TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 16, Number 1 December 16, 1969

VARIATION AND RELATIONSHIP OF THE STUDFISHES, *FUNDULUS CATENATUS* AND *FUNDULUS STELLIFER* (CYPRINODONTIDAE, PISCES)

JAMIE E. THOMERSON

Faculty of Biological Science, Southern Illinois University Edwardsville, Illinois 62025

Abstract

Fundulus catenatus and *Fundulus stellifer* are recognized as valid allopatric (with the exception of a problematic syntopic record) species differing in pigmentation, male breeding coloration, distribution of male contact organs and pharyngeal dentition. On the basis of meristic and morphometric differences eight populations (Ozarks, Ouachita, Homochitto River, Tennessee R., Virginia, Cumberland R., Green R. and Indiana) of *F. catenatus* and six populations (Upper Coosa R., Middle Coosa R., Alabama R., Cahaba R., Tallapoosa R. and Chattahoochee R.) of *F. stellifer* are recognized. The Homochitto population seems to be dwarfed and no black-banded males were recorded. In both species, males occur in two breeding color forms: those with and those without a black band on the caudal fin. *Fundulus stellifer* males with the black caudal band have black terminal dorsal bands also. The black caudal band is usually subterminal in *F. catenatus* and terminal in *F. stellifer* males. The more massive pharyngeal bones and teeth of *F. stellifer* are regarded as evidence for further specialization for snail feeding. *Fundulus catenatus* probably originated in the Eastern Highlands and the Ozarks and Ouachita populations may be the result of separate invasions of the Interior Highlands. *Fundulus stellifer* was derived from a *F. catenatus*-like ancestor isolated in the Alabama River system by minor stream capture.

Introduction

The northern studfish, *Fundulus catenatus* (Storer) 1846, is a large active killifish which inhabits the clear sand and gravel bottom streams draining the upland areas of the central United States. It is known only from streams ultimately tributary to the Mississippi River and is one of a number of animal species distributed disjunctly in the Interior Highlands of Missouri and Arkansas west of the Mississippi River and in the Cumberland and Appalachian uplands east of the Mississippi River (see Conant, 1960, for a discussion of this distributional pattern). With the exception of an isolated population in the Homochitto River drainage in Mississippi, *F. catenatus* is absent from the intervening Mississippi Embayment of the Gulf Coastal Plain to the south and the predominantly prairie state of Illinois to the north. *Fundulus stellifer* (Jordan) 1876, the southern studfish, has its main distribution in the upland tributaries of the Alabama River in Alabama and Georgia and few of the headwater tributaries of the Chattahoochee River in northern Georgia. With the exception of a single problematic syntopic record discussed below, the two studfishes appear to be completely allopatric. Though extensive comparative life history data are not yet available, they occupy similar habitats and *F. stellifer* may be thought of as replacing *F. catenatus* in its range.

The studfishes are quite similar morphologically (Figure 1) and were even considered conspecific by Garman (1895, pp. 107-108), but presently (Moore, 1968;

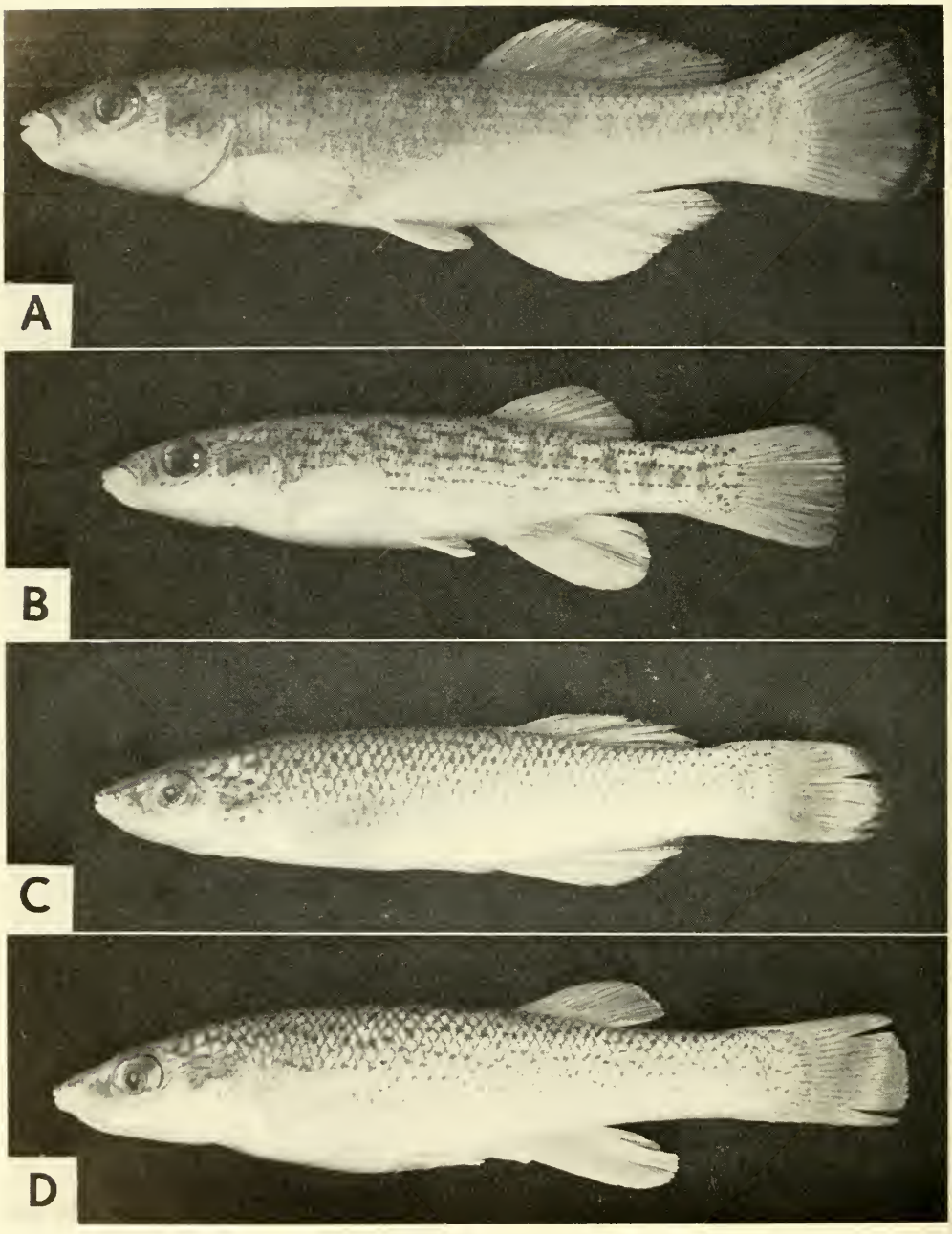

Figure 1. A. Male *Fundulus catenatus* (SL 86.6 mm), and B. female *F. catenatus* (SL 69.4 mm) from SIUE collection JET 66-10, Ozarks Population. C. Male *Fundulus stellifer* (SL 68.5 mm), and D. female *F. stellifer* (SL 68.8 mm) from TU 37703, Cahaba River Population.

Bailey, *et al.*, 1960) they are considered distinct species. However, Miller (1955) has reasonably suggested that further study might show them to be subspecies rather than allopatric species. The purpose of this study is to describe and compare variation in the two forms and to clarify their relationship. The problem is simplified in that the studfishes

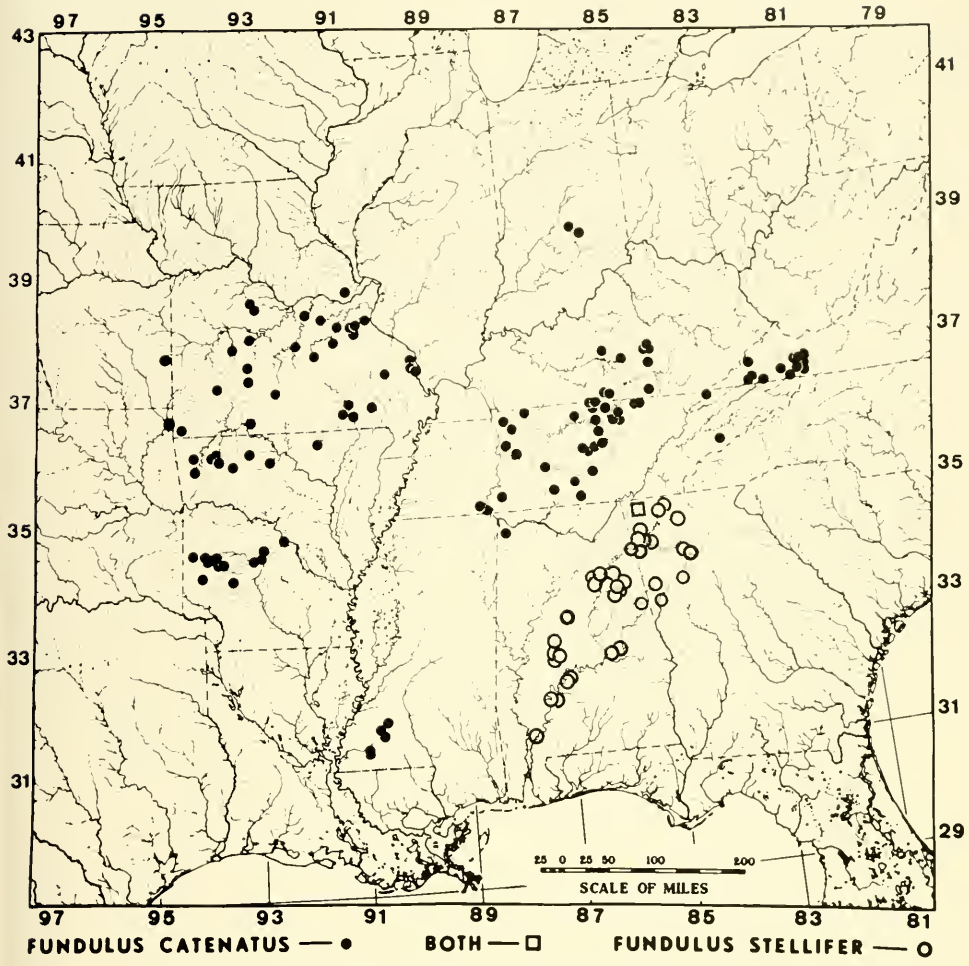

Figure 2. Distribution of studfish collections listed in Material Examined and peripheral localities in Kansas and Oklahoma.

have not been described several times, confused, or misidentified as has so often happened to members of the genus *Fundulus*. Even though the two forms show considerable overlap in meristic and morphometric characters, consistent differences in pigmentation, male breeding colors, and pharyngeal dentition lead me to regard *F. catenatus* and *F. stellifer* as valid allopatric species.

Key to the Studfishes

Eight to ten continuous rows of lateral dots centered on each scale; dots brown or olive in females and juveniles, orange to orange-red in nuptial males; scale outlines not sharp, particularly in males; males without black margin on dorsal fin but some males with black subterminal caudal band; pharyngeal teeth of large individuals at most peg-like; nuptial males usually without contact organs on dorsal fin or caudal peduncle; lateral scale rows usually 12-14. In streams ultimately tributary to the Mississippi River ..... *Fundulus catenatus*.

Dots randomly distributed or at most in six to nine irregular rows on upper sides, dots not centered on each scale, size of dots irregular; dots brown or olive in females and juveniles, orange to dark red in nuptial males; scale outlines sharp, particularly in

females and juveniles; some males with black margins on both dorsal and caudal fins; some pharyngeal teeth in large individuals molariform; males often with contact organs on dorsal fin and caudal peduncle; lateral scale rows usually 14-16. In streams ultimately tributary to the Alabama or Chattahoochee Rivers ..... *Fundulus stellifer.*

Range

Distribution of Material Examined and Peripheral Records (Figure 2) gives a good representation of the range of the studfishes. A few of the apparent distributional gaps are not real but reflect that no material from those areas was studied.

Fundulus catenatus

Moore (1968, p. 112) gave the range of *Fundulus catenatus* as:

> "Upland tributaries of the Tennessee, Cumberland, and Green Rivers in Kentucky, Tennessee, Virginia, and Alabama: clear streams of the Ozark region in Kansas, Missouri, Oklahoma, and Arkansas; Red River tributaries in southwestern Arkansas; the Homochitto River in Mississippi; and the upper part of the East Fork of White River, Indiana."

Previous records of *F. catenatus* in Kansas are probably not valid (Cross, 1967, pp. 230-231), however, Bass and Triplett (1967) have taken a single specimen from Drywood Cr., Crawford County Kansas, a stream ultimately tributary to the Little Osage River. The populations cited in this paper represent geographical areas from which samples seemed to me to be reasonable homogeneous and statistically distinct from those of adjacent areas.

The "Ozarks Population" inhabits the small creeks draining into the Mississippi River on the Missouri (western) side of the river from just north of the confluence of the Missouri and Mississippi Rivers south to Cape Girardeau Co., Missouri. Smith (1965) included *F. catenatus* as a hypothetical addition to the fish fauna of Illinois because of its occurrence in these small tributaries in adjacent Missouri counties. The populations north of the Missouri River in the Big Creek system seem to have crossed the river from the south and established themselves in historical times (W. L. Pflieger, in litt., 1966). It thus seems possible that pioneers from the Ozarks population in Missouri may someday cross the Mississippi River into Illinois. The specimens included in the Ozarks population are generally distributed throughout the Missouri Ozarks and south into central Arkansas where samples from tributaries to the Arkansas River were referred to this population. I have not examined material from the Neosho R. in NE Oklahoma (Branson, 1967).

The "Ouachita Population" includes samples from the Ouachita River drainage in Arkansas and one sample from the Saline River of southwestern Arkansas, a tributary of the Red River.

The "Homochitto River Population" is confined to the Homochitto River system in the southwestern corner of Mississippi.

The "Tennessee River Population" includes samples from the Tennessee and Duck Rivers and their tributaries in Tennessee, Alabama, and Georgia. CU 50009 (22 specimens) from Powell River, Claiborne Co., Tenn., just south of the western tip of Virginia (see Figure 2) clearly belongs with the Tennessee River population and not with the Virginia population.

The "Virginia Population" includes samples from the Clinch River and the North Fork of the Holston River in Virginia. Although several of the collections I examined had locality data simply as "Holston River, Va." or just as "Va.," I assume that they came from the North Fork of the Holston River or the Clinch River. Ross and Carico (1963) listed 25 localities for *F. catenatus* from the North Fork drainage and none for the Middle Fork or South Fork of the Holston River.

The "Cumberland River Population" includes samples from the Cumberland River and its tributaries in Tennessee and Kentucky. The "Green River Population" includes samples from Green River drainage in Kentucky and Tennessee. The "Indiana Population" is a relict population in tributaries to the East Fork of the White River in Indiana (see Gerking, 1945, p. 22; Map 69, p. 78).

Fundulus stellifer

Fundulus stellifer occurs in Alabama River tributaries in Alabama, Georgia and Polk

Co., Tennessee, but is not known from the Tombigee River which joins the Alabama River from the west just north of Mobile Bay. It also occurs in several of the upper tributaries of the Chattahoochee River in northern Georgia (Figure 2). There is a problematic record of one specimen from West Fork Chickamauga Creek, a Tennessee River tributary in northeastern Georgia (see Material Examined). This record is of considerable interest because it is from the range of *F. catenatus* and an *F. catenatus* was present in the collection. I believe this is a valid record of *F. stellifer* syntopic with *F. catenatus* rather than the result of mixing of specimens from two different localities or some similar mistake. However, intensive collecting of this locality 17 September 1967 netted a single juvenile *F. catenatus*. All other easily accessible sites in the small drainage were visited also; two offered no studfish habitat, one seemed suitable but no studfish were present and *F. catenatus* only was present at two other sites. One party of fishermen was present at the syntopic locality when we arrived at 0900 and another party came before 1030. Perhaps the record of *F. stellifer* at this locality indicates bait release rather than a natural population, but it seems doubtful that fishermen would transport bait from the sparsely populated Alabama River tributaries of the area when bait fishes are so abundant in the Tennessee River tributaries.

The "Upper Coosa River Population" includes samples from northern Georgia, except for those from Chattahoochee tributaries. Included were samples from Walker, Murray, Whitfield, Cobb, Gordon and Pickens Cos. The "Middle Coosa River Population" comprises all samples from the Coosa River and its tributaries in Alabama and in Chattooga and Cherokee Cos., Ga.

The "Alabama River Population" included samples from the Alabama River proper and its small tributaries. The "Cahaba River Population" and the "Tallapoosa River Populations" included samples from tributaries to those streams respectively in Alabama and Georgia. The "Chattahoochee River Population" includes all samples from the Chattahoochee system.

Methods

All rays of the dorsal, anal and left pectoral fins were counted at their bases. Caudal ray number is total branched caudal rays plus 2 and counts were made only on large individuals since the number of branched rays increases with ontogeny. Lateral scales were counted as described by Hubbs and Lagler (1947). Lateral scale rows were counted on the left side only in a zig-zag fashion from and including the scale on the dorsal midline at the anterior of the dorsal fin base ventrally to the last scale before the ventral midline.

Standard Length measurements were made to the nearest mm for the fish discussed in the section on contact organs. All other measurements, including Standard Length, were made with Helios mm dial calipers to three figures. Standard Length (SL), Predorsal Length (PDL), Caudal Peduncle Depth (CPD), Pelvic Fin Length (P2L), Depressed Dorsal Fin Length (DL), Depressed Anal Fin Length (AL), and Anal Fin Base Length (AB) were taken as described by Hubbs and Lagler (1947). Body Depth (BD) and Head Width (HW) were taken as described by Thomerson (1966). Head Length (HL) was taken from the rear of the bony operculum at the dorsal terminus of the gill slit to the tip of the snout. Head Depth (HD) was taken at the level of the posterior margin of the preopercle.

Color descriptions were made from 35 mm color slides of live and preserved specimens, from field notes and from live specimens kept in aquaria. All adult males in the collections listed under Material Examined were examined with a dissecting microscope and sketches were made showing distribution of contact organs. Notes on pigmentation were also made for these males.

Variation in Meristic Characters

Meristic data are presented in tabular form (Tables 1-6). Populations are not considered to have significant differences for a given count unless the sum of 2 standard errors (2SE) of one plus 2SE of the other is less than the difference between the two means. This interpretation and that of Figures 5 and 6 presenting morphometric data follow Hubbs and Hubbs (1953).

Table 1. Number of dorsal rays in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	12	13	14	15	16	17	N	Average	SD	2SE
Fundulus catenatus										
Ozarks			14	188	58	9	269	15.2	.58	.07
Ouachita	1	5	64	29	1		100	14.2	.60	.12
Homochitto R.		10	71	19			100	14.1	.53	.11
Tennessee R.		13	65	48	2		128	14.3	.54	.09
Virginia		18	38	9			65	13.9	.63	.16
Cumberland R.		3	29	56	12		100	15.2	.81	.16
Green R.		3	45	62	7		117	14.6	.64	.12
Indiana				3	3		6			
Fundulus stellifer										
Upper Coosa R.		6	30	19	3		58	14.3	.74	.19
Middle Coosa R.		43	76	6	1		126	13.7	.58	.10
Alabama R.	1	27	44	1			73	13.6	.54	.12
Cahaba R.		33	55	1			89	13.6	.50	.10
Tallapoosa R.	1	7	1				9	13.0		
Chattahoochee R.		5	14	11	1		31	14.3	.77	.28

Fundulus catenatus

Observed range of variation in dorsal ray number is 12 to 17 (Table 1). Specimens from the Ozarks and Cumberland River populations tend to have relatively high dorsal ray numbers (avg. 15.2 for both) and these populations are significantly different from all other populations of *F. catenatus* in this character. The two populations with lowest average number of dorsal rays are the Homochitto River (14.1) and Virginia (13.9) populations. The Homochitto River population is not separable from either the Ouachita or Tennessee River populations with this character; however, the Virginia and Tennessee River populations can be separated.

Anal ray number (Table 2) varies from 13 to 18. The highest averages are again those of the Ozarks and Cumberland River populations (avg. 16.2 for both), but the Green River Population also tends toward high counts (avg. 16.1). The Homochitto River, Ouachitas, and Virginia populations tend toward low counts (avgs. 14.9, 15.2, and 15.3 respectively). Distribution of anal ray counts tends to parallel distribution of

Table 2. Number of anal rays in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	13	14	15	16	17	18	N	Average	SD	2SE
Fundulus catenatus										
Ozarks			12	138	48	6	204	16.2	.60	.08
Ouachita	2	10	53	33	2		100	15.2	.72	.14
Homochitto R.	1	13	78	8			100	14.9	.50	.10
Tennessee R.		2	47	68	19		136	15.8	.70	.12
Virginia		2	39	22	1		64	15.3	.57	.14
Cumberland R.			14	59	24	3	100	16.2	.68	.14
Green R.			12	69	19		100	16.1	.55	.11
Indiana				2	4		6			
Fundulus stellifer										
Upper Coosa R.	1	15	34	9			59	14.9	.69	.18
Middle Coosa R.	3	58	59	5	1		126	14.5	.65	.12
Alabama R.	1	31	37	3			72	14.5	.61	.14
Cahaba R.	2	56	30				88	14.3	.52	.11
Tallapoosa R.		4	5				9	14.6		
Chattahoochee R.	1	8	21	1			31	14.7	.59	.21

Table 3. Number of left pectoral rays in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	14	15	16	17	18	19	N	Average	SD	2SE
Fundulus catenatus										
Ozarks			38	131	31		200	17.0	.58	.08
Ouachita			25	67	8		100	16.8	.55	.11
Homochitto R.		1	4	21	63	11	100	17.8	.72	.14
Tennessee R.	1	4	41	66	9	1	122	16.7	.73	.13
Virginia		11	44	8			63	16.0	.55	.14
Cumberland R.	1	1	34	61	3		100	16.6	.61	.12
Green R.		7	48	39	6		100	16.4	.71	.14
Indiana				4	2		6			
Fundulus stellifer										
Upper Coosa R.		1	11	38	8		58	16.9	.63	.17
Middle Coosa R.		4	49	60	12	1	126	16.7	.74	.13
Alabama R.			33	39	1		73	16.6	.57	.13
Cahaba R.		8	60	22			90	16.2	.56	.12
Tallapoosa R.		1	1	4	3		9	17.0		
Chattahoochee R.		1	13	17			31	16.5	.57	.20

dorsal ray counts; most specimens have one more anal than dorsal ray but some have the same number, one less, or two more.

Number of left pectoral rays (Table 3) varies from 14 to 19. The Virginia sample average (16.0) is significantly the lowest and the average (17.8) for the Homochitto River sample is significantly the highest. Coefficient of Difference between these two populations is 1.38, slightly above the conventional criterion for subspecific differentiation (Mayr, Linsley, and Usinger, 1953, p. 146). However, Coefficients of Difference between the Homochitto population and the Ozarks, Ouachita, or Tennessee River populations are all less than 1.0. The same is true of Coefficients of Difference between the Virginia population and the Tennessee River, Cumberland River, or Green River populations.

Caudal Ray number (Table 4) varies from 15 to 18. All populations tend to have subequal proportions of individuals with 16 or 17 caudal rays. The lowest average number of caudal rays is 16.2 (Green River) and the highest is 16.7 (Homochitto River). There is thus a weak trend from higher number of caudal rays in the south to lower number of caudal rays in the north.

Observed range of lateral scale row num-

Table 4. Number of caudal rays in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	14	15	16	17	18	N	Average	SD	2SE
Fundulus catenatus									
Ozarks		2	57	24	3	86	16.3	.58	.13
Ouachita		3	17	18	3	41	16.5	.74	.23
Homochitto R.			18	22	4	44	16.7	.63	.20
Tennessee R.		1	19	24	2	46	16.6	.61	.18
Virginia			11	7		18	16.4	.25	.12
Cumberland R.		3	20	27	1	51	16.5	.64	.18
Green R.		6	31	13	2	52	16.2	.69	.19
Indiana			6			6			
Fundulus stellifer									
Upper Coosa R.		1	11	17		29	16.6	.57	.21
Middle Coosa R.		5	26	27		58	16.4	.64	.17
Alabama R.	1		36	17		54	16.3	.56	.15
Cahaba R.	1	17	33	1		52	15.7	.58	.16
Tallapoosa R.			6	3		9	16.3		
Chattahoochee R.		5	14	4		23	16.0	.64	.27

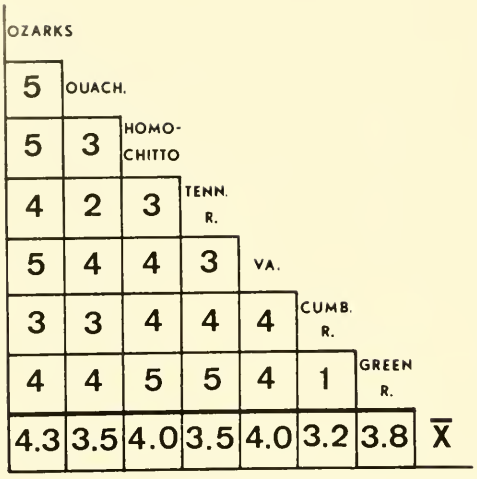

Figure 3. Matrix giving the number (out of 6) of meristic characters in which the various populations of *Fundulus catenatus* differ significantly. $\bar{X}$ is the arithmetic average number of significantly different characters for each population. Population labels apply to the horizontal row to the left of the label and the vertical column below the label.

ber (Table 5) is 11 to 16. Average number of lateral scale rows ranges from 13.2 (Ouachita, Green River) to 14.4 (Virginia). The Virginia sample average differs significantly from the Tennessee River average (13.7).

Number of lateral scales is given in Table 6. In the aquarium studfish fight and individuals may be almost completely scaled. Though such intensive fighting may be an artifact caused by crowding in the aquarium, many studfish collected in the wild show patches of regenerated scales. These individuals were not counted unless the original number of scales was obvious. However, there is also considerable irregularity of scale rows that does not involve regenerated scales. When I felt that the lateral scale count was questionable, I counted the lateral scales on the right side and discarded the counts if there was more than 1 scale difference. Thus, even though the count is often difficult to make, the wide range of variation (38–52) seems real. The average (42.4) for the Homochitto River Population is significantly the lowest. Other populations with low average number of lateral scales are the Ozarks (avg. 43.5) and Ouachita (avg. 44.5) populations. These southern and western populations thus contrast with the eastern populations which have averages ranging from 45.3 to 46.4. These differences are, however, far below the level required to justify recognition of subspecies.

Figure 3 is a matrix showing the number of meristic characters (out of six) in which the various populations of *F. catenatus* differ. The average number given for each population is the arithmetic mean and is an unweighted estimate of the amount of divergence of each population from all other *F. catenatus* populations. The Ozarks population is most divergent and the Cumberland River population the least divergent.

Table 5. Number of lateral scale rows in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	11	12	13	14	15	16	17	18	N	Average	SD	2SE
Fundulus catenatus												
Ozarks		6	70	112	12				200	13.6	.68	.10
Ouachita		20	46	31	3				100	13.2	.78	.16
Homochitto R.	1	22	29	37	10	1			100	13.4	1.00	.20
Tennessee R.		6	35	67	13	1			122	13.7	.74	.13
Virginia			8	24	23	5			60	14.4	.99	.26
Cumberland R.	2	12	42	37	7				100	13.3	.85	.17
Green R.		15	48	37					100	13.2	.69	.14
Indiana			2	4					6			
Fundulus stellifer												
Upper Coosa R.			1	11	21	13	2		48	15.1	.87	.25
Middle Coosa R.			3	27	36	35	17	1	119	15.4	1.09	.20
Alabama R.				12	46	12	3		73	15.1	.70	.16
Cahaba R.				5	42	26	14		87	15.6	.83	.18
Tallapoosa R.					6	2	1		9	15.4		
Chattahoochee R.			1	7	15	6	2		31	15.0	.91	.33

Table 6. Number of lateral scales in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	N	Average	SD	2SE
Fundulus catenatus																			
Ozarks		5	13	18	35	33	30	27	15	13	8		1	1		199	43.5	2.29	.33
Ouachita			1	8	11	13	16	24	12	10	1	3	1			100	44.5	2.04	.40
Homochitto R.	3	6	12	5	27	17	12	12	6							100	42.4	2.01	.40
Tennessee R.		2	2	6	9	12	16	14	25	13	11	4	5	2	1	122	45.3	2.60	.47
Virginia				3	1	8	3	10	13	7	8	4	2	1		60	45.7	2.34	.60
Cumberland R.				2	5	6	14	10	11	18	15	8	6	2	3	100	46.4	2.56	.51
Green R.		1		5	7	12	13	11	14	16	14	2	3	2		100	45.4	2.46	.49
Indiana					2				3	1						6			
Fundulus stellifer																			
Upper Coosa R.		1	2	5	4	6	5	6	5	5	5		4	1		49	44.7	3.01	.86
Middle Coosa R.		2	1	4	5	10	14	19	21	18	17	9	6	3		129	45.9	2.51	.44
Alabama R.	1	3	3	9	12	12	13	7	4	6	2	1				73	43.3	2.36	.55
Cahaba R.	3	3	7	15	12	17	12	8	6	3	2					88	42.7	2.27	.49
Tallapoosa R.							1	2		1		1	3		1	9	42.2		
Chattahoochee R.					1	6	5	6	7	6						31	44.9	1.52	.55

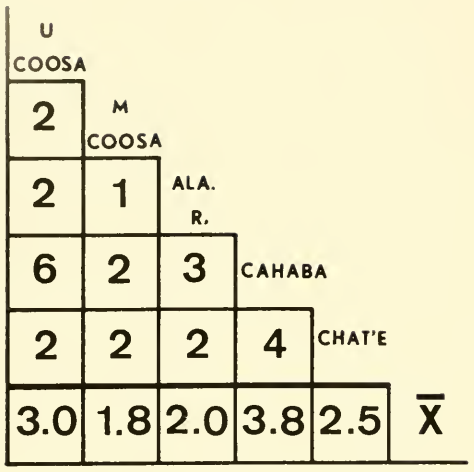

Figure 4. Matrix giving the number (out of 6) of meristic characters in which the various populations of *Fundulus stellifer* differ significantly. Interpretation as for Figure 3.

Fundulus stellifer

Fundulus stellifer populations from the Alabama River–Coosa River system show a trend toward high average number of rays in all fins (pelvic not counted) upstream and low average number of rays downstream. The Cahaba River sample tends to have the lowest average numbers of fin rays.

Number of dorsal rays (Table 1) varies from 12 to 16 and all populations have a modal number of 14. However, means (14.3) for the Upper Coosa River and Chattahoochee River samples are significantly higher than means for the other populations. Number of left pectoral rays (Table 3) varies from 15 to 19 and the Cahaba River average (16.2) is significantly lower than averages for other Alabama drainage populations. Caudal ray number (Table 4) varies from 14 to 17. With the exception of the Cahaba River and the Chattahoochee River samples, individuals with 16 or 17 caudal rays occur in all populations in subequal proportions. These samples have unusually high percentages of individuals with 15 caudal rays and the Cahaba River average (15.7) is significantly the lowest for the Alabama drainage samples.

Trends in distribution of average numbers of scales do not parallel distribution of fin ray averages. Left lateral scale row number varies from 13 to 18 (Table 5). The Cahaba River sample has the highest average number (15.6) and the Chattahoochee River sample the lowest (15.0). The remarks above regarding the causes of extreme variation in lateral scale number of *F. catenatus* also apply to *F. stellifer*. Observed range of variation in lateral scale number (Table 6) is 38 to 52. The Cahaba and Tallapoosa River samples have the lowest average number of lateral scales (42.7, 42.2) and the Middle Coosa River sample the highest (avg. 45.9).

Figure 4 is a matrix for *F. stellifer* drawn in the same fashion as Figure 3. The Cahaba River sample has the highest average number of significantly different meristic characters and the Middle Coosa River sample the lowest.

Comparison of *Fundulus catenatus* and *Fundulus stellifer*

Dorsal Rays—*Fundulus stellifer* tends to have fewer dorsal rays than *F. catenatus* but there is almost complete overlap in observed range of variation (none with 17 rays for *F. stellifer*, 9 from the Ozarks sample for *F. catenatus*). The Middle Coosa River, Alabama River, Cahaba River and Tallapoosa River samples of *F. stellifer* have lower average numbers of dorsal rays than any *F. catenatus* sample (Table 1), but the Upper Coosa River and Chattahoochee River samples have higher average numbers than three of the *F. catenatus* samples and are identical to the Tennessee River sample (avg. 14.3) in this parameter.

Anal Rays—The Homochitto River *F. catenatus* sample is not separable from the Upper Coosa River and Chattahoochee River *F. stellifer* samples of this character. The other three large samples of *F. stellifer* had lower averages than all *F. catenatus* and the other six large *F. catenatus* samples had higher averages than all *F. stellifer* samples.

Left Pectoral Rays—Range of variation in average number of left pectoral rays (16.0 to 17.8) for the *F. catenatus* samples includes the range of variation (16.2 to 16.9) seen in *F. stellifer* samples.

Caudal Rays—Only the Cahaba River *F. stellifer* sample average (15.7) is significantly outside the range of variation in this parameter for *F. catenatus* samples (16.2 to 16.7).

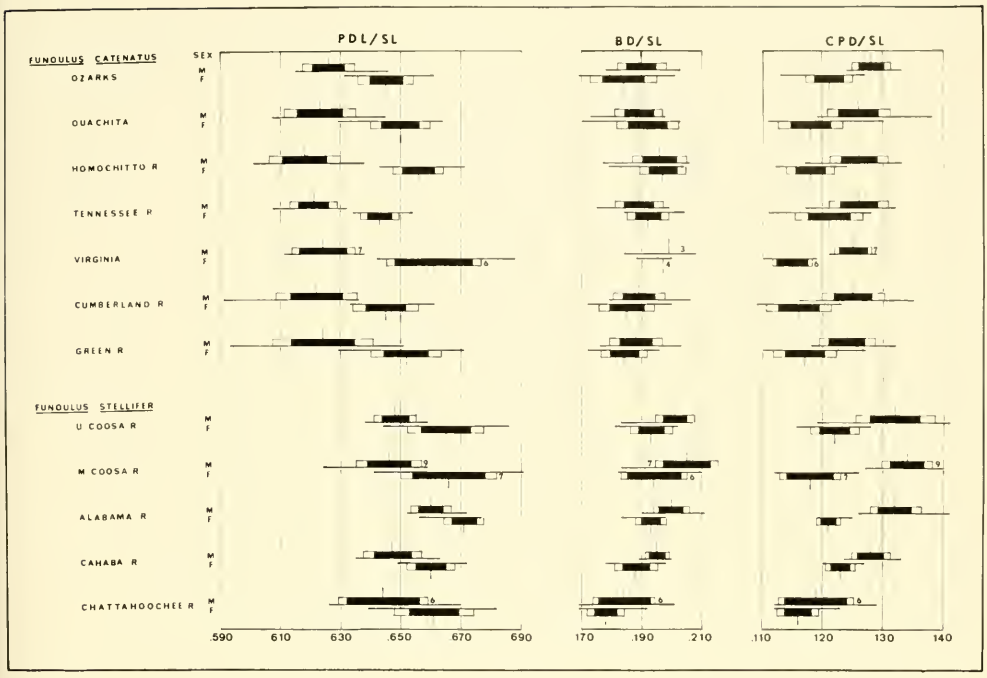

Figure 5. Geographic variation in morphometric characters in *Fundulus catenatus* and *Fundulus stellifer*. Samples are 10 individuals except where number is given. PDL-Predorsal Length, BD-Body Depth, CPD-Caudal Peduncle Depth, SL-Standard Length. Drawn following Hubbs and Hubbs (1953).

Lateral Scale Rows—There is considerable overlap in range of variation in this character (*F. catenatus*, 11 to 16; *F. stellifer*, 13 to 18), but it is the most divergent of the meristic characters studied. The highest average for an *F. catenatus* sample (14.4, Virginia Population) is significantly lower than the lowest *F. stellifer* average (15.0, Chattahoochee River Population).

Lateral Scales—The range of average number of lateral scales for *F. catenatus* samples (42.4 to 46.4) includes the range of variation (42.7 to 45.9) for *F. stellifer* samples.

Morphometric Characters

There is considerable variation in body proportions in both species of studfish. Several characters also exhibit marked sexual dimorphism. In addition to the characters shown in Figures 5, 6, and 7, other proportional measurements involving characters mentioned above in the section on Material and Methods were made but showed only random variation and are not presented.

There is striking sexual dimorphism in Predorsal Length (Figure 5) in *F. catenatus* and to a lesser extent in *F. stellifer*. Even though the body outline of males and females is different (Figure 1) there is no sexual dimorphism of Body Depth in either species but males do tend to have deeper caudal peduncles than females. This character is fairly consistent from population to population in *F. catenatus*, but there is considerable variation in *F. stellifer*. Male *F. stellifer* from the Coosa River and Alabama River populations tend to have deeper caudal peduncles than most *F. catenatus* males. The Cahaba River population resembles *F. catenatus* in this character and the Chattahoochee River population appears most slender.

Head Length (Figure 6) varies considerably within populations but there does not seem to be a consistent pattern of either sexual or geographic variation in *F. catenatus* except that Tennessee River females have significantly shorter heads than males. The Alabama River *F. stellifer* also show signifi-

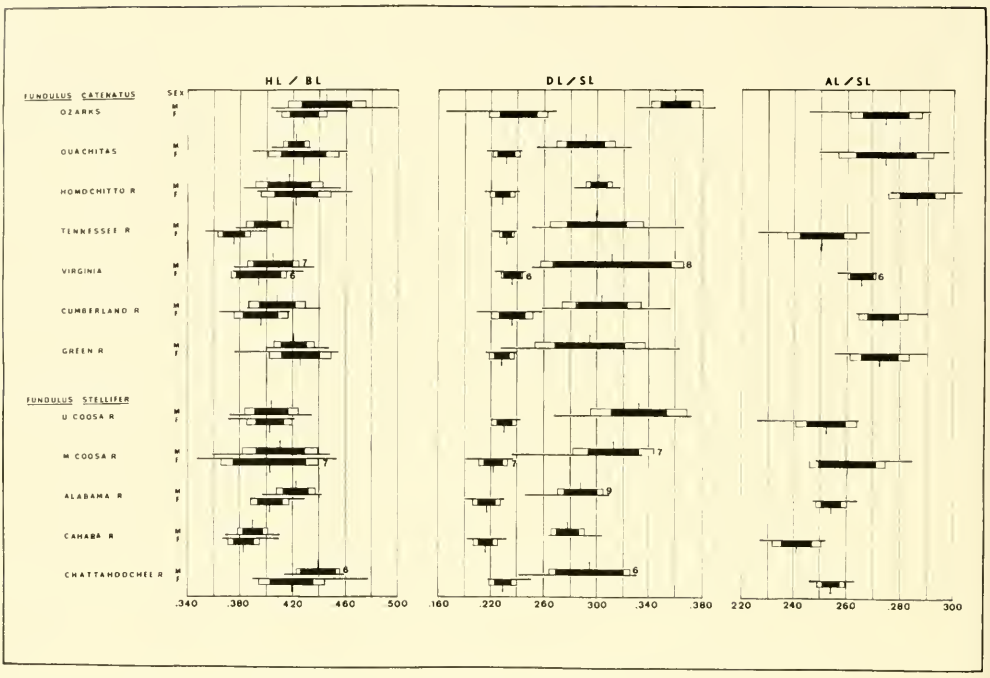

Figure 6. Geographic variation in morphometric characters in *Fundulus catenatus* and *Fundulus stellifer*. Samples are 10 individuals except where number is given. HL-Head Length, BL-Body Length, DL-Depressed Dorsal Fin Length, AL-Depressed Anal Fin Length, SL-Standard Length. Drawn following Hubbs and Hubbs (1953).

cant sexual dimorphism in this character and difference between the Alabama and Cahaba River populations is significant when males are compared with males and females with females. There is also a significant difference between Cahaba and Chattahoochee River populations.

Dorsal Fin Length (Figure 6) shows a high degree of sexual dimorphism with little overlap between the sexes in either species. With the exception of Ozarks population *F. catenatus*, there is little variation in female dorsal fin length. Part of the variation seen in the males is seasonal. Nuptial males have slightly elongated dorsal fins.

Male studfish have dorsal and anal fins of approximately the same length but anal fin length averages 17% greater than dorsal fin length in female *F. catenatus* and 13% greater in female *F. stellifer*. The anal fin of the female digs into the substrate during spawning and her anal rays are stouter than the dorsal rays. In female studfish longer anal fins tend to be elongate and pointed but shorter anal fins tend to be rectangular. The Tennessee River females have significantly shorter anal fins than those of other *F. catenatus* populations. The Homochitto River females have significantly longer anal fins than females from other eastern populations of *F. catenatus*. The means for *F. stellifer* samples, except the Middle Coosa River sample, are significantly lower than those of *F. catenatus* samples except for the Tennessee River population. None of the *F. stellifer* samples can be separated from the Tennessee River *F. catenatus* sample using this character. The Cahaba River sample mean is significantly lower than the other *F. stellifer* sample means except for the Upper Coosa River sample mean.

Both species show sexual dimorphism in Pelvic Fin Length. The observed range of P2L/SL for *F. catenatus* females is 0.102 to 0.136, for *F. stellifer* females 0.106 to 0.131, average for both 0.115. This average ratio is compared with the distribution of P2L/SL for males in Figure 7. Large males and

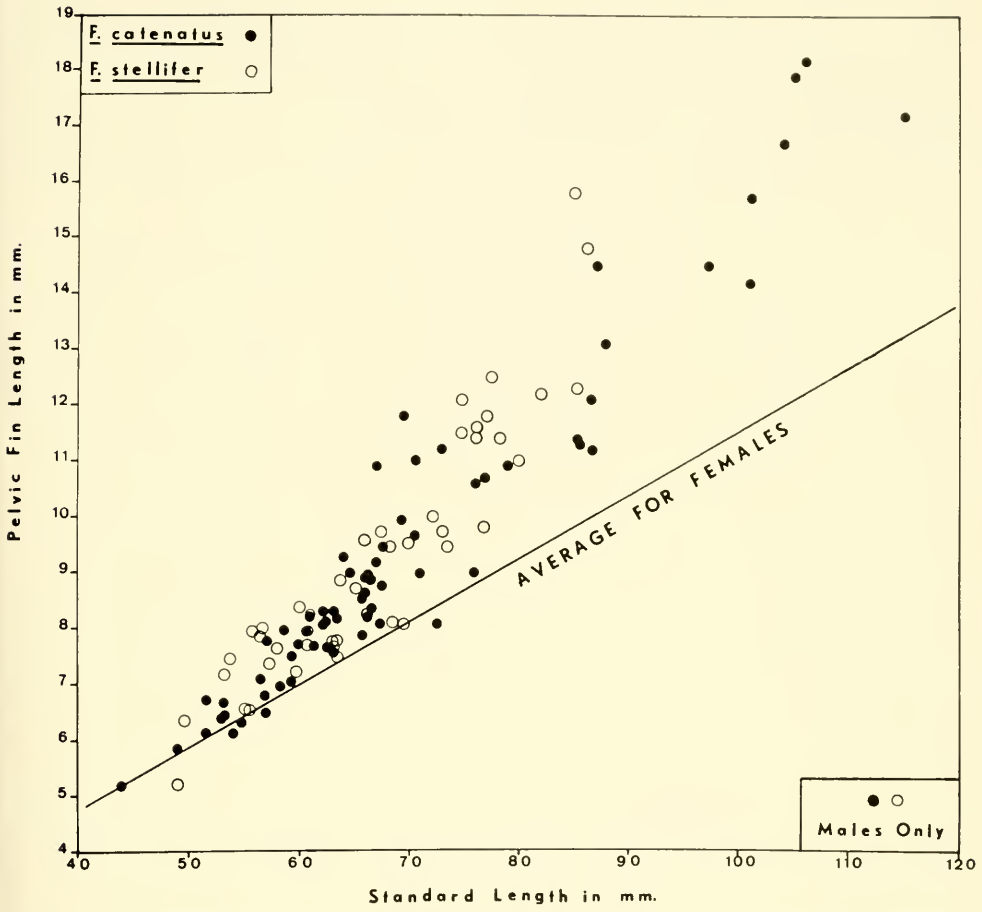

Figure 7. Relationship between Pelvic Fin Length and Standard Length in *Fundulus catenatus* and *Fundulus stellifer*. Pooled data from all populations, including largest males from each.

smaller males in breeding condition tend to have proportionately longer pelvic fins in both species.

Male Contact Organs and Breeding Colors

During the breeding season, males of *F. catenatus* and *F. stellifer* develop contact organs (Newman, 1907, 1909). These are particularly noticeable on the anal fin rays, and the presence of contact organs on the anal fin of *F. stellifer* was noted by Fowler (1916, Pl. 1). The distribution of contact organs is similar in the two studfishes (Figure 8), but usually *F. catenatus* males are less "prickly" than *F. stellifer* males, and contact organs on the sides of the body are confined to an area between the bases of the dorsal and anal fins. Figure 8A shows the distribution of contact organs usually seen on breeding *F. catenatus* males, but there are often no contact organs on the dorsal or pectoral fins in this species. In both species a few anal fin contact organs may be present in males taken at any time of year. As the fish come into breeding condition, the anal fin organs are proliferated and contact organs on the cheeks and opercles develop concurrently or soon after. Development of the lateral contact organs begins at midbody between the bases of the dorsal and anal fins and in general proceeds further anteriad and posteriad

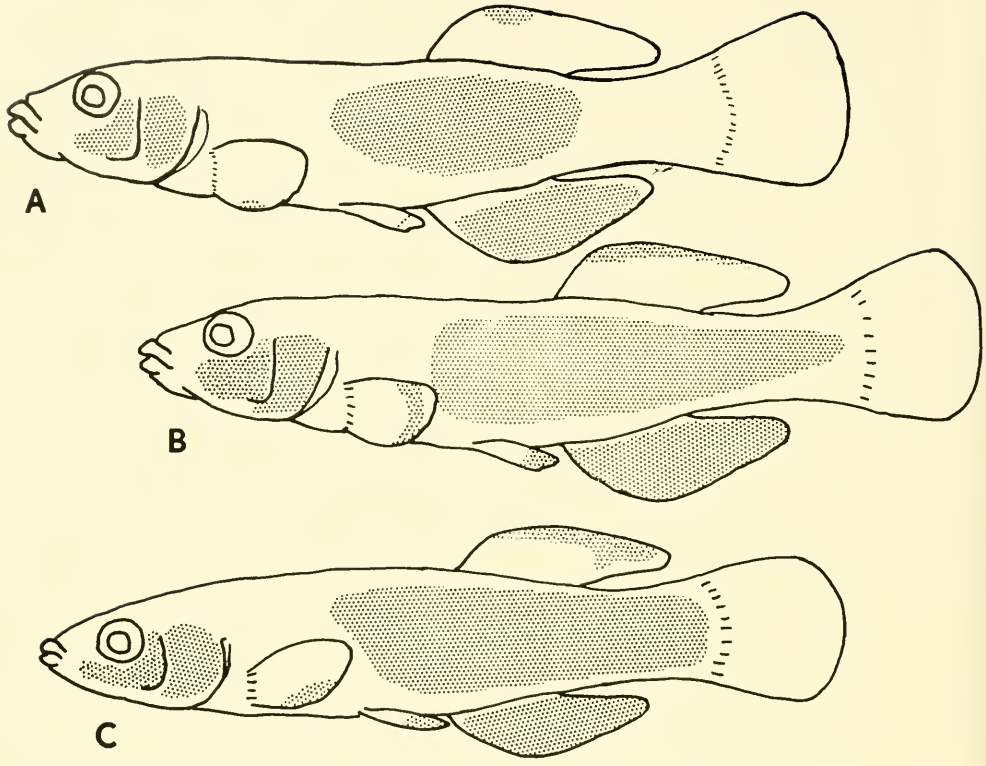

Figure 8. Sketches of studfish males; dotted area represents extent of development of contact organs. A. Usual extent of contact organs in *Fundulus catenatus*. B. Unusually extensive development of contact organs in *Fundulus catenatus*. C. Usual extent of contact organs in *Fundulus stellifer*.

in *F. stellifer* than in *F. catenatus* (Figure 8A and C). I have seen only two specimens of *F. catenatus* with contact organs on the lateral scales of the caudal peduncle; one of these is sketched in Figure 8B. Development of contact organs on the pelvic rays, on both sides of the fin, is seen in most high males but presence of contact organs on the pectoral fins is less common. About half the breeding males of both species have a few organs on the anteroventral surface of the pectoral fin. Occasional males have one or two contact organs on the posterodorsal surface of the pectoral fin. Less than half the *F. catenatus* males examined had contact organs on the dorsal fin, and these were generally confined to the anterior half of the fin. Almost all *F. stellifer* males had dorsal fin contact organs with the greatest concentration in the posterior half of the fin. I examined a number of breeding female studfish and found no contact organs.

Female studfish do not show seasonal color changes. The patterns shown in Figure 1B and D are seen in live specimens in varying shades and intensities of brown. Nonbreeding males resemble the females in drab coloration and pattern, but nuptial males are spectacularly colored.

Fundulus catenatus males occur in two color forms. As given in Table 7, various percentages of males exhibit a subterminal black band in the caudal fin. This band intensifies during the breeding season but is discernable in all months of the year. Placement and sharpness of the band are variable. Some males, particularly those from the Cumberland and Green rivers, have a wide (about 2 mm) yellow to orange band distal to the black band. In others, particularly those from the Ouachita and Ozarks popu-

Table 7. Occurrence of males with black caudal fin band in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	Number	Percent with Band
Fundulus catenatus		
Ozarks	109	44
Ouachita	12	42
Homochitto	60	0
Tennessee	30	20
Virginia	14	36
Cumberland	30	43
Green	34	12
Fundulus stellifer		
All	142	58

lations, the yellow to orange band may be quite narrow. In two of the Ouachita specimens, the black band is essentially terminal, as it is in *F. stellifer*. The margins of the band, particularly the distal margin, are usually sharp, but in some males it is a black zone rather than a sharply defined band. The band is represented by disconnected blotches of black pigment in many males from the Ozarks population.

Only one of the males examined showed any concentrated black pigments at the margin of the dorsal fin (CU 49857, Cumberland River population). His black dorsal pigment resembles that of an *F. stellifer* male with less than maximum expression of this character. Dorsal fin coloration in breeding *F. catenatus* males varies from dark slate blue overall, which appears blue in the water, to yellow distally and translucent yellow-grey proximally, which looks yellow in the water. When the dorsal fin is dark there is sometimes a narrow yellow or orange margin but I have never seen the white or cream margin of the dorsal and caudal fin described by Garman (1895). The interradial membranes of the dorsal and the proximal halves of the anal, caudal, and sometimes the pelvic and pectoral fins are marked with elliptical orange spots. These are largest and most intense in the dorsal fin. The anal fin is transparent yellow-grey proximally and bright translucent yellow distally. The color pattern of the pectoral and pelvic fins is similar but not so intense. The caudal fin is greyish and translucent in transmitted light but blue in reflected light. Males without the black subterminal band exhibit the yellow to orange terminal band on the caudal fin.

The head pattern is similar to that of *F. stellifer*. There is a very conspicuous light blue or blue-green iridescent patch from the upper anterior quarter of the orbit to the corner of the gape. The iris is bright yellow-green to dark with a silver reflecting margin around the pupil. In some specimens there is an area of dark pigment directly ventral to the preocular light patch. The cheeks and opercular area are marked with a random pattern of circular orange spots. Those on the operculum are about twice the diameter of the others on head and body. The lower half of the head and the gular and branchiostegal regions are yellow, but the upper lateral surfaces of the head are livid yellow-green. The dorsum and top of the head are olive grading into either sky blue or green laterally. The color of the sides depends on the angle and quality of the light striking them. There may be an area of disordered orange spots just behind the head or all the spots may be linearly arranged, one spot per scale, from the gill openings to the bases of the caudal rays. The spots are slightly separated but give the impression of 10 to 12 continuous orange lines down the sides. Viewed in the water in sunlight against a dark background, a male in high color gives the impression of a fish with a solid red-orange body.

Fundulus stellifer males also occur in two color forms. A black margin on the dorsal and caudal fins may be either present or absent. Data from all populations are pooled in Table 7, but males of both kinds were present in all populations where reasonable size samples were available. A few males with black borders on the dorsal and caudal fins also had less distinct black borders on the pectoral and pelvic fins.

Body color in males is a livid sky blue, grading into white on the belly and bluish-brown on the dorsum. The fins are clear yellow, and there are rows of elliptical orange spots in the interradial membranes of the dorsal fin and in the basal halves of the caudal and anal fins. There may also be a few such spots near the base of the pectoral fins. If the caudal fin border is absent the caudal fin may be slate grey rather than yel-

low. There is a brilliant iridescent pre-ocular patch as in *F. catenatus*, but it is yellow-green rather than bluish. The iris is also yellow-green, and there is a light blue-green, diffuse iridescent patch on the gill cover behind the eye. The orange spots on the head are irregular in size and arrangement like those of *F. catenatus* and the body pattern is similar to the head pattern. Dark orange spots are concentrated on the dorsolateral region of the body with only a few scattered on the lower sides. The spots on the caudal peduncle are linearly arranged but not so consistently as those of *F. catenatus*.

Other Characters

Male studfish average larger than females in most collections; however, the largest *F. catenatus* I have seen was a 118 mm SL female from the Ozark population. Dr. David A. Etnier kindly informed me of an unusually large 98 mm SL male *F. stellifer* from the Conasauga River in Polk Co., Tennessee. The largest males in the collections listed under Material Examined were 86 or 87 mm SL. With the exception of the Homochitto population, a large *F. catenatus* male is over 100 mm SL. The Homochitto population seems dwarfed and the largest specimen (of 768) from there was an asexual individual 76 mm SL.

Fundulus catenatus has regular rows of spots on the sides of the body. These dots are red or red-orange in breeding males but an alcoholic male specimen appears plain because of leaching of pigment by the preservative. The pattern in *F. stellifer* is similar but with fewer spots not necessarily on the centers of the exposed scale fields nor arranged in the orderly manner seen in *F. catenatus*. The few Tallapoosa River specimens seem more *F. catenatus*-like than specimens from other *F. stellifer* populations in the arrangement of their lateral spots. In addition to the difference in arrangement of the lateral dots there is a consistent difference in the pigmentation of the scale borders. As seen in Figure 1, *F. stellifer* has a regular cross-hatched appearance in contrast to the more uniform background pattern of *F. catenatus*. The cross-hatching extends to the base of the anal fin in *F. stellifer* and stops a few scales short in *F. catenatus*. The differences in development of scale border pigmentations allow identification of juveniles, although they are more similar than are the adults (Figure 9). I have not seen enough very small specimens of the two species to point out differences between them at sizes below approximately 14 mm SL.

The intestinal contents of *F. stellifer* seem finely ground in comparison to those of *F. catenatus*, probably as a result of chewing with the stout pharyngeal molars (Figure 10). The pharyngeal bones of *F. stellifer* are massive compared to those of similar size *F. catenatus* and molars are developed both on the inferior pharyngeal bones and on the pharyngobranchials. The corresponding teeth in *F. catenatus* are pegs with hooked tips. They resemble the hooked blade-like teeth of other species of *Fundulus*, for example *F. notatus*, but are stronger with an expanded circular cross section. Snails form an important item of diet for *F. stellifer* (J. D. Satterfield, personal communication) and I have seen snail shells in the feces of *F. catenatus*. One might guess from its comparatively more massive pharyngeal bones and dentition that of the two, *F. stellifer* eats more mollusks.

Discussion

Fundulus catenatus is an aggressive and adaptable small-stream fish widely distributed in the upland areas of the Mississippi Valley. It probably originated in the eastern uplands where I have recognized four distinct populations in roughly a third of the range. The distribution of *F. catenatus* crosses a number of zoogeographic barriers. Particularly striking is the uniformity of the Ozarks population over an area approximately equal to the eastern uplands. Many Ozarkian fishes have been sufficiently isolated in the White River system and the Missouri Ozark streams tributary to the Missouri and Mississippi Rivers to diverge even to the species level (Gilbert, 1964, pp. 104-5), but *F. catenatus* samples from the two areas are not significantly different.

The broadly-ranging Ozark population is the most divergent in terms of meristic characters studied (Figure 3). It seems closest to the Cumberland River population, than to the Tennessee and Green River populations. Not only does relative morphological uniformity over such a large area suggest

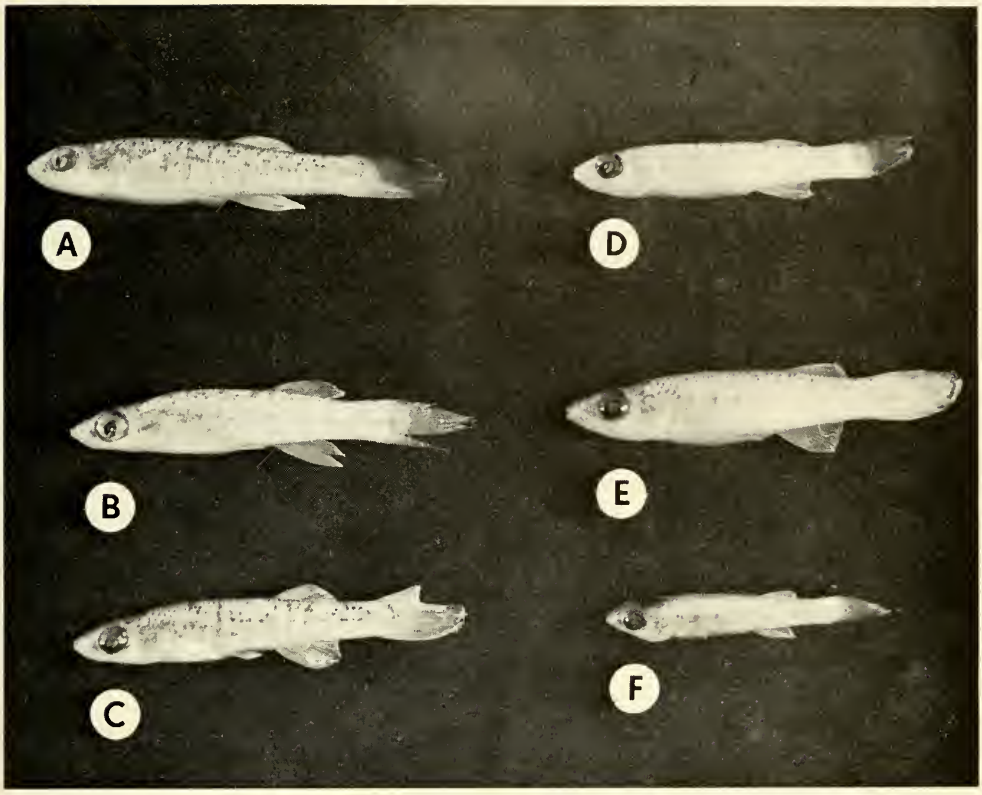

Figure 9. Juvenile studfish—*Fundulus catenatus*: A. TU 15132 (SL 24.6 mm), B. KU 6661 (SL 24.1 mm), C. KU 11550 (SL 24.2 mm). *Fundulus stellifer*: All from JDS, D. SL 22.1 mm, E. SL 25.4 mm, F. SL 17.2 mm.

that the Ozarks population is of recent origin compared to the populations in the eastern uplands, but there is evidence that Ozarkian *F. catenatus* are still rapidly moving into suitable habitats around the margins of the Ozarks. As mentioned above, *F. catenatus* seems to have crossed the Missouri River and become established in the Big Creek system in recent historical time. The recent Neosho River records may be from a population established naturally from the White River (Branson, 1967) or from bait releases (Hall, 1956). In any case, *F. catenatus* is common there now. It seems significant that *F. catenatus* is absent from the Flint Hills region of Kansas, even though several other species with Ozarkian affinities occur there (Cross, 1967). Probably *F. catenatus* was not present in the Ozarks when access to the Flint Hills was possible.

The Ouachita population shows surprising divergence from the Ozarks population, is most like the Tennessee River population and is not particularly divergent from the other eastern populations. It thus seems probable that the Ozarks and Ouachita populations originated from separate invasions of the Interior Highlands by fish from the eastern populations.

The widely disjunct Homochitto population does not show as much divergence in meristic characters as the Ozarks population but seems unique in the absence of black-banded males and the small maximum adult size. Conditions in the Homochitto drainage are considerably different from those in the Interior Highlands or eastern uplands and the characters mentioned above could have strong adaptive significance. The small size of the Homochitto fish may be correlated with reduced food supply. In any case, the numbers taken in the collections I have ex-

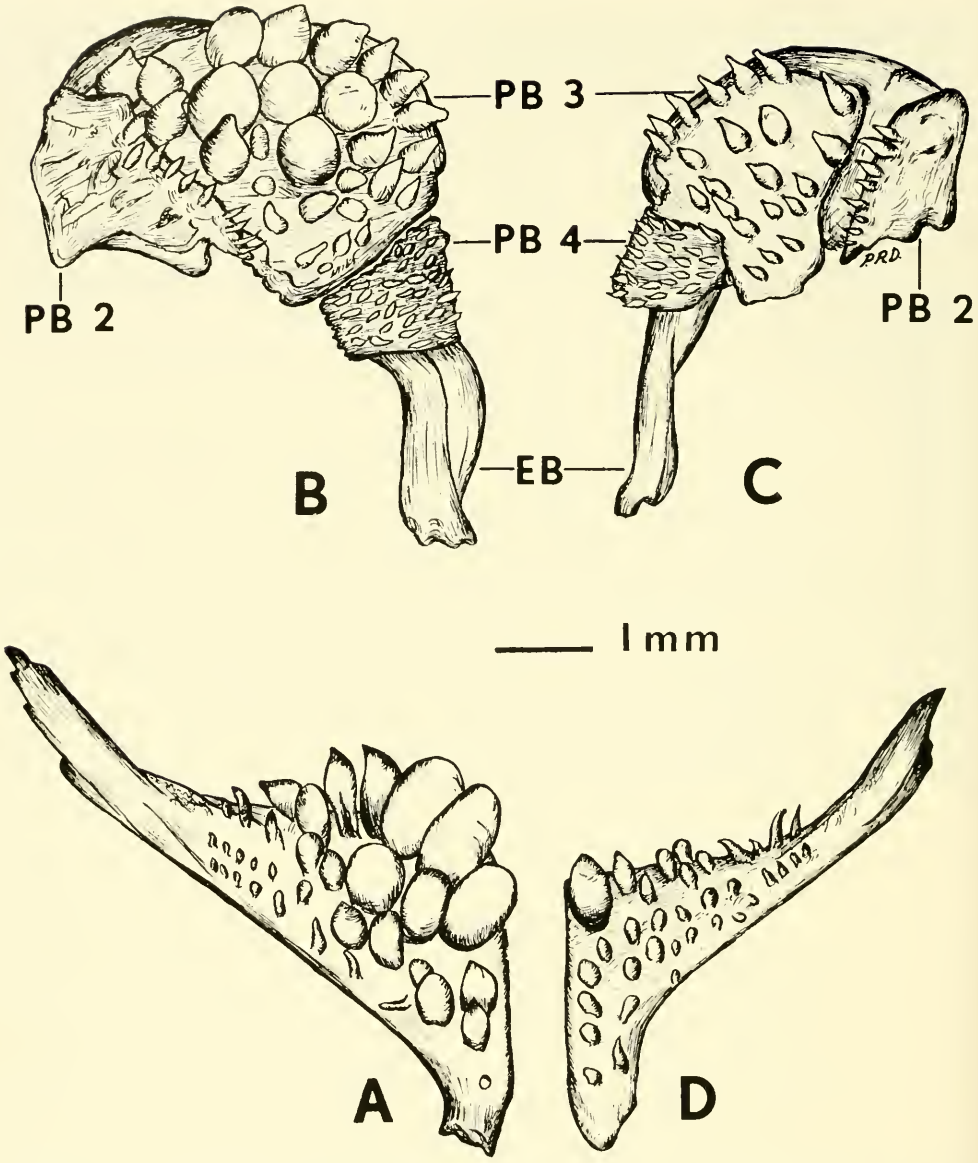

Figure 10. Pharyngeal arches of studfish; A. and B. from a 71.4 mm SL *Fundulus stellifer* (TU 35029), C. and D. from a 70.0 mm SL *Fundulus catenatus* (SIUE, JET 66-10). A. Right lower arch, dorsal view, anterior down. B. Right upper arch, ventral view, anterior to the upper left. C. Left upper arch, ventral view, anterior to upper right. D. Left lower arch, dorsal view, anterior down.

amined indicate that *F. catenatus* is successful in maintaining relatively dense populations in the Homochitto River system. The small fish and southern location of this population suggest a similarity to *F. stellifer*, but their pharyngeal teeth, lateral scale row count and pigment patterns show no such similarity. Perhaps gene flow with other populations of *F. catenatus* is maintained even though there is a broad expanse of unsuitable habitat separating the Homochitto River from the *F. catenatus* populations in the cen-

tral highlands. The Homochitto fish may represent a postglacially isolated relict of a population distributed through the Lower Mississippi Valley during glacial periods when lowered sea level caused rejuvenation of small tributaries of the Lower Mississippi River. Alternatively the population could have been established by individuals tributary-hopping during interglacial periods when the Mississippi River was cooler, clearer and swifter flowing than it is today. If this were the case, the Homochitto population might have received immigrant individuals from both eastern and western populations.

The major observed differences between *F. catenatus* and *F. stellifer* are: general pigmentation, distribution of contact organs, male breeding colors and pharyngeal dentition. *Fundulus stellifer* could be duplicated by relatively slight changes in an *F. catenatus* stock and indeed a few *F. catenatus* individuals, as noted above, show tendencies toward the *F. stellifer* condition. Pharyngeal dentition is very similar in small individuals of the two species. Greenwood (1964) found differences of approximately the same magnitude between the pharyngeal bones and associated structures of wild individuals and an aquarium-raised specimen of the snail-eating cichlid *Astatoreochromis alluaudi*. The aquarium-raised specimen had an adequate diet but did not receive snails until late in life. Its pharyngeal teeth and bones were less massive (Figure 3, p. 5, Greenwood, 1964) than those of any of the wild individuals. The differences between the pharyngeal teeth and bones of larger *F. catenatus* and *F. stellifer* (Figure 10) may thus be correlated with difference in food habits rather than with difference at the genetic level. Whatever their cause, differences between the two species seem to be consistent.

The ancestors of *F. stellifer* were probably a stock much like present day *F. catenatus* which became isolated in the Alabama River system. Whether this was the result of a major faunal exchange between the Tennessee and Alabama systems or the result of local stream capture is not clear, but the latter seems more likely. If *F. catenatus* had entered the Alabama system in large numbers, stabilizing selection acting on the somewhat generalized and flexible *F. catenatus* gene pool would probably have produced just another population of *F. catenatus*, one perhaps resembling the Homochitto population.

If the ancestor of *F. stellifer* was a *F. catenatus*-like fish, the more massive pharyngeal dentition of *F. stellifer* is thus probably a result of further specialization for snail eating. It is my impression that, even though the faunas of the Alabama and Chattahoochee systems are rich in fish species, the density of small fishes in streams inhabited by *F. catenatus* is much higher than in streams inhabited by *F. stellifer*. The varieties and kinds of habitats seem to be similar in the two areas, so perhaps the greater number of individual fishes in *F. catenatus* habitat is correlated with availability of food organisms. If *F. stellifer* lives in a less rich habitat, further specialization of snail eating would be of adaptive value by increasing utilization of a food supply little used by other small stream fishes. The evolution of *F. stellifer* may have been relatively rapid and recent because the characters separating it from *F. catenatus* seem of obvious adaptive significance but characters of less obvious adaptive significance show little divergence.

Material Examined

Collections are listed by population, state, county and museum number. Collections deposited Illinois Natural History Survey (INHS) and Southern Illinois University, Edwardsville (SIUE) are not given catalog numbers. Complete data are given for the syntopic collection. Other museum abbreviations are used as follows: The Academy of Natural Sciences of Philadelphia, ANSP; Auburn University, AU; University of Alabama Ichthyological Collection, UAIC; Cornell University, CU; Indiana University, IU; University of Kansas, Museum of Natural History, KU; University of Michigan, Museum of Zoology, UMMZ; Smithsonian Institution, USNM; personal collection of James D. Satterfield, JDS; Tulane University, TU; University of Richmond, UR. Number of specimens in each collection is given in parentheses. All specimens were examined and counts were made on 885 *F. catenatus* and 386 *F. stellifer* from the collections listed below. Distribution of these collections is shown in Figure 2.

Allopatric *Fundulus catenatus*

Ozarks.—Missouri: Lincoln Co.; SIUE (14), SIUE (44)—Franklin Co.; INHS (7)—Carter Co.; UMMZ 104684 (25)—Wright Co.; INHS (3)—Osage Co.; INHS (6)—Phelps Co.; INHS (25)—Morgan Co.; KU 6501 (11)—Camden Co.; UMMZ 150336 (14)—Dallas Co.; KU 7837 (19)—Hickory Co.; KU 7811 (6)—Crawford Co.; UMMZ 148448 (9)—Dent Co.; INHS (9), INHS (7), KU 7614 (11)—Wayne Co.; UMMZ 117246 (12)—Cape Girardeau Co.; INHS (8), INHS (2), INHS (25)—Madison Co.; INHS (6)—Shannon Co.; KU 7652 (10), KU 7674 (2), UMMZ 102491 (38)—Dade Co.; KU 5503 (50)—Green Co.; KU 7856 (19)—Taney Co.; KU 10926 (112)—McDonald Co.; CU 42324 (6). Arkansas: Sharp Co.; UMMZ 116378 (40)—Marion Co.; KU 8012 (53), KU 9864 (31)—Boone Co.; UMMZ 123522 (88), KU 6661 (8)—Newton Co.; UMMZ 175430 (6)—Madison Co.; UMMZ 123892 (43), UMMZ 123425 (54), UMMZ 123859 (27)—Washington Co.; UMMZ 127769 (7), CU 36506 (2).

Ouachita.—Arkansas: Pulaski Co.; INHS (2)—Saline Co.; CU 42245 (17)—Garland Co.; TU 14250 (3)—Montgomery Co.; KU 6166 (25), KU 6143 (7)—Pike Co.; KU 6133 (48), UMMZ 81112 (8), KU 6135 (11)—Howard Co.; KU 6115 (5)—Polk Co.; KU 6907 (10), UMMZ 81110 (2).

Homochitto River.—Mississippi: Amite Co.; UMMZ 144728 (2), UMMZ 155340 (12), TU 7447 (18)—Franklin Co.; TU 11991 (12), TU 16623 (142), TU 19766 (57), TU 19851 (32), TU 15132 (141), TU 23952 (78), UMMZ 161204 (4), TU 7208 (176)—Lincoln Co.; TU 32916 (32), TU 28895 (60)—Copiah Co.; UMMZ 154371 (2).

Tennessee River.—Tennessee: Sevier Co.; KU 8935 (1)—Coffee Co.; TU 30299 (61)—Bedford Co.; UMMZ 121529 (1)—Lincoln Co.; TU 30289 (7)—Marshall Co.; KU 10684 (12)—Marshall and Maury Cos.; UMMZ 121477 (44)—Lewis Co.; UMMZ 105213 (28)—Wayne Co.; UMMZ 177703 (4)—Humphrey Co.; UMMZ 168314 (33)—McNairy Co.; TU 10593 (2). Tennessee: Claiborne Co.; CU 56009 (22). Alabama: Franklin Co.; UMMZ 177723 (6).

Virginia.—Virginia: ? Co.; (Holston R.), ANSP 7304-35 (32)—Smyth Co.; UR 1979 (1), UR 899 (2), UR 940 (1), USNM 40368 (3), UMMZ 96899 (11), USNM 102428 (1)—Washington Co.; UMMZ 130779 (1), UMMZ 130808 (4), UMMZ 130788 (3)—Scott Co.; CU 50078 (1), ANSP 74207 (4), ANSP 74235 (1)—Lee Co.; USNM 104043 (1).

Cumberland River.—Kentucky: Pulaski Co.; CU 50059 (26)—Wayne Co.; CU 50090 (8)—Cumberland Co.; CU 50042 (3), KU 11554 (1), INHS (2). Tennessee: Fentress Co.; KU 11532 (14), CU 50191 (6)—Overton Co.; UMMZ 125196 (2)—Clay Co.; UMMZ 125228 (3), UMMZ 125258 (13), UMMZ 125341 (3)—Jackson Co.; KU 11550 (24), CU 50028 (9)—Smith Co.; CU 49857 (19)—Putnam Co.; KU 8947 (1)—Warren Co.; UMMZ 175257 (5)—Cannon Co.; KU 11678 (10)—Sumner Co.; UMMZ 96323 (26)—Wilson Co.; KU 11588 (15)—Rutherford Co.; KU 11482 (7)—Montgomery Co.; INHS (1)—Houston Co.; INHS (8).

Green River.—Kentucky: Lincoln Co.; KU 5722 (17), KU 7253 (41)—Casey Co.; UMMZ 178028 (17)—Taylor Co.; KU 11620 (26)—Allen Co.; KU 11641 (4), INHS (20), INHS (13). Tennessee: Macon Co.; UMMZ 165377 (42), TU 14532 (25).

Indiana.—Indiana: Shelby Co.; IU 397 (5)—Johnson Co.; INHS (2).

Syntopic Collection

Tennessee River.—Georgia: Walker Co.; W Fork Chickamauga Cr. 1.3 mi. W jct. Hwy. 143 and Hwy. 341 on Hwy. 143, 23 June 1964, R. D. Suttkus and Env. Biol. Class, TU 34975 (1 ♂ *F. stellifer*, 1 ♀ *F. catenatus*).

Allopatric *Fundulus stellifer*

Upper Coosa River.—Georgia: Pickens Co.; TU 38346 (9), TU 40732 (9)—Murray Co.; TU 7334 (4), TU 27974 (5), TU 37542 (27)—Gordon Co.; TU 35029 (85)—Walker Co.; TU 27575 (1)—Whitfield Co.; USNM 200704 (4).

Middle Coosa River.—Georgia: Chattooga Co.; TU 34978 (2), TU 33367 (3)—Floyd Co.; USNM 31070 (8), USNM 101159 (1), JDS (2), JDS (140). Alabama: Cherokee Co.; JDS (73)—Etowah Co.; USNM 43475 (3)—Calhoun Co.; TU 40782 (2), UAIC 636 (6), USNM 63136 (4), USNM 200705 (6)—St. Clair Co.; UAIC 648 (6), UAIC 657 (4)—Talladega Co.; UAIC 639 (5), UAIC 880 (1), UAIC 890 (2).

Alabama River.—Alabama: Dallas Co.; TU 35357 (39), TU 32640 (28)—Wilcox Co.; TU 40325 (1), TU 2971 (1), TU 3058 (5)—Clark Co.; TU 35344 (1).

Cahaba River.—Alabama: Shelby Co.; USNM 43504 (8)—Bibb Co.; UAIC 2035 (1)—Perry Co.; TU 29899 (18), TU 30095 (15), TU 37703 (11), UAIC 962 (49).

Tallapoosa River.—Georgia: Carroll Co.; UAIC 1312 (1). Alabama: Randolph Co.; UAIC 1379 (2)—Elmore Co.; TU 15280 (3), UAIC 1279 (3).

Chattahoochee River.—Georgia: Fulton Co.; CU 28249 (2), TU 12167 (1), TU 26125 (1), AU 718 (24)—Heard Co.; AU 512 (3).

Acknowledgments

I wish to express my appreciation to curators who loaned specimens from their collections: Dr. James E. Böhlke, ANSP; Dr. John S. Ramsey, AU; Dr. H. T. Boschung, UAIC; Dr. Edward C. Raney, CU; Dr. Joseph S. Nelson, IU; Dr. Ernest A. Lachner, USNM; and Dr. W. S. Woolcott, UR. The following persons also extended every courtesy during

visits to their institutions; Dr. Philip W. Smith, INHS; Dr. Frank B. Cross, KU; Dr. Robert R. Miller, UMMZ; and Dr. Royal D. Suttkus, TU.

Drs. Reeve M. Bailey, W. L. Burger, David A. Etnier, Neal Foster, Mr. Robert E. Jenkins, Dr. George A. Moore, Mr. William L. Pflieger, Dr. John S. Ramsey, Mr. William Smith-Vaniz, and Mr. James D. Williams all aided the study by supplying color notes, locality data or other useful information. Mr. William L. Pflieger also read the manuscript and offered many helpful comments. Mr. James D. Satterfield kindly supplied considerable information from his study of *Fundulus stellifer* and allowed me to examine specimens from his personal collection. A number of SIUE students and former students, particularly Mrs. Norma Brown, Leland Hill, Dennis Trotter, Steven L. Smith and Gerald L. Smith, helped with various aspects of the study. Ronald Twillman, Gary D. Waller and Drs. Robert J. and Joyce Goldstein helped make the collections from W Fork Chickamauga Cr. in Georgia. We thank the Goldsteins for their hospitality during this collecting trip.

Figure 10 was drawn by Pamela R. Drake. The University Photographic Service assisted in preparing the Figures. Dr. Leonard C. Jones wrote a program and showed me how to operate the GE 265 time sharing computer facility at SIUE to treat the data presented in Figures 5 and 6. The study was supported by a Faculty Research Grant from the Graduate School, Southern Illinois University.

Literature Cited

Bailey, Reeve M., *et al.* 1960. A list of common and scientific names of fishes from the United States and Canada. Second Edition. *Amer. Fish. Soc. Sp. Publ.* 2:1-102.

Bass, J. C., and J. R. Triplett. 1967. An addition to the known Kansas fish fauna. *Trans. Kansas Acad. Sci.* 70(3):411.

Branson, Branley A. 1967. Fishes of the Neosho River system in Oklahoma. *Am. Midland Naturalist* 78(1):126-154.

Conant, Roger. 1960. The queen snake, *Natrix septemvittata*, in the Interior Highland of Arkansas and Missouri, with comments upon similar disjunct distributions. *Proc. Acad. of Nat. Sci. Philadelphia* 112(2):25-40.

Cross, Frank B. 1967. Handbook of fishes of Kansas. *Mus. Nat. History, Univ. Kansas Misc. Publ.* 45:1-357, 20 Figs., 4 color pl.

Fowler, Henry W. 1916. Some features of ornamentation in the killifishes or toothed minnows. *American Naturalist* 50:743-750.

Garman, S. 1895. The cyprinodonts. *Memoirs Mus. Comp. Zool.* 19(1):1-179, pls. 1-12.

Gerking, Shelby D. 1945. The distribution of the fishes of Indiana. *Investigations of Indiana Lakes and Streams* 3(1):1-137.

Gilbert, Carter R. 1964. The American cyprinid fishes of the subgenus *Luxilus* (Genus *Notropis*). *Bull. Florida State Mus.* 8(2):95-194.

Greenwood, P. H. 1964. Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis alluaudi*, and their taxonomic implications. *Proc. Linn. Soc. Lond.* 176(1):1-10.

Hall, Gordon E. 1956. Additions to the fish fauna of Oklahoma with a summary of introduced species. *Southwestern Nat.* 1(1):16-26.

Hubbs, Carl L., and Clark Hubbs. 1953. An improved graphical analysis and comparison of series of samples. *Syst. Zool.* 2:49-56, 92.

Hubbs, Carl L., and K. F. Lagler. 1947. (2nd printing, 1949). Fishes of the Great Lakes Region. *Bull. Cranbrook Inst. Sci.* 26:1-186, pls. 1-26, Figs. 1-251.

Mayer, Ernst, G. E. Linsley and R. L. Usinger. 1953. Methods and Principles of Systematic Zoology. McGraw-Hill Book Co., N. Y., i-ix, 1-328, Figs. 1-45.

Miller, Robert R. 1955. An annotated list of the American cyprinodontid fishes of the genus *Fundulus*, with the description of *Fundulus persimilis* from Yucatan. *Occas. Pap. Mus. Zool., Univ. Mich.* 568:1-125, 1 pl.

Moore, George A. 1968. Fishes, Part II, pp. 21-165, Figs. 1-112. *In*: Vertebrates of the United States (2nd Ed.), by W. F. Blair, A. P. Blair, P. Brodkorb, and F. R. Cagle. McGraw-Hill Book Co., N. Y., 616 pp.

Newman, H. H. 1907. Spawning behavior and sexual dimorphism in *Fundulus heteroclitus* and allied fish. *Biol. Bull.* 12(5):314-345, 2 pls.

Newman, H. H. 1909. Contact organs in the killifishes of Woods Hole. *Biol. Bull.* 17(2):170-180.

Ross, Robert D., and J. E. Carico. 1963. Records and distribution problems of fishes of the North, Middle, and South Forks of the Holston River, Virginia. *Virg. Agr. Exper. Station Tech. Bull.* 161:1-24.

Smith, Philip W. 1965. A preliminary annotated list of the lampreys and fishes of Illinois. *Ill. Nat. Hist. Surv. Biol. Notes.* 54:1-12.

Thomerson, Jamie E. 1966. A comparative biosystematic study of *Fundulus notatus* and *Fundulus olivaceus* (Pisces: Cyprinodontidae). *Tulane Stud. Zool.* 13(1):29-47.