THE SOUTHWESTERN NATURALIST 26(1):31-36 FEBRUARY 21, 1981

DIEL FEEDING CHRONOLOGIES IN TWO SONORAN DESERT STREAM FISHES, *AGOSIA CHRYSOGASTER* (CYPRINIDAE) AND *PANTOSTEUS CLARKI* (CATOSTOMIDAE)

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ABSTRACT.—Diel feeding chronologies in two desert fishes, *Agosia chrysogaster* (longfin dace) and *Pantosteus clarki* (Gila mountain sucker), were determined by examining the foregut contents of fishes taken from Sycamore Creek, Maricopa Co., Arizona. A comparison of algae in foreguts with algae collected from the stream suggests that these species have distinct feeding chronologies and foraging areas. *Pantosteus clarki* consumes benthic diatoms and small amounts of detritus while *A. chrysogaster* feeds on filamentous green algae, benthic and epiphytic diatoms, and detritus. Peaks of ingested food volume indicate that *A. chrysogaster* is a diurnal feeder whereas *P. clarki* feeds both day and night, with crepuscular peaks.

Fishes may assume an important role in ecosystem metabolism through feeding activities. To evaluate their role in the metabolism of a desert stream, we asked the following questions: 1) What do the dominant fish species eat? 2) How is feeding activity distributed in time? 3) How do the two species in our study area interact with respect to food?

The importance of fishes to freshwater ecosystem metabolism is often considered minor because many fishes require a large percentage of protein in their diets and find structural carbohydrates to be rather indigestible (Phillips, 1969; National Research Council, 1977). The two species considered here have been reported to consume substantial quantities of algal material within a broader, omnivorous diet. *Pantosteus clarki* was a selective algal feeder when compared to six other native fishes in a Sonoran Desert stream (Schreiber, 1978). In the same study, *Agosia chrysogaster*, the longfin dace, was a generalist, feeding on a variety of foods, including benthic algae.

Diel feeding chronologies have been described for a variety of carnivorous freshwater fish species (Spencer, 1939; Mathur and Robbins, 1971; Baumann and Kitchell, 1974; Sarker, 1977); however, to our knowledge, feeding chronology has not been examined in predominantly herbivorous freshwater fishes, the foods of which are equally available day and night.

Resource partitioning is apparent in a variety of assemblages of fishes in various ecosystems, often taking the form of feeding separations in space or divisions of food types among several species (Fryer and Iles, 1972; Kawanabe, 1959; Keast, 1978). In this study, we examine both spatial and temporal partitioning of feeding between two fishes in a desert stream in autumn.

METHODS.—All samples were from Sycamore Creek, a Sonoran Desert stream 65 km northeast of Phoenix, Arizona. It is a relatively unshaded, moderately hardwater stream (conductivity = 600 μS cm^{-1}) with sand substrates and low turbidity except during floods. Site one (1785 m elevation), sampled for fish on 8 September 1978, consisted of a uniform riffle 1.0 m wide and 5.0 cm deep. Discharge was 0.05 $m^3 \cdot s^{-1}$ and maximum temperature 32.7° C. A well developed algal mat domi-

TABLE 1.—*Percent abundance of diatoms associated with* Cladophora glomerata *mats, stream sediments in pools and riffles, and foreguts of the fishes* Agosia chrysogaster *and* Pantosteus clarki.

	Stream habitat		Fish guts	
SITE 1	*C. glomerata* mat	Riffle sediments	*A. chrysogaster*	*P. clarki*
Cymbella hustedtii	13.9	25.7	22.5	20.6
Gomphonema lanceolata	45.7	10.8	40.0	6.8
Navicula radiosa tenella	15.2	14.1	9.7	18.4
Navicula viridula	8.4	29.5	19.1	41.3
other species	16.8	19.9	8.7	12.9

	Stream habitat		Fish guts			
			A. chrysogaster		*P. clarki*	
SITE 2	Riffle	Pool	Riffle	Pool	Riffle	Pool
Achnanthes lanceolata	9.8	11.5	4.2	7.8	10.1	6.8
Cocconeis pediculus	3.1	4.2	5.4	25.8	3.6	7.0
Cocconeis placentula	23.1	8.4	14.8	7.9	13.7	6.7
Gomphonema lanceolata	38.1	12.3	52.1	19.9	40.7	13.2
Melosira varians	2.3	35.0	7.4	19.6	3.6	43.4
other species	23.6	28.6	16.1	19.0	28.3	22.9

nated by *Cladophora glomerata* covered the riffle bottom and food abundance was very high. Site two (2335 m elevation) was sampled 13 October when discharge was 0.02 m^3 s^{-1} and maximum temperature was 25.1°C. Both pool (10 m × 8 m wide by 0.65 m deep) and contiguous upstream riffle areas were sampled. The riffle was similar to that at site one, except that algal abundance was much lower. No algal mats were present in the pool, and the bottom consisted of sand covered by detritus, some algae, and fish feces.

The riffle at site one and both riffle and pool at site two were sampled every 3 to 4 hours for 24 hours with electrofishing gear. Four to six individuals each of *A. chrysogaster* and *P. clarki*, 40 - 50 mm SL, were immediately preserved in 10% formalin, and returned to the laboratory for analysis. Contents of the anterior 1.5 cm of digestive tract were removed, suspended in water, and drawn onto a Millipore filter. The filter was cleared with oil, mounted on a glass slide with Permount, and examined at 400 ×. Volumes of filamentous algae were estimated with a grid method (Olson, 1950) and diatom taxa by the product of numerical and mean volume based on geometric shape.

Algal samples were taken from macroscopically evident patch types at sites where fish were collected (Busch, 1979). These samples were processed in a manner identical to those from fish digestive tracts.

RESULTS.—Simple inspection revealed algal standing crops to be markedly different at sites one and two. A dense *Cladophora glomerata* mat with associated epiphytes was present at site one riffle. In areas devoid of *C. glomerata*, an assemblage of epipelic diatoms was present (Table 1). Filamentous algae were much less abundant on the site two riffle and consisted of *Zygnema* sp., various blue-green algae, and the diatom *Melosira varians*. No algal mats were present in the pool at site two. Several diatom species were present in both pool and riffle habitats; however, their relative abundances differed (Table 1). The blue-green algae *Calothrix parietina, Schizothrix calcicola*, and *Oscillatoria lutea* were very abundant on cobbles and rocks in the pool and riffle at site two.

Because relative abundance of algal species (particularly diatoms) was characteristic of a given microhabitat, and since diatoms are too small to be selected individually by these fishes, analysis of foregut contents should

TABLE 2.—*Mean volume of algae in foreguts of* Pantosteus clarki *and* Agosia chrysogaster *in Sycamore Creek, Arizona. Volumes in* 10^7 μm^3.

	Filamentous green algae	Diatoms	Total
P. clarki			
Site 1, riffle	0.06	2.03	2.09
Site 2, riffle	0.00	1.36	1.36
Site 2, pool	0.00	1.58	1.58
A. chrysogaster			
Site 1, riffle	2.39	1.67	4.06
Site 2, riffle	1.18	0.71	1.89
Site 2, Pool	0.20	0.46	0.66

indicate the microhabitats in which each fish species fed. At site one, *Agosia chrysogaster* fed predominantly on the *C. glomerata* mat assemblage as indicated by the large percentage of both *C. glomerata* and its epiphytes (e.g., the diatom *Gomphonema lanceolata*) in its foregut (Tables 1, 2). *Pantosteus clarki* contained mostly epipelic diatoms such as *Cymbella hustedtii* and *Navicula viridula*, both of which were less common in the *C. glomerata* mat. This and the rarity of *C. glomerata* filaments in their guts suggest that *P. clarki* fed away from mats, on epipelic associations of riffles. Invertebrates and detritus were only incidentally encountered in foreguts; thus both fish species were predominantly herbivores during the study at these sites.

Not only did the two fishes feed in different areas and on different algal species at site one, but they also fed at different times of day (Fig. 1a). Longfin dace was a diurnal feeder while mountain sucker fed both day and night with peaks shortly after dusk and dawn.

At site two, fishes from the riffle showed a feeding pattern similar to that at site one. *P. clarki* guts always contained algae, mostly epipelic diatoms characteristic of the riffle habitat (Table 1, Fig. 1b). *Agosia chrysogaster* again fed mostly in daylight and largely on filamentous algae, in this case *Zygnema*. *Zygnema* has few epiphytes and the diatoms found in *A. chrysogaster* guts were largely epipelic forms characteristic of the riffle (Table 1). The total volume of food taken by both *A. chrysogaster* and *P. clarki* at site two was considerably lower than at site one where food was more abundant (Table 2).

Agosia chrysogaster from the site two pool consumed even less algae but fed continuously (Table 2, Fig. 1c). *Zygnema* did not grow in the pool but was particularly abundant in foreguts of *A. chrysogaster* taken in the pool at night. Apparently *A. chrysogaster* fed on the riffle and occasionally moved back to the pool. Diatoms in pool *A. chrysogaster* foreguts were, however, typical of the pool flora. Other abundant diatoms in foreguts were *Melosira varians*, an epipelic form; and *Cocconeis pediculus*, a species rare in both riffles and pools (Table 1) but abundant within the detrital matrix of pool bottoms. Detritus was a significant dietary item only in pool-caught *A. chrysogaster* and then did not exceed 50% of total food volume in any individual fish.

Pantosteus clarki from the pool always contained diatoms typical of the pool flora (Table 1, Fig. 1c). Volumes were similar to those of riffle fish but

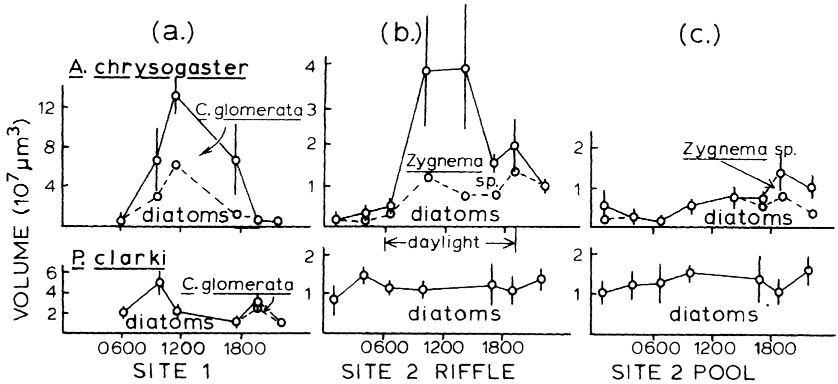

FIG. 1.—Volumes of algae (*Cladophora glomerata, Zygnema* sp., and diatoms) in foreguts of *Agosia chrysogaster* and *Pantosteus clarki* collected at Sycamore Creek, Arizona. Solid lines indicate total algal volume; dashed lines denote diatom abundance. Vertical bars are ± one SE of the mean of total food volume. a., Site one riffle; b., site two riffle; c., site two pool.

lower than those of *P. clarki* taken at site one where food was more abundant (Table 2). Blue-green algae were locally abundant at site two but were rarely encountered in foreguts of either fish, indicating that these species avoided blue-greens.

DISCUSSION.—*Agosia chrysogaster* is native to southern Arizona, southwestern New Mexico, and northern Sonora, Mexico, and is the most common fish of low Sonoran Desert streams (Miller, 1961). *Pantosteus clarki* overlaps *A. chrysogaster* in much of its range but tends to occur at higher elevations. Both prefer shallow water, with *A. chrysogaster* in slow flowing water over sandy bottoms and *P. clarki* in riffles with coarse bottoms (Minckley, 1973). Together they comprise 99% of the fish fauna of Sycamore Creek. *Pimephales promelas* and *Notropis lutrensis* have both been introduced, but are rarely encountered. At the time of this study, *P. clarki* population size had increased following two extremely wet winters. In dry years, Sycamore Creek is reduced to a few hundred meters of permanent channel and only *A. chrysogaster* remains abundant. The two species characteristically dominate a depauperate fauna and achieve high densities in low desert streams.

Pantosteus clarki is an herbivore in Sycamore Creek and elsewhere; however, *A. chrysogaster* tends to be omnivorous (Schreiber, 1978) and opportunistic. *Agosia's* primarily herbivorous habit in Sycamore Creek may have been a partial function of food availability. Baetid mayflies were the preferred food of *A. chrysogaster* on an annual basis in Aravaipa Creek, Arizona; however, during July, when algae were abundant, nearly 53% of their food was filamentous algae (Schreiber, 1978).

Both species showed pronounced temporal patterns of feeding at site one where food was abundant. At this time and place, *A. chrysogaster* fed exclusively during daylight and *P. clarki* fed continuously with crepuscular peaks. When food was less abundant, this pattern disappeared and in the pool where fish were abundant and food scarce, both fed continuously. Since foreguts were consistently fuller when food was abundant, we suggest that each species has a preferred feeding time which is extended when food is scarce.

Diel patterns in herbivore feeding are obviously not generated by food activity patterns, as is the case with carnivorous fishes (Mathur, 1973; Keast and Welsh, 1968; Nikolsky, 1963). Omnivorous fishes may also exhibit discontinuous feeding activity (Al-Daham, 1977; Darnell and Meierotto, 1962) which may correspond to other activity cycles such as metabolism and migration (Baumann and Kitchell, 1974). Herbivorous marine fishes are largely diurnal feeders, inactive at night to avoid piscivorous predators (Ogden and Lobel, 1978). Whatever the proximal causes in *A. chrysogaster* and *P. clarki*, diel patterns of feeding obviously must be considered in studies of herbivorous as well as carnivorous fishes.

While both species in Sycamore Creek are herbivorous, direct competition is probably minimal when food is abundant. Not only are feeding chronologies different, but the fishes feed upon different resources as well. *Pantosteus clarki*, with its ventral mouth vested with cartilagenous scraping sheaths, is capable of removing algae (largely diatoms) from coarse sand and gravel substrates. The more terminal mouth of *A. chrysogaster* is well suited for engulfing algal filaments, which it may do as much for epiphytic diatoms as for the filamentous alga itself. When this complex is unavailable (e.g., site 2 riffle), *A. chrysogaster* feeds alongside *P. clarki* on epipelic diatoms. Thus food habits overlap and potential for competition is greater at low food densities.

Desert streams in the American Southwest depend heavily on autochthonous primary production instead of the allochthonous detrital base which supports streams of more mesic, forested regions. Both primary production rates and algal standing crops are very high in streams like Sycamore Creek (Busch and Fisher, 1981). Fishes tap this resource directly and the top carnivores in the ecosystem are insects (e.g., belastomid and nepid hemipterans). In such a system fishes attain high densities, especially as ecosystem boundaries retreat during summer drying. Selective feeding by fishes can affect the abundance and kinds of algae present in the system. For example, the predominance of blue-greens over preferred diatoms at the site two riffle may have resulted from cropping by fishes. By so shaping primary producer communities, these fishes may also influence rates of production, food availability to other consumers, nutrient cycling pathways, and a host of other ecosystems properties.

We thank Cheryl Bronk for technical assistance on this project. W. L. Minckley provided valuable advice during the course of the study and a thorough, critical review of the manuscript. This material is based upon work supported by the National Science Foundation under grant no. DEB 77-24478 to S. Fisher.

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