, since the fish had empty intestines on which starvation would have little effect. The quantity digested (Table 3) appeared to be more related to the amount of food in the intestine than to temperature. The highest amount was between 2100-2400 hr when the intestine was full. Daylight consumption per hour averaged 0.0144 ml/g body wt (SE = 0.0012).

The daily ration (daily meal as a % of body weight; Ricker, 1946) for all time periods was 0.213 ml/g body wt. The food had a wet weight of 1.27 g/ml (n = 3), and thus Flat Creek stonerollers consumed 27% of their body weight daily in September.

DISCUSSION

Food habits. —Kraatz (1923), Starrett (1950), Mathur (1972) and Burkhead (1980)

TABLE 3.—Diel feeding periodicity, digestion and consumption amounts from the index of fullness data (ml food/gram body weight) for young-of-the-year *Campostoma* in Flat Creek on 17-18 September 1982. (SE = standard error)

Time	Index of fullness ml/g	± SE	Digestion ml/g	Consumption ml/g	Temperature C
0600	0.0215[1]	0.0041			18
0600(S)[2]	0.0156	0.0015	0.0059	0.0467	
0900	0.0623	0.0035			19
0900(S)	0.0346	0.0037	0.0277	0.0437	
1200	0.0783	0.0081			21
1200(S)	0.0545	0.0047	0.0238	0.0295	
1500	0.0840	0.0054			22
1500(S)	0.0554	0.0052	0.0287	0.0480	
1800	0.1034	0.0059			21
1800(S)	0.0696	0.0029	0.0338	0.0483	
2100	0.1179	0.0082			20.5
2100(S)	0.0585	0.0070	0.0594	−0.0166[3]	
2400	0.0418	0.0052			20
2400(S)	0.0080	0.0026	0.0338	0.0114[3]	
Daily ration				0.2130	

[1]mucous clumps, negligible food volume
[2](S) = starved
[3]−0.0032 ml/g experimental error due to sample variance

used the entire intestinal tract or sections thereof to determine the food habits of the central stoneroller. Lotrich's (1973) method of examining only the foregut contents has several advantages since the foregut contents have had minimal time for digestion. The pharyngeal teeth appear to do little damage to diatoms and green algae filaments. Further maceration occurs throughout the intestine by mixing with mineral particles (Kraatz, 1923; Burkhead, 1980), which increases the amount of detritus and the difficulty in identification of food items. As food material is digested and assimilated, it is no longer available for food habit analysis, and would tend to increase the relative amounts of inorganic material. It is suggested that future workers consider this method when investigating the food habits of fishes lacking an anterior diverticulum.

The results of food habit analysis for the central stoneroller were in general agreement with previous studies (Kraatz, 1923; Starrett, 1950; Mathur, 1972). Each of these workers used visual estimation of percent volume for various food categories. The use of a Whipple disc in a microscope aided in making consistent volumetric estimates.

Feeding periodicity. — Mathur (1972) found two feeding peaks for central stonerollers, in April, at 1100 and 2000 hr, and in September at 0800 and 1700, by visually estimated percent fullness of digestive tract. Mathur's (1972) peaks were based on one or two specimens while April peaks were based on six or nine specimens. Southwest Missouri *Campostoma* did not show feeding peaks during the day. Possibly Mathur's sample size and the difficulty in making accurate visual estimates of the fullness account for the difference. It appears from our samples and observations that, in the absence of major disturbance, stonerollers feed continually during the daylight hours.

Feeding ecology. — The attached microfloral community in riffles, according to Round (1973), is composed of epilithic and epiphytic nonmotile diatoms, desmids, filamentous green and bluegreen algae and associated flagellate unicells. The genera of algae found in intestines of *Campostoma* correlate very closely with the typical genera that Round (1973) lists for the attached riffle community including *Gomphonema, Synedra, Cymbella, Cocconeis, Cladophora, Mougotia, Cosmarium* and *Oscillatoria. Gomphonema, Synedra* and *Cymbella* are epilithic or epiphytic in flowing water, attaching by a gelatinous stalk (Patrick, 1977). *Cymbella* can also occur in a gelatinous tube. These diatom genera should be more easily scraped off rocks with the specialized lower jaw of *Campostoma* than *Cocconeis* or *Navicula* which are appressed to the substrate. Round (1973) also indicated that in pockets where the rate of flow was slower, silt was trapped and epipelic genera such as *Navicula* invaded. This may explain the presence of epipelic genera in the foregut of SW Missouri *Campostoma* and may also account for the large amounts of detritus and inorganic matter ingested. All motile and monmotile diatom genera present in the riffle environment may not be available to the stonerollers. *Campostoma* apparently grazes the attached community including epiphytic and epilithic stalked diatoms such as *Gomphonema* and *Cymbella* and epiphytes such as *Cocconeis* appressed to attached filamentous algae. These forms are easily accessible when compared to *Navicula* and *Nitzschia* which are motile on the rock surface or sand/silt substrate. Selection of certain attached epilithic and epiphytic genera is occurring and appears to be for morphologic forms which are more accessible.

Burr and Smith (1976) described ecological separation for a syntopic population of *Campostoma anomalum pullum* and *C. oligolepis* in which *C. oligolepis* preferred faster water and large riffles while *C. a. pullum* was taken in smaller riffles and to some extent in the quiet water habitats. The restricted habitat associations of *C. oligolepis* (Burr and Smith, 1976; Pflieger, 1975) suggest that they are more of a specialist (Rakocinski, 1980) and better adapted to faster water (Rakocinski, 1977). Ingestion by the central stoneroller of more inorganic material than the large-scale stoneroller suggests a feeding microhabitat with slower water velocity where small inorganic particles are more prevalent and supports the concept of spatial separation. Spring River central stonerollers ingested less inorganic matter than central stonerollers in James and Pomme de Terre rivers ($F = 10.45$, $P < 0.0005$); however, this difference may be a reflection of greater surface area of slow riffle microhabitat in the latter rivers. Central stonerollers ingested more of the epipelic genus *Navicula* than large-scale stonerollers at all locations and this is a further indication of different feeding microhabitats. Although the food habits of the central and large-scale stoneroller overlap greatly, the separation in feeding microhabitat supports the current hypothesis of two separate species held by most modern workers (Pflieger, 1971; Burr and Smith, 1976; Rakocinski, 1977, 1980; Cloutman, 1976).

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