A SYSTEMATIC STUDY OF TWO SPECIES COMPLEXES
OF THE GENUS *FUNDULUS*
(PISCES: CYPRINODONTIDAE)

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ABSTRACT: Two *Fundulus* species complexes, the *Fundulus heteroclitus-F. grandis* and *F. majalis* species complexes, have nearly identical overall geographic ranges (Canada to northeastern Mexico and New England to northeastern Mexico, respectively; both disjunctly in Yucatan). *Fundulus heteroclitus* (Canada to northeastern Florida) and *F. grandis* (northeastern Florida to Mexico) are valid species distinguished most readily from one another by the total number of mandibular pores (8 and 10, respectively) and the long anal sheath of female *F. heteroclitus*. *Fundulus majalis* and *F. similis* are conspecific (*F. majalis* has nomenclatural priority) and intergrade in northeastern Florida in the same region in which *F. heteroclitus* and *F. grandis* are sympatric. Overlapping populations in other species groups of fishes, notably *Sphoeroides*, *Chasmodes*, and *Menidia*, occur in the same northeastern Florida area. Both *Fundulus* population complexes have disjunct Gulf and Atlantic populations, differentiated allopatric populations in the Florida Keys (and Cuba for *F. grandis*), and allopatric related species in Yucatan (*F. grandissimus* and *F. persimilis*). Presumably *F. grandis* and southerly *F. majalis* ("*similis*-type") evolved in the Gulf of Mexico in isolation from Atlantic coast ancestors during some Pleistocene interglacial period, and have recontacted Atlantic populations in northeastern Florida since the Wisconsin glaciation. Yucatan populations of *Fundulus*, *Floridichthys*, *Menidia*, and *Cyprinodon* and Florida Keys populations of *Fundulus*, *Menidia*, *Syngnathus*, and possibly *Lucania* and *Cyprinodon* are considered to be glacial relicts.

RESUMEN: Dos complejos de especies del género *Fundulus*: *Fundulus heteroclitus-F. grandis* y *F. majalis* tienen una distribución geográfica general casi idéntica (desde Canadá al noreste de México y desde Nueva Inglaterra al noreste de México, respectivamente, siendo ambas disyuntivas en Yucatán). *Fundulus heteroclitus* (desde Canadá al noreste de Florida) y *F. grandis* (desde el noreste de Florida a México) son especies válidas distinguibles fácilmente entre sí por el número total de poros mandibulares (ocho y diez, respectivamente) y la larga membrana anal en la hembra de la especie *F. heteroclitus*.

Fundulus majalis y *F. similis* son coespecíficos (*F. majalis* tiene prioridad en la nomenclatura) y se alternan al noreste de Florida, en la misma región en la cual *F. heteroclitus* y *F. grandis* son simpátricas. Poblaciones de otros grupos de peces con distribución superpuesta como es el caso de *Sphoeroides*, *Chasmodes* y *Menidia*, se presentan en esa misma área del noreste de Florida.

Ambas poblaciones del complejo *Fundulus* tienen distribución disyuntiva en el Golfo de México y en la costa Atlántica, así como poblaciones alopátricas en los Cayos de Florida (y Cuba en el caso de *F. grandis*) y especies alopátricas relacionadas en el Yucatán (*F. grandissimus* y *F. persimilis*).

Presumiblemente, *F. grandis* y *F. majalis* (tipo *similis*) se originaron en el Golfo de México, aisladas de sus ancestros de la costa Atlántica durante algún periodo interglacial del Pleistoceno y posteriormente recontactaron a las poblaciones del noreste de Florida a partir de la glaciación del Wisconsin. Las poblaciones de *Fundulus*, *Floridichthys*, *Menidia* y *Cyprinodon* en Yucatán, así como las poblaciones de *Fundulus*, *Menidia* *Syngnathus* y probablemente *Lucania* y *Cyprinodon* en los Cayos de Florida, son consideradas como relictos vivientes del periodo glacial.

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INTRODUCTION

The North American killifishes of the genus *Fundulus* are relatively well known taxonomically. Two general reviews of the genus have appeared (Miller 1955, Brown 1957), and Rosen (1973) included it in his general discussion of the brackish water species of Cyprinodontidae. All studies at the species level have dealt with freshwater forms (*Fundulus rathbuni* Brown 1955; *F. catenatus* and *F. stellifer* Thomerson 1969; *F. cingulatus* and *F. chrysotus* Brown 1956a; *F. olivaceus* and *F. notatus* Brown 1956b, Braasch and Smith 1965, Thomerson 1966; *F. notti* and *F. lineolatus* Brown 1958, Rivas 1966, Wiley 1977; *F. blairae* Wiley and Hall 1975; *F. waccamensis* Hubbs and Raney 1946; *F. diaphanus* Shapiro 1947). The last species often enters brackish water. Other freshwater species would be worthwhile candidates for taxonomic analysis.

No systematic study has been concerned with brackish water forms, of which 10 species are currently recognized in the Atlantic Ocean and Gulf of Mexico. This study deals with two brackish water species complexes, the *Fundulus heteroclitus-F. grandis* and *F. majalis-F. similis* population complexes, which have remarkably similar overall distributions.

The *F. heteroclitus-F. grandis* complex ranges continuously (or nearly so) from Labrador (Kendall 1909) to northeastern Mexico (Miller 1955). Allopatric populations occur on Bermuda (*F. bermudae* and *F. rhizophorae*) and the Yucatan Peninsula of Mexico (*F. grandissimus*) (Hubbs 1936). The *F. majalis-F. similis* complex ranges from New Hampshire (Jackson 1953) to northeastern Mexico (Miller 1955). The similarity of the distribution of these two population complexes allows comparison of geographic variation between them, and provides a basis for zoogeographical interpretations.

Although Brown (1957:73) placed members of both species complexes in the subgenus *Fundulus,* it is not certain that the two groups are closely related (Miller 1955:7-9).

METHODS

Counts and measurements used follow the methods proposed by Hubbs and Lagler (1958), with exceptions as noted below. The lateral scale count was made by counting

anteriorly from the caudal base to the scale at, or just posterior to, the dorso-posterior rim of the operculum, in the manner proposed by Brown (1957:70). The last two dorsal and anal rays were counted as separate rays. Caudal ray counts refer to branched rays only; no ontogenetic changes in this character occur in these species complexes. Vertebral counts include the hypural plate. Body depth was measured at the level of the pelvic fin base. Gill-raker counts were made on the first (anterior most) arch.

Morphometric data, expressed as thousandths of standard length (hereafter referred to as "SL") were maintained separately for the sexes, whereas meristic data for both sexes were combined. For body proportions, 10 males and 10 females were measured for each species from a given geographic area with the following exceptions: *Fundulus grandissimus* (Yucatan), 3 specimens of each sex; *F. majalis* from the Savannah River to Matanzas Inlet, and from Mosquito Lagoon southward, 15 specimens of each sex. Most morphometric data were not significant and are not included in this paper; significant items are discussed. Morphometric features examined were: lengths of head, snout, orbit, caudal peduncle, predorsal area, and anal and dorsal fin bases; height of pectoral and pelvic fins; interorbital width; caudal peduncle and body depth; and length of the anal sheath (ovipositor, females only).

Cephalic sensory pore and pit organ arrangements were also examined using Gosline's (1949) study as a basis.

The statistical procedure used was the t-test (N > 30, two-tailed, p = .01) (see Sokal and Rohlf 1969:220-221). The test is designed to compare population sample means by using the formula:

$$t = \frac{\overline{X}_1 - \overline{X}_2}{\sqrt{\dfrac{S_1^2}{N_2} + \dfrac{S_2^2}{N_1}}}$$

where $\overline{X}_1$ and $\overline{X}_2$ are the means to be compared, S is the standard deviation, and N the number of individuals of each sample to be compared. The null hypothesis in all cases is: The means being compared are not different. A value of t of 2.58 or less would mean acceptance of the null hypothesis with a 1% chance of error. Values of t greater than 2.58 suggest rejection of the null nypothesis (i.e. the means can be considered significantly different at the level of p = .01). These numbers do not mean that a population can automatically be considered a subspecies or species. This is still a matter of judgment. The fragmentation of each species into populations is arbitrary, but necessary for comparisons, and must be taken into account in making taxonomic decisions.

Institutions from which specimens were examined are: Academy of Natural Sciences of Philadelphia (ANSP), United States National Museum of Natural History (USNM), University of Michigan Museum of Zoology (UMMZ), Cornell University (CU), Tulane University (TU), Florida State University (FSU)[1], University of Florida (UF), University of Miami (UMIM), University of Miami Institute of Marine Science[2], (UMML), and Jacksonville University (JU).

KEY TO THE SPECIES OF THE *Fundulus heteroclitus—Fundulus grandis* AND *Fundulus majalis* SPECIES COMPLEXES

1 a. Preorbital region scaled.................................2
   b. Preorbital region unscaled 3
2 a. Dorsal fin rays 12-16, rarely 11 (only 12 of 1780
       specimens examined had 11); New Hampshire to
       northeastern Mexico................................*Fundulus majalis*
   b. Dorsal fin rays 9-11, usually 10; known only from
       Yucatan, Mexico ....*Fundulus persimilis*

SYSTEMATIC ACCOUNTS
THE *FUNDULUS HETEROCLITUS-FUNDULUS GRANDIS* SPECIES COMPLEX
A. *Fundulus heteroclitus* AND BERMUDA POPULATIONS
Fundulus heteroclitus (LINNAEUS)
FIGURE 1

Cobitis heteroclita Linnaeus 1766:500 (original description of *F. heteroclitus*, Charleston, South Carolina; type specimen now in Linnaean Society of London collection); Goode and Bean 1885:204-205 (type examined); specimen skinned and glued to herbarium sheet; skin 122 mm TL; counts: dorsal rays 12, anal rays 10, lateral scales 33); Jordan and Evermann 1896:641 (synonymy).

Cobitis killifish Walbaum 1792:12 (original description, Long Island, New York); Jordan and Evermann 1896:641 (synonymy).

Poecilia macrolepidota Walbaum 1792:11 (original description, Long Island, New York); Jordan and Evermann 1896:641 (synonymy).

Poecilia fasciata Bloch and Schneider 1801:453 (original description); Jordan and Evermann 1896:641 (synonymy).

Poecilia coenicola Bloch and Schneider 1801:452 (original description, Carolinas); Jordan and Evermann 1896:641 (synonymy).

Hydrargyra swampina Lacépède 1803:378 (original description, South Carolina); Jordan and Evermann 1896:641 (synonymy); Bailey and Wiley 1976:477-840 (evidence for retention of *H. swampina* as a synonym of *Fundulus heteroclitus*).

Fundulus mudfish Lacépède 1803:37 (Carolinas); Jordan and Evermann 1896:641 (synonymy).

Esox pisciculus Mitchill 1815:440 (original description, New York); Jordan and Evermann 1896:641 (synonymy).

Esox pisculentis Mitchill 1815:441 (original description, New York); Jordan and Evermann 1896:641 (synonymy).
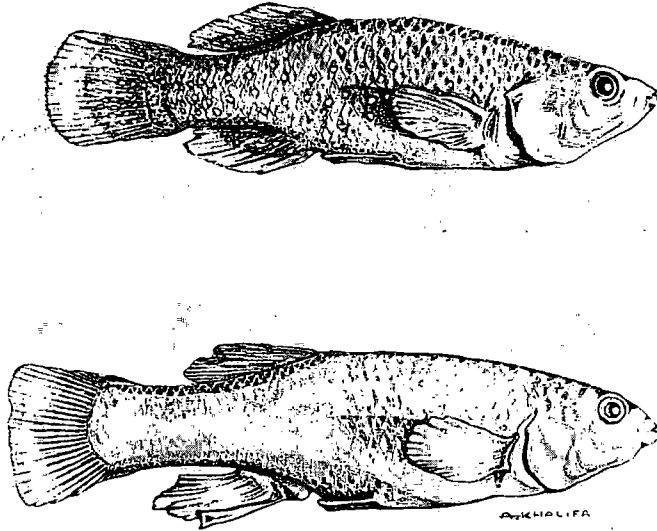
FIGURE 1. *Fundulus heteroclitus* (JU 775), St. Johns County, Florida. Upper: male, 60 mm SL; Lower: female 64 mm SL.

Hydrargira nigrofasciata LeSeur 1817:133-134 (original description, Newport, Rhode Island); Jordan and Evermann 1896:641 (synonymy).

Fundulus nigrofasciata Storer 1837:295 (original description, Massachusetts); Jordan and Evermann 1896:641 (synonymy).

Fundulus pisculentis Storer 1837:294 (original description, Massachusetts); Jordan and Evermann 1896:641 (synonymy).

Fundulus viridescens DeKay 1842:217 (original description, New York); Jordan and Evermann 1896:641 (synonymy).

Fundulus zebra DeKay 1842:218 (original description, New York); Jordan and Evermann 1896:641 (synonymy).

Fundulus fonticola (?) Cuvier and Valenciennes 1846:198 (original description, Puerto Rico); Jordan 1887:528 (examination of type specimen); Jordan and Evermann 1896:643 (description, Puerto Rico); Hubbs 1926:7 (*F. fonticola* = *F. antillarum?*); Jordan, Evermann, and Clark 1930:175 (West Indies); Hildebrand 1935:49 (existence of *F. fonticola* doubtful); Myers 1938:358-360 (existence doubtful); Rivas 1948:216-217 (existence doubtful); Miller 1955:3 (status of *F. fonticola* unclear).

Fundulus nisorius Cope 1870:490 (original description, Gaboon, West Africa); Fowler 1916:417-418 (species redescribed; allied to *Fundulus heteroclitus*); Hubbs 1926:6 (synonymy; West African type locality presumably in error); Miller 1955:3 (synonymy).

Fundulus fasciatus Uhler and Lugger 1876:126 (original description, Maryland); Jordan and Evermann 1896:641 (synonymy).

Fundulus vinctus Jordan and Gilbert 1882:354-356 (original description, Cape San Lucas, California); Hubbs 1931:2-3 (synonymy; type locality presumably in error).

Fundulus antillarum Fowler 1916:418-420 (original description, St. Martins, West Indies); Myers, 1938:358-360 (type locality *F. antillarum* doubtful); Rivas 1948:216-217 (synonymy); Miller 1955:3 (synonymy; ANSP types examined; type locality presumably in error).

Fundulus heteroclitus grandis Bean 1891:92 (Chesapeake Bay).

Fundulus heteroclitus badius Garman 1895:96 (original description, Gulf of St. Lawrence, Canada).

Fundulus heteroclitus heteroclitus Jordan and Evermann 1896:640-641 (original description, Virginia to Florida); Brown 1957:73 (Gulf of St. Lawrence to Matanzas River, Florida).

Fundulus heteroclitus macrolepidotus Jordan and Evermann 1896:641 (original description, Maine to Virginia); Breder 1948:83 (Gulf of St. Lawrence to Virginia); Brown 1957:73 (synonymy).

MATERIAL EXAMINED.—(The number of specimens follows catalogue number in parentheses.) LABRADOR: USNM 86223(2); NOVA SCOTIA: UMMZ 138840(36), 138834(15), USNM 35339(14); QUEBEC: CU 18357(34), UMMZ 174659(4); MAINE: TU 43451(20), 43452(4), UMMZ 145494(80); NEW HAMPSHIRE: UMMZ 140525(80); MASSACHUSETTS: CU 31101(46), 47234(31), TU 19743(10), 23221(9); CONNECTICUT: UMMZ 138841(100); NEW YORK: UMMZ 103897(80), CU 38503(36); NEW JERSEY: CU 26970(12), 32197(7), 30365(4), UMMZ 109874(100); PENNSYLVANIA: UMMZ 99463(100); DELAWARE: UMMZ 99430(43), 99428(5), 99429(5); MARYLAND: TU uncatalogued (68), UMMZ 159890(22); VIRGINIA: UMMZ 156714(6), 171290(20); NORTH CAROLINA: ANSP 80837(6), UMMZ 132806(3), 65237(1), 55997(4), 126285(29); SOUTH CAROLINA: ANSP 7509-19(11), UMMZ 139418(100); GEORGIA: ANSP 80833(29), 80834(36), TU 21339(160), 21232(477); FLORIDA: FSU 6525(82), 10432(8), 8896(19), JU 36, 60, 111, 673, 644, 790, 476, 457, 252, 154, 1463, 709, 876, 838, 794, 806, 796, 775, 786, TU 41592(2), 41583(13), 41588(3), 41843(1), UF 2980(4), USNM 104956(7).

DIAGNOSIS.—A species of *Fundulus* most closely related to *F. bermudae* and *F. rhizophorae*, with which it shares the characters of 8 total mandibular pores and a long anal sheath in females (Table 6). Somewhat less closely related to *F. grandis* (with which it is partly sympatric), from which it differs in having 8 (vs. 10) total mandibular pores and a longer anal sheath in females (see Table 6). Also distinguished from *F. grandis* by gill raker number (8-17), usually 10-13, versus 8-12, mode 10, in sympatric *F. grandis*), vertebral number (30-36, usually 32-34, vs. 33-37, usually 35-36), and length of the anal sheath of females (59-233, population means are 87-200 expressed as thousandths of standard length; vs. 52-80, mean 69.0, in sympatric *F. grandis*). *Fundulus heteroclitus* is distinguished from *F. bermudae* by anal rays (9-12, usually 11, vs. 11-14, usually 12-13) and predorsal scales (13-21, usually 15-16, vs. 12-16, usually 14); and from *F. rhizophorae* by predorsal scales (13-21, usually 15-16, vs. 11-17, usually 12-14), caudal peduncle circumferential scales (17-22, usually 19-20, vs. 15-18, usually 16-17), and pectoral fin rays (16-21, usually 17-19, vs. 15-18, usually 16-17). Maximum body size in about 120 mm SL.

DESCRIPTION.—Meristic data, in addition to that given in the diagnosis and in Tables 1-5, are as follows: pelvic fin rays 6-6; branchiostegal rays 5 + 5; dorsal fin rays 10-15 (mode = 12); anal fin rays 9-12 (mode = 11); branched caudal rays 14-21, usually 16-18; caudal peduncle circumferential scales 17-22, usually 19-20; and pectoral fin rays 16-21 (mode = 18-19).

The preorbital area is naked, and 4 irregular scale rows occur on the operculum. There is an enlarged interorbital scale surrounded by a rosette

of 7 smaller scales.

Cephalic sensory pore arrangement has been described by Gosline (1949). There are 4 preorbital pores. In northern populations a pit organ lies between preorbital pores 2 and 3, but anterior of a line connecting those 2 pores. This pit organ is absent in many individuals in southern populations. Of 68 specimens examined, 66 had 14 preopercular pores, 1 had 15, and 1 had 16.

The lower pharyngeal plates are narrow and elongated and have numerous, small, conical teeth. The upper pharyngeal plates are rounded.

Mature males in life are colored blue to olive dorsally, shading to a lighter olive ventro-laterally. The ventral region is bright yellow in breeding males (hence the common name yellow bellied cobbler). Small, light spots occur on the body, especially posteriorly. The median fins are blue with light spots, and have a yellow or orange margin. Pelvic and pectoral fins are also yellow or orange. An ocellus occurs in the dorsal fin of males, but this is obscured by increasing pigmentation in the dorsal fin as the fish matures (Fig. 1).

In males, 7-10 contact organs appear on the posterior rim of each body scale, and numerous contact organs are found on the margins of the head scales. These structures also occur on the rays of the dorsal and anal fins, and occasionally on the pectoral fins.

Lateral scale number (Table 1) and predorsal scale number (Table 2) show general north-south clines, with numbers decreasing southward, and with significant differences in means between populations. These characters will not separate *F. heteroclitus* and *F. grandis*.

The mean number of gill rakers (Table 3) for *F. heteroclitus* south of the St. Johns River, Florida (12.36), is statistically different from the mean for Florida east coast *F. grandis* (9.95), where the two species are sympatric. Northern specimens of *F. heteroclitus* (Chesapeake Bay northward) have significantly fewer gill rakers (8-13, usually 10-12) than southern specimens (10-17, usually 11-13).

There is no difference in number of caudal-peduncle circumferential scales between *F. heteroclitus* and *F. grandis*, and little variation among *F. heteroclitus* populations. The mode is 20 in all populations.

The pectoral ray mean for *F. heteroclitus* south of the St. Johns River (18.50) differs from the mean for Florida east coast *F. grandis* (17.95). As with gill rakers, northern and southern populations of *F. heteroclitus* may also be indicated here (means < 18.28 vs. means > 18.50, respectively).

Vertebral number (Table 4) generally decreases southward with significantly different means between populations suggesting strong clinal patterns. The mean number of vertebrae for southern *F. heteroclitus* (33.27) differs significantly from the means for Florida east coast *F. grandis* (35.27).

The total number of mandibular pores (Table 5) completely separates *F. heteroclitus* and *F. grandis* (and *F. grandissimus*), and is the best single diagnostic character. The mode for *F. heteroclitus* is 8 (mean 7.95) and for *F. grandis* is 10 (mean 9.94) with no overlap in counts.

MORPHOMETRIC VARIATION.—No significant variation in morphometric features was found. See discussion of morphometric variation for *F. grandis* for comparisons with that species, and Table 6, which shows intraspecific and interspecific variation for anal sheath length in females.

RANGE.—This species is known from northeastern Florida to southern Newfoundland (Fig. 2).

DISCUSSION.—Four subspecies of *Fundulus heteroclitus* have been recognized (see synonymy). Bean (1891:92) recognized *F. h. grandis* from Chesapeake Bay, but my data show no distinctive differences for any feature for Chesapeake Bay populations. Garman (1895:96) described *F. h. badius* from the Gulf of St. Lawrence, Canada, and this was later retained as a valid form by Jordan et al. (1930:176). Breder (1948:83) included Gulf of St. Lawrence specimens in *F. h. macrolepidotus* (Gulf of St. Lawrence to Virginia), and Brown (1957:73) included Gulf of St. Lawrence specimens in *F. h. heteroclitus*. Obviously, these latter authors did not consider *F. h. badius* to be valid, and my data support this. *Fundulus heteroclitus* ranges continuously from the Gulf of St. Lawrence to Florida, and Canadian populations differ in no way from New England specimens. These are included together in my tabulation of meristic features.

Although Brown (1957:73) recognized one subspecies from Canada to Florida, *F. h. heteroclitus,* Jordan and Evermann (1896:640-641) had delineated *F. h. heteroclitus* (Virginia to Florida) and *F. h. macrolepidotus* (Maine to Virginia). My data suggest some differentiation of populations from Cape Lookout northward through Canada from populations to the south of Cape Lookout (see Remarks). One meristic feature, gill raker number, does show a significant difference between populations north and south of Cape Lookout, but a vague cline is indicated. Other meristic features do not show significant differences, or clinal trends are clearly evident if differences are apparent. One morphometric character, anal sheath length of females, is shorter in populations north of Chesapeake Bay, but this does not coincide with the defined subspecies *F. h. heteroclitus* and *F. h. macrolepidotus*. In addition, a general increase in anal sheath length southward is clear from Table 6.

Some meristic variation may be expected on the basis of environmental temperatures, but characters such as anal sheath length and gill raker number point to more specific reproductive and feeding differences. Brummett's (1966:616-620) demonstration that eggs of *F. heteroclitus* from Woods Hole have chorionic fibrils, in contrast to eggs from Beaufort specimens, points to further differences between northern and southern
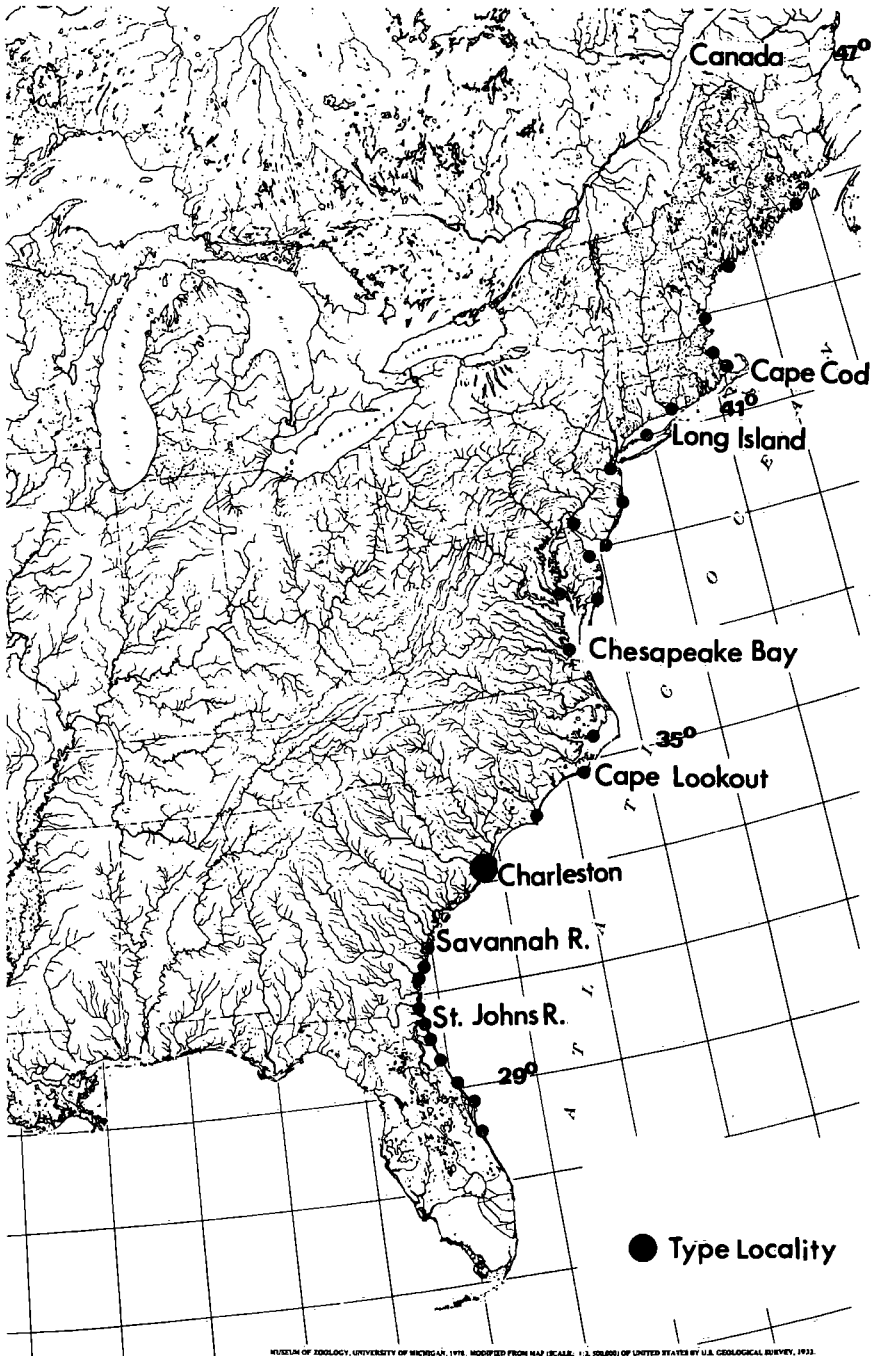
FIGURE 2. Map of the geographic distribution of *Fundulus heteroclitus*.

populations. These meristic, morphometric, and egg morphology differences could be interpreted as evidence for the validity of the nominal subspecies *F. h. heteroclitus* and *F. h. macrolepidotus*. However the differences do not coincide along distributional lines, and some variability should be expected in a wide ranging species such as *F. heteroclitus*. I choose not to fragment *F. heteroclitus* into subspecies, and in doing so follow Brown (1957).

Fundulus bermudae GÜNTHER
FIGURE 3
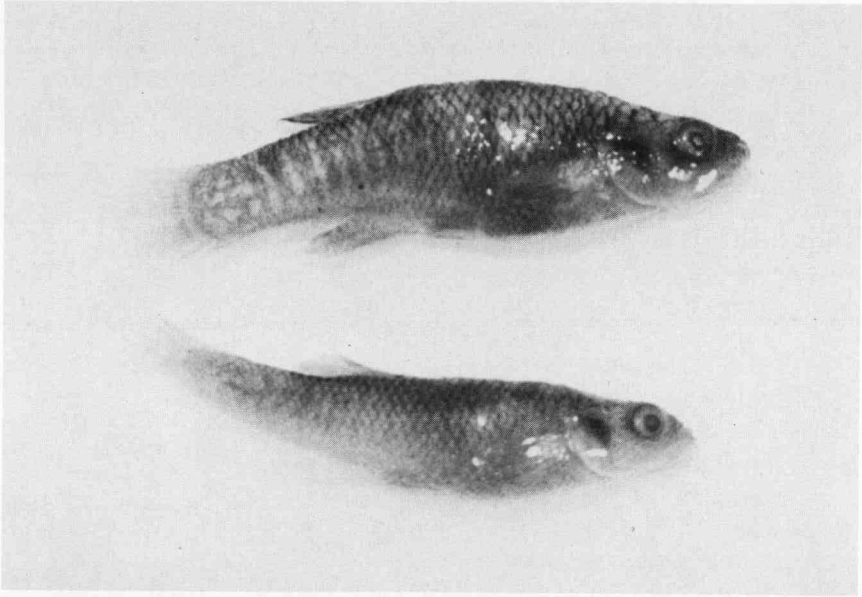
FIGURE 3. *Fundulus bermudae* (USNM 164795), Mangrove Lake, Bermuda. Upper: male 85 mm SL; Lower: female 78 mm SL.

Fundulus bermudae Günther 1874:370 (original description, Bermuda; precise type locality unknown; present location of types unknown; counts: dorsal rays 14, anal rays 12, lateral scales 35); Jordan and Evermann 1896:643-644 (in part: description); Bean 1906:35 (in part: distribution); Beebe and Tee-Van 1933:57 (in part: description).

Fundulus heteroclitus bermudae Hubbs 1926:8 (synonymy); in part: distribution); Jordan, Evermann, and Clark 1930:175 (synonymy); in part: distribution); Miller 1955:3, 7 (in part: distribution); Brown 1957:69, 73 (in part: distribution); Collette 1962:438 (Bermuda endemic).

MATERIAL EXAMINED.—The number of specimens follows catalogue number in parentheses. BERMUDA: USNM 164793(105), 164794(127), Mangrove Lake.

DIAGNOSIS.—A species of *Fundulus* most closely related to *F. heteroclitus* and *F. rhizophorae*, with which it shares the characters of eight total mandibular pores and a long anal sheath in females (Table 6). It is sympatric with *F. rhizophorae*, from which it is distinguished by number of dorsal

fin rays (11-15, usually 13-14, vs. 10-13, usually 11-12), anal fin rays (11-14, usually 12-13, vs. 9-12, usually 11), branched caudal fin rays (16-19, usually 17-18, vs. 13-18, usually 15-16), predorsal scales (12-16, usually 14-15, vs. 11-17, usually 12-14), gill rakers (12-15, usually 12-13, vs. 9-14, usually 10-11), caudal peduncle circumferential scales (18-20), vs. 15-18), and pectoral fin rays (17-20, usually 18-19, vs. 15-18, usually 16-17). *Fundulus bermudae* may be distinguished from *F. heteroclitus* by number of anal fin rays and predorsal scales; *F. heteroclitus* has 9-12, usually 11, anal fin rays and 13-21, usually 15-16, predorsal scales.

DESCRIPTION.—*Fundulus bermudae* has 31-36 (usually 33-34) vertebrae, 31-36 (usually 33-35) lateral scales, 14 preopercular pores, 5 branchiostegal rays, and 6 rays in each pelvic fin, in addition to the meristic features given in the diagnosis. See Table 7 for a summary of meristic features. Head scalation and sensory pore arrangement are similar to those occurring in *F. heteroclitus*.

I have not seen living material of this species. Günther (1874:370) described this species as being brownish-olive with faint dark green cross-bands. There seems to be little difference between this species and *F. rhizophorae* and *F. heteroclitus* in coloration of preserved specimens, with the exception that *F. bermudae* has a wide cream-colored band extending above the lateral line from the operculum to the caudal peduncle. As in the other species, the median fins are heavily pigmented (presumably blue) in males, and pale or clear in females. The anal sheath of females is long as in the other two species, to which *F. bermudae* is obviously closely related (see Table 6 for comparison of anal sheath length).

Maximum body size is about 100 mm SL.

RANGE.—This species is known only from Bermuda. Its current prevalence and distribution there are undetermined.

DISCUSSION.—Hubbs (1926) considered *F. bermudae* to be a subspecies of *F. heteroclitus*. Because of its isolation and the degree of morphological divergence from *F. heteroclitus*, I believe that Günther's (1874) original interpretation of *F. bermudae* as a distinct species should be accepted. The long anal sheath of females and the eight total mandibular pores clearly ally *F. bermudae* with *F. rhizophorae*, which also occurs on Bermuda, but which is distinguished by several meristic features (see Diagnosis). The two Bermuda species probably represent two invasions of Bermuda by *heteroclitus* or pre-*heteroclitus* populations, or (less likely) one invasion followed by separation in isolated lacustrine situations.

Fundulus rhizophorae Goode 1877:298 (original description, Basden Pond, Bermuda; types USNM 21943, but present whereabouts unknown; counts: dorsal rays 12, anal rays 11, lateral scales 35).

Fundulus bermudae Jordan and Evermann 1896:643-644 (synonymy; in part: description); Bean 1906:36 (in part: description); Beebe and Tee-Van 1933:57 (in part: description).

Fundulus heteroclitus bermudae Hubbs 1926:8 (synonymy; in part: distribution); Collette 1962:440 (synonymy).

MATERIAL EXAMINED.—The number of specimens follows catalogue number in parentheses. BERMUDA: JU 1550 (150), USNM 175776 (70), 112083 (247), all from St. George I., Lover's Lake.

Fundulus rhizophorae GOODE

FIGURE 4
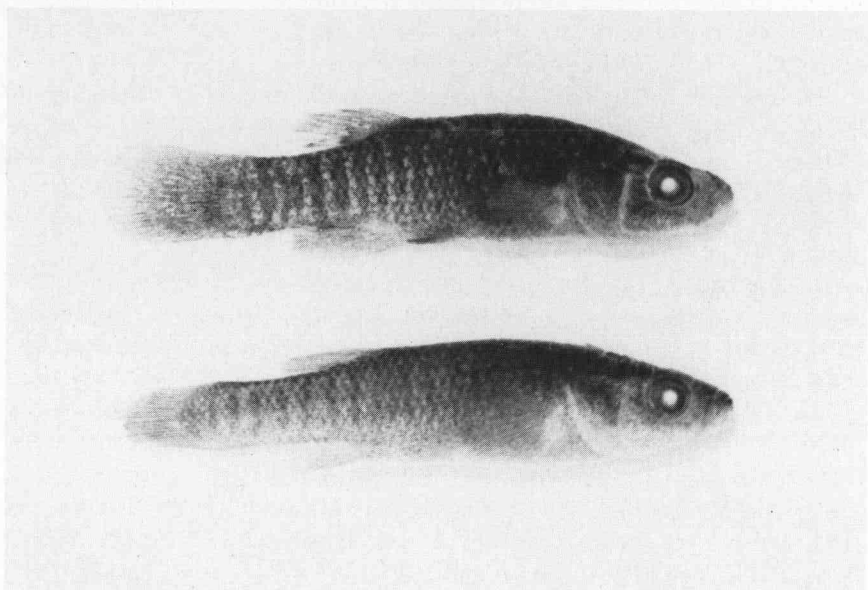
FIGURE 4. *Fundulus rhizophorae* (JU 1550), Lover's Lake, Bermuda. Upper: male 42 mm SL; Lower: female 43 mm SL.

DIAGNOSIS.—A species of *Fundulus* most closely related to *F. bermudae* and *F. heteroclitus*, with which it shares the characters of eight total mandibular pores and a long anal sheath in females (Table 6). It is distinguished from *F. bermudae* by number of dorsal fin rays (10-13, usually 11-12, vs. 11-15, usually 13-14), anal fin rays (9-12, usually 11, vs. 11-14, usually 12-13), branched caudal fin rays (13-18, usually 15-16, vs. 16-19, usually 17-18), predorsal scales (11-17, usually 12-14, vs. 12-16, usually 14-15), gill rakers (9-14, usually 10-11, vs. 12-15, usually 12-13), caudal peduncle circumferential scales (15-18, usually 16-17, vs. 18-20, usually 19), and number of pectoral fin rays (15-18, usually 16-17, vs. 17-20, usually 18-19). *Fundulus rhizophorae* is distinguished from *F. heteroclitus* by number of predorsal scales, caudal peduncle circumferential scales, and pectoral fin rays; *F. heteroclitus* has 13-21 (usually 14-18) predorsal scales, 17-22 (mode 19-20) caudal peduncle circumferential scales, and 16-21 (usually 17-19) pectoral fin rays.

DIAGNOSIS.—A species of *Fundulus* most closely related to *F. bermudae* and *F. heteroclitus,* with which it shares the characters of eight total mandibular pores and a long anal sheath in females (Table 6). It is distinguished from *F. bermudae* by number of dorsal fin rays (10-13, usually 11-12, vs. 11-15, usually 13-14), anal fin rays (9-12, usually 11, vs. 11-14, usually 12-13), branched caudal fin rays (13-18, usually 15-16, vs. 16-19, usually 17-18), predorsal scales (11-17, usually 12-14, vs. 12-16, usually 14-15), gill rakers (9-14, usually 10-11, vs. 12-15, usually 12-13), caudal peduncle circumferential scales (15-18, usually 16-17, vs. 18-20, usually 19), and number of pectoral fin rays (15-18, usually 16-17, vs. 17-20, usually 18-19). *Fundulus rhizophorae* is distinguished from *F. heteroclitus* by number of predorsal scales, caudal peduncle circumferential scales, and pectoral fin rays; *F. heteroclitus* has 13-21 (usually 14-18) predorsal scales, 17-22 (mode 19-20) caudal peduncle circumferential scales, and 16-21 (usually 17-19) pectoral fin rays.

DESCRIPTION.—*Fundulus rhizophorae* has 31-34 (usually 32-33) vertebrae, 14 preopercular pores, 5 branchiostegal rays, and 6 rays in each pelvic fin, in addition to the characteristics given in the diagnosis. Table 7 summarizes meristic data.

Goode (1877:298) described *F. rhizophorae* as being a light, tawny yellow with transverse bands of greenish-brown. I have examined freshly preserved material, from which I present the following additional information: Males resemble *F. heteroclitus* males. The body is olive to blue in life with light spots, especially posteriorly. The ventral region is yellow, as in *F. heteroclitus.* Median fins are heavily pigmented (blue) with light spots. Females are drab brown (tawny?) with faint, dark vertical bars, as is true also of *F. heteroclitus.*

Males possess 7-10 extremely long contact organs on the rim of each body scale. Contact organs also occur on the head, dorsal fin, and anal fin.

Maximum size attained is about 65 mm SL. This is somewhat smaller than the maximum size of *F. bermudae* and *F. heteroclitus.*

RANGE.—*Fundulus rhizophorae* is known only from Bermuda. In addition to the type locality, the species is known from Lover's Lake on St. Georges Island (USNM 175776, USNM 112083, JU 1550). The species is particularly abundant at this latter locality, and seems to be isolated from *F. bermudae.* Even though two species of *Fundulus* occur on Bermuda, they apparently are not sympatric.

DISCUSSION.—Jordan and Evermann (1896) placed *F. rhizophorae* in the synonymy of *F. bermudae.* In my opinion, these two forms are distinct species, both derived from *F. heteroclitus,* and I believe that the meristic data presented here argue for that conclusion. In addition, *F. rhizophorae* appears to be smaller than the other two species. The possibility exists that the degree of difference between *F. rhizophorae* and *F. bermudae* could

be interpreted as merely ecophenotypic variation. However, given the allopatric distribution of both Bermuda forms and *F. heteroclitus* and the meristic differences existing among them, specific status for each seems reasonable.

B. *Fundulus grandis grandis* AND *Fundulus grandis saguanus*
Fundulus grandis grandis BAIRD AND GIRARD
FIGURE 5
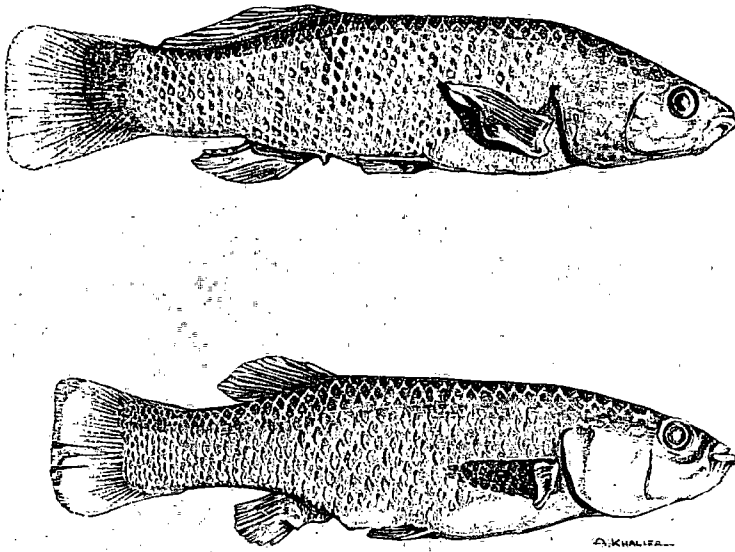
FIGURE 5. *Fundulus grandis grandis* (JU 842), Franklin County, Florida. Upper: male 105 mm SL; Lower: female 104 mm SL.

Fundulus grandis Baird and Girard 1853:389 (original description, Indianola, Texas; two male syntypes, 99-101 mm SL, USNM 15298).

Fundulus grandis grandis Rivas 1948:215-222 (original description of *F. g. saguanus* and comparison with *F. g. grandis*); Brown 1957:73 (identification in key; distribution).

Fundulus pallidus Evermann 1892:84 (original description, Galveston, Texas); Garman 1895:96 (*F. pallidus* placed in synonymy of *F. grandis*); Miller 1955:5-7 (synonymy).

Fundulus floridensis Girard 1859:157 (original description, Charlotte Bay, Florida); Garman 1895:96 (*F. floridensis* placed in synonymy of *F. grandis*); Jordan and Evermann 1896:641-642 (synonymy).

Fundulus heteroclitus Jordan and Gilbert 1883:334 (distribution); Evermann 1892:84 (Texas); Nichols 1942:125-126 (Gulf coast of Florida).

Fundulus heteroclitus grandis Jordan and Swain 1884:230 (Cedar Keys, Florida); Garman 1895:96 (*F. grandis* and *F. heteroclitus* clearly distinguished); Jordan and Evermann, 1896:641-642 (Gulf of Mexico); Jordan, Evermann, and Clark 1930:176 (Gulf of Mexico); Brown 1957:73 (distributions of *F. grandis* and *F. heteroclitus* delineated and species recognized as distinct).

MATERIAL EXAMINED.—The number of specimens follows catalogue number in paren-
theses. FLORIDA: Florida State Board of Conservation 1225(6), 1288(9), 903(6); FSU
11210(55), 11474(110), 12413(12); JU 113, 1618, 44, 1730, 1499, 1464, 1011, 1024, 903, 912, 922,
875, 890, 891, 691, 686, 780, 770, 798, 842, 839, 639, 530, 475, 453, 367, 164, 86, 82; TU 39581(10),
38091(4), 39587(1), 39616(8), 20477(11), 20477(11), 20388(9), 18183(5), 12539(5), 41206(14),
21261(57), 20366(11), 2273(112), 41387(2), 42448(1), 41069(133), 40562(9), 9742(37), 21385(61),
18421(29), 20959(6), 18355(44), 20424(1), 41069(133), 40562(9), 9742(37), 21385(61), 18421(29),
20959(6), 18355(44), 20424(1), 18220(4), 41566(15), 41077(11), 17815(15), 17846(5), 18389(129),
17915(4), 41584(3); UF 9693(1), 3483(5), 4013(8), 5215(1), 4014(4), 12279(1), 1490(8), 4662(11),
6683(5), 2980(11), 3116(10); UMIM 3152(3); UMML 3264(50); USNM 62668(2), 25310(1).
ALABAMA: TU 8577(9), 14514(2), 15854(2). MISSISSIPPI: JU 235(100); TU 10861(32),
16109(107). LOUISIANA: TU 11492(27), 19048(11), 4344(11), 37219(6), 1394(4), 6425(16),
9253(21), 6546(81), 17338(16), 8271(4). TEXAS: JU 1639, 1645, 1657, 1683, 1688; TU 39872(4),
2163(75), 22190(76), 21505(195), 22063(15), 21474(6), 41099(7); USNM 15298(2), Indianola,
1853, (Cotypes). MEXICO, TAMAULIPAS: TU 38959(14), Rio Purificacion, 38.5 km NW of
Victoria, Hwy 85, 25 Dec. 1964; TU uncat. (18), 11 km W of Tampico on Hwy 110, 23 May
1961; TU uncat. (59), Rio Purificacion, Caracol, Hwy 85, 20 May 1961; TU uncat. (8), Arroyo
Chorreras, S of San Jose las Norias, 17 Dec. 1960; TU uncat. (3), Arroyo Chorerras, 19 km S of
San Fernando, Hwy 101, 22 May 1962; UF 25975 (30)

DIAGNOSIS.—A subspecies of *Fundulus grandis* most closely related to
F. g. saguanus, *F. grandissimus*, and slightly less closely related to *F.
heteroclitus*, *F. bermudae*, and *F. rhizophorae*. Distinguished from *F.
heteroclitus* by number of gill rakers (7-13, usually 9-11, vs. 10-15, usually
12-13 in sympatric *F. heteroclitus*), vertebrae (31-36, usually 34-35, vs.
31-37, usually 33-34), total mandibular pores (10 vs. 8), and the short anal
sheath of females (34-103, as thousandths of standard length, vs. 166-194 in
sympatric *F. heteroclitus*). *Fundulus g. grandis* is distinguished from *F.
grandissimus* by number of lateral scales (30-38, usually 33-36, vs. 36-42,
usually more than 38), predorsal scales (13-19, usually 15-17, vs. 21-25,
usually 23-24), caudal peduncle circumferential scales (17-23, usually 20,
vs. 21-25, usually 24), and total mandibular pores (10 vs. 12). *Fundulus
grandis grandis* is distinguished from the allopatric *F. g. saguanus* by
number of lateral scales (30-38, usually 33-36, vs. 30-35, usually 32-33), gill
rakers (7-13, usually 9-11, vs. 7-11, usually 9), vertebrae (31-36, usually
34-35, vs. 31-35, usually 32-33), and pectoral fin rays (15-21, usually 17-19,
vs. 16-19, usually 17).

DESCRIPTION.—Meristic features, in addition to those in Tables 1-5 and
in the Diagnosis, are pelvic fin rays 6-6, branchiostegal rays 5+5, dorsal fin
rays 10-14 (usually 11-12), anal fin rays 10-15 (usually 11), branched caudal
fin rays 15-21 (usually 16-18). Of 136 specimens examined, 132 had 14
preopercular pores, 3 had 15, and 1 had 16. Four irregularly arranged scale
rows occur on the preoperculum. The preorbital area is naked, and the
preorbital pore series consists of four pores with a pit organ directly
between numbers two and three. An enlarged interorbital scale is sur-
rounded by a rosette of seven smaller scales.

Males have 7-10 contact organs on the posterior rim of each scale on the body, and many small contact organs on each head scale. Contact organs also occur on the rays of the dorsal and anal fins, and occasionally on the pectoral fins.

The lower pharyngeal plates are elongate and narrow, and have many small conical teeth. The upper pharyngeal plates are rounded.

Breeding males are deep blue in color dorsally, shading to a lighter olive ventrally. The body coloration is interrupted by light, narrow, vertical, irregular bars. Numerous small, light spots occur on the body, especially posteriorly. The median fins are blue, with numerous light spots, and have a yellow or orange margin. The pelvic fins are yellow or orange, and have many scattered melanophores.

A prominent dark blotch on the operculum and a dark predorsal stripe that fades with age are present in both sexes. Many scattered melanophores occur on the anterior and posterior portions of the pectoral fin base of both sexes.

Females are drab olive dorsally, shading to white ventrally and the fins are cream colored or yellow. Juveniles are generally olive, but their most distinctive coloration feature is a bright yellow anal fin. Some juveniles have darker vertical bars on the lighter olive ground color, but these disappear at 15-20 mm SL.

Maximum size is about 145 mm SL.

TYPES.—Of the two syntypes, the smaller (99 mm SL) has 12 dorsal rays, 11 anal rays, 19 branched caudal rays, 35 lateral scales, 14 predorsal scales, 10 gill rakers, 19 pectoral rays, and 21 caudal peduncle circumferential scales. The other syntype (101 mm SL) has 13 dorsal rays, 12 anal rays, 18 branched caudal rays, 35 lateral scales, 9 gill rakers, 17 pectoral rays, and 19 caudal peduncle circumferential scales. The predorsal region of this specimen is damaged. Both specimens have a total of 10 mandibular and 14 preopercular pores.

RANGE.—*Fundulus grandis grandis* ranges from Laguna de Tamiahua, Veracruz, Mexico (Miller 1955), eastward along the coast of the Gulf of Mexico to at least Collier County, Florida (southwest Florida, UMIM 3152 and 3264), and disjunctly on the east coast to Florida from Nassau County (northeastern Florida, JU 36, 44, 111, 113, 1618) southward to Lake Worth, Palm Beach County (UF 1490, 4662). The gap between the east coast and Gulf of Mexico populations is occupied by *F. g. saguanus* (extreme southern Florida, Florida Keys, Cuba). *Fundulus grandis* is sympatric with *F. heteroclitus* for about 100 miles of coastline in northeastern Florida (Fig. 6).

MERISTIC VARIATION.—The modal number of dorsal rays is 12 in populations in the Gulf of Mexico east of the Mississippi River and 11 in populations west of the Mississippi River and on the east coast of Florida. Most specimens of *F. grandis* have either 11 or 12 dorsal rays. Atlantic and Gulf
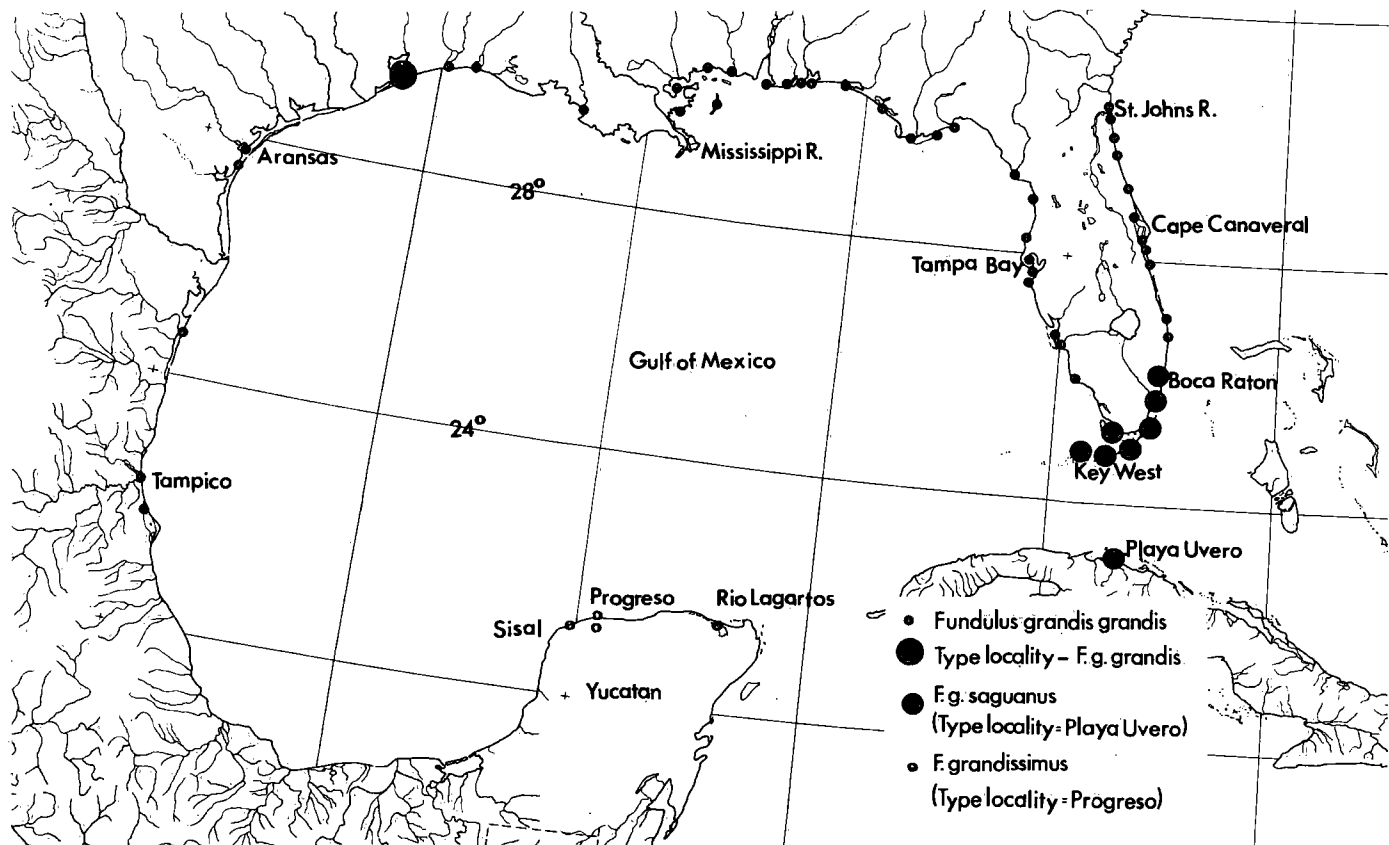
FIGURE 6. Map of the geographic distribution of *Fundulus grandis* and *Fundulus grandissimus*.

coast means are statistically different (11.41 and 12.04, t=7.87), and signifi-cantly different means between Gulf of Mexico populations may indicate strong clinal patterns.

The mode of anal rays is 11 in all populations, and means only show significant variation in the western Gulf of Mexico. *Fundulus heteroclitus* also has 11 anal fin rays.

The number of branched caudal rays is extremely variable, no clear modes are evident, and any statistical difference in means is slight. Approx-imately 89% of all specimens examined had either 16, 17, or 18 branched caudal rays.

The modal number of lateral scales (Table 1) is 35 in Gulf of Mexico populations and 34 on the east of Florida. The east coast race mean (34.37) is significantly different from the southwestern Florida population mean (34.72). No major significant variation occurs in Gulf populations, and no clinal patterns are evident.

The modal number of predorsal scales (Table 2) is 16 in all populations except in the western Gulf of Mexico (mode = 15), but no difference is apparent in the western and eastern Gulf means. The Atlantic coast popula-tion mean differs from the southwestern Florida mean.

The modal gill raker count west of the Mississippi River is 10 (Table 3), shifts to 9 in the region from the Mississippi River to Cape San Blas, is 10 again farther east and south in the Gulf, and is 10 on the Florida east coast.

The modal number of caudal peduncle circumferential scales is 20 in all populations. The mean number increases clinally southward along the Florida Gulf coast, but statistical differences are marginal for compared means.

The modal number of pectoral rays is 18 in all populations. There is a distinct increase in mean number from north to south in the Gulf of Mexico. The western Gulf mean (18.21) differs statistically from eastern Gulf means (17.90), and the Florida east coast mean (17.95) differs significantly from the southwestern Florida mean (18.38).

No significant variation occurs for vertebral number (Table 4), the mode remaining 35 in all populations. Mean vertebral number differs significantly between southern *F. heteroclitus* (33.27) and Florida east coast *F. grandis* (35.27).

Total mandibular pores (Table 5) are typically 10 in nearly all specimens.

MORPHOMETRIC VARIATION.—Although no significant morphometric data were obtained, one feature is worth noting. The length of the anal sheath in females (Table 6) permits separation of nearly all populations of *F. grandis* and *F. heteroclitus* (except for *F. heteroclitus* north of Cape Cod where *F. grandis* does not occur). The length of the anal sheath of female *F. g. grandis* (Florida east coast) ranges from 52 to 80 (thousandths of stand-ard length, mean 69.0), whereas the longer anal sheath of female *F. heteroc-

litus ranges from 166 to 194 (mean 178.8). In *F. grandis*, the sheath encloses only about one-half the length of the first anal ray, whereas in *F. heterocli-tus* the first anal ray is completely enclosed. This character is useful for field identification.

Fundulus grandis saguanus RIVAS
FIGURE 7
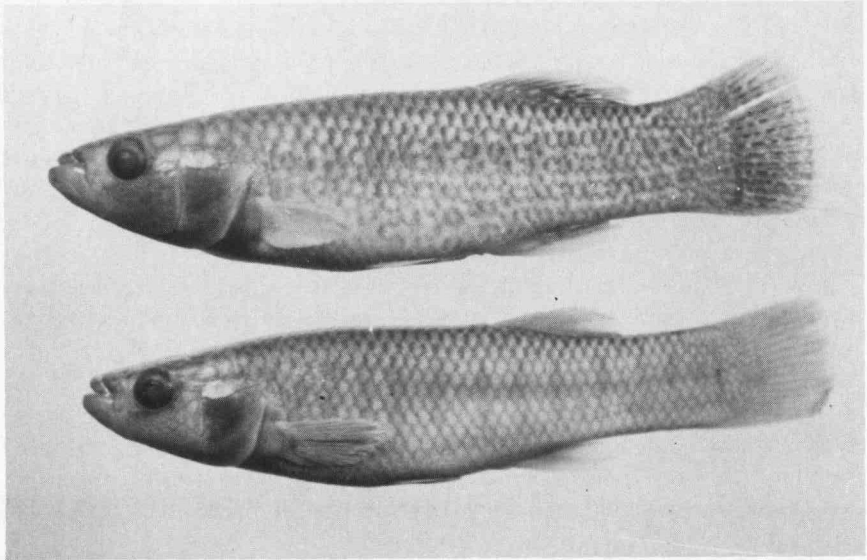
FIGURE 7. *Fundulus grandis saguanus* (CU 23975), Monroe County, Florida. Upper: male 92 mm SL; Lower: female 87 mm SL.

Fundulus grandis saguanus Rivas 1948:215-222 (original description, Playa Uvero, Cuba, holotype, USNM 132419, 75 mm SL; 14 paratypes, USNM 132420, 49-65 mm SL); Miller 1955:6, 8 (Cuba); Brown 1957:69 (Cuba).

Fundulus grandis Kilby and Caldwell 1955:203 (ecology; Snake Bight Canal, Florida); Briggs 1958:265 (in part: distribution); Tabb and Manning 1961:614 (ecology; Florida Bay).

MATERIAL EXAMINED.—The number of specimens follows catalogue number in parentheses. CUBA: USNM 132419(1), Holotype; USNM 132420(10), Paratypes. FLORIDA: ANSP 79273(4), 97096(6), 89772(1), 74883(6); CU 587(2), 48360(50), 48374(55), 48340(1), 48354(17), 48294(18), 48335(9), 48330(135), 23975(8), 45408(12); FSU uncatalogued (8); JU 718, 869, 938, 951, 1029, 1448; TU 37200(2); UMIM 5727(5), 5723(17); UMML 419(2), 4374(2), 319(2), 3306(2), 6585(8), 772(1), 3112(28); UF 8632(1), 5091(43); USNM 131871(2), 126799(2), 124660(2), 116897(2).

DIAGNOSIS.—A subspecies of *Fundulus grandis*, distinguished from the typical subspecies by number of lateral scales (30-35, usually 32-33, vs. 30-38, usually 33-36), gill rakers (7-11, usually 9, vs. 7-13, usually 9-11), vertebrae (31-36, usually 32-33, vs. 31-36, usually 33-35), and pectoral fin rays (16-19, usually 17, vs. 15-21, usually 17-19). *Fundulus g. saguanus* has the 10 mandibular pores and short anal sheath of *F. g. grandis*, and may be

distinguished from *F. heteroclitus* on the basis of those characters. The total of 10 mandibular pores also distinguishes *F. g. saguanus* from *F. grandissimus*, which has 12 mandibular pores.

DESCRIPTION.—See Tables 1-6 for summary of meristic characters. Except for those features noted above, these characters are the same as those found in the typical subspecies.

Coloration is similar to that of *F. grandis grandis*, but overall coloration is much lighter. The blue color of males is pale, and the ventral area is white. Median fins are not so heavily pigmented as in *F. grandis grandis*, and the light spots on the body are more prominent. This lighter coloration may be correlated with the clear or milky colored water in which this subspecies lives.

Melanophores are not scattered along the base of the pectoral fin as in *F. g. grandis*, but are concentrated into a distinct blotch around the dorsal origin of the pectoral fin. Usually no melanophores occur on the rest of the fin base, but on some individuals a few scattered melanophores may occur there anteriorly and posteriorly. The pelvic fins of males also lack melanophores, or have only a few, which is in sharp contrast to *F. g. grandis*, in which the pelvic fins have a heavy concentration of melanophores.

Contact organs are poorly developed on *F. g. saguanus* males. They are neither as large nor as numerous as on *F. g. grandis*, and do not appear at all on many specimens in breeding condition.

The pharyngeal plate is similar to that of *F. g. grandis*, but the individual teeth are somewhat larger and more recurved.

Maximum size is about 150 mm SL.

TYPES.—The holotype (USNM 132419), a female 75 mm in standard length, was collected 18 km northeast of Sagua La Grande, at Playa Uvero, Las Villas Province, Cuba. The 14 paratypes (USNM 132420: 9 females 38-66 mm SL, 5 males 49-65 mm SL), bear the same locality data as the holotype. Four of the paratypes are no longer at the USNM and presumably are deposited elsewhere. These are the only Cuban specimens known.

RANGE.—This subspecies ranges from Cuba (type material) and the Dry Tortugas (USNM 116897) northward through the Florida Keys and Florida Bay (westward to Cape Sable, UMIM 5723) to Boca Raton on the Florida east coast (JU 951, 2 specimens). It is common at least as far north as the Miami area. It does not appear to contact or intergrade with populations of *F. g. grandis* on either the Gulf or Atlantic coasts (Fig. 6).

MERISTIC VARIATION.—Little variation in meristic features occurs throughout the range of the subspecies, and Cuban specimens closely resemble specimens from the Florida Keys and Florida bay. *Fundulus g. saguanus* differs from *F. g. grandis* in a number of meristic features (Tables 1-4; and the Diagnosis). In addition, the mean number of pectoral fin rays for *F. g. saguanus* (17.44) differs significantly from populations of the

typical subspecies from southwestern Florida (mean 18.38) and from the Florida east coast (mean 17.95). The mode for the latter two populations is 18, and is 17 for *F. g. saguanus* from the Florida Keys and Cuba. Also of note is that clinal trends in pectoral fin ray and predorsal scale numbers seen in *F. g. grandis* are reversed in *F. g. saguanus*.

MORPHOMETRIC VARIATION.—*Fundulus g. saguanus* differs little from *F. g. grandis* in morphometric features, and consequently these data are not presented here. However, Rivas (1948:219), in his description of *F. g. saguanus* from Cuba, distinguished this form from *F. g. grandis* (including Florida Keys specimens in *F. g. grandis*) on the basis of several morphometric features. Although the Cuban specimens may differ from the *F. g. grandis* in the northern Gulf of Mexico, they do not differ from Keys specimens. Rivas (1948) reported the range for caudal peduncle length of the Cuban specimens as 4.1-4.5 (ratio of standard length), and the range for head length as 2.7-3.0 (also in standard length). My data for specimens from the Florida Keys give a range of 3.5-4.3 and 2.8-3.4 for these characters, respectively. Rivas (1948) also reported the caudal peduncle depth as 1.9-2.2 in head length, and the interorbital width as 2.1-2.4 in head length. My figures for these characters are, respectively, 1.8-2.1 and 2.2-2.4, for Keys' specimens. Subsequently, on the basis of these morphometric data and previously discussed meristic data, the Florida Keys' populations are placed with *F. g. saguanus*.

DISCUSSION OF *Fundulus grandis*.—Populations of *F. grandis* from the Gulf of Mexico seem to be continuous from Mexico (several TU collections) to southwestern Florida, over which range little morphological variation occurs. Slight differences in meristic features can be seen to the east and west of the Mississippi River, but recognition of subspecies is not warranted.

The allopatric population of *F. grandis* on the Atlantic coast is much more similar to the Gulf populations than to those from extreme south Florida and Cuba. If there are *F. grandis* between Boca Raton and Lake Worth, they are very rare, and gene flow is surely minimal.

The extreme south Florida population, *F. g. saguanus* (including the lower Florida east coast, Florida Keys, and Cuba) appears to be allopatric to both the Gulf and Atlantic populations, and differs markedly from both in most meristic characters (Tables 1-4). There are no characters that will distinguish Florida Keys (north to Boca Raton) populations from the nominal Cuban subspecies *F. g. saguanus* (Rivas 1948), and they should be referred to that subspecies. My original inclination (Relyea 1967) to elevate *F. g. saguanus* (inclusive of the Florida Keys) to species level may well be correct. Allopatric populations such as this, however, with a low degree of differentiation, cannot be easily placed taxonomically. Obviously what is important is the elucidation of the population as allopatric and somewhat

distinct. Perhaps other workers using different criteria (i.e. biochemical or chromosomal) will now be able to progress with the species concept in allopatric killifish populations, such as in the Florida Keys. In my opinion, killifish populations are too ecophenotypically plastic to be readily and simply alloted to species or subspecies on the basis of variable body proportions or indices derived from combinations of traits. Different populations differ in different ways.

Experimental work with the influence of temperature and other environmental factors on development of morphometric, meristic, and pigmentary features is needed. Studies of zygote viability in intraspecific crosses would also be of interest (i.e. Gulf of Mexico vs. Atlantic coast populations of *F. grandis*).

Fundulus grandis from the Gulf of Mexico and Atlantic coast of Florida are more like one another than either is to extreme south Florida *F. g. saguanus* and should be recognized as disjunct populations of the same subspecies, *F. g. grandis*.

C. YUCATAN POPULATIONS, *Fundulus grandissimus*
FIGURE 8
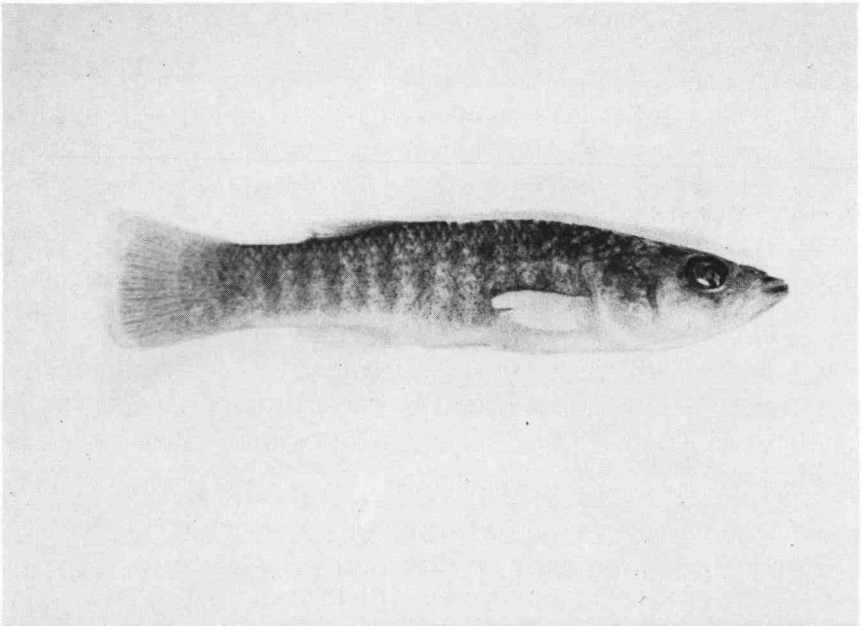
FIGURE 8. *Fundulus grandissimus* (JU 1699), Chiquila, Quintana Roo, Yucatan Peninsula, Mexico. Male 68 mm SL.

Fundulus grandissimus Hubbs 1936:209-210 (original description, Progreso, Yucatan, Mexico; Holotype, MCZ 32909, 179 mm SL); Miller 1955:1 (Yucatan); Brown 1957:69 (Yucatan); Miller 1966:788 (Yucatan).

Fundulus grandis Evermann and Goldsborough 1902:149 (Yucatan; error in identification);
  Barbour and Cole 1906:156 (Yucatan; error in identification).

MATERIAL EXAMINED.—The number of specimens follows catalogue number in parentheses. MEXICO, YUCATAN: TU uncatalogued (11), Lagoon 0.5 mi. S. of Progreso, 31 May 1961; USNM 50513(15), Progreso, 1935, Paratypes; FSU 27222(18), Progreso Mexico, Quintana Roo: JU 1679(20), at Chiquila, March 1979.

DIAGNOSIS.—A species of *Fundulus* most closely related to *F. grandis*, but differing from that species in the number of lateral scales (36-42, usually 38-41, vs. 30-38, usually 33-36), predorsal scales (21-25, usually 23-24, vs. 13-19, usually 15-17), caudal peduncle circumferential scales (21-25, usually 22-24, vs. mode of 20 in *F. grandis*), pectoral fin rays (15-18, usually 16, vs. mode of 18), and total number of mandibular pores (12, vs. 10). It also reaches a larger maximum size, the holotype measuring nearly 30 mm longer than the largest known specimens of *F. grandis* (179 mm vs. 150 mm SL).

DESCRIPTION.—In addition to the meristic features summarized in Tables 1-5 and in the Diagnosis, *F. grandissimus* has 14 preopercular pores, 5+5 branchiostegal rays, 6 rays in each pelvic fin, 10-12 dorsal fin rays, 10-12 anal fin rays, and 15-18 branched caudal fin rays. Cephalic squamation and sensory pore arrangement are similar to those of *F. grandis*.

Coloration is similar to that of *F. grandis*. Males are blue to olive with light vertical streaks and light spots, especially posteriorly, whereas females are drab olive. Median fins are blue with light spots.

Maximum size is about 180 mm SL.

Contact organs appear to be poorly developed. Females have a short anal sheath, a feature that allies this species with *F. grandis* (see Table 6).

TYPES.—The holotype (MCZ 32909) is a female, 179 mm SL collected at Progreso, Yucatan, Mexico. The USNM collection has 15 paratypes (USNM 50513), consisting of 12 females 108-131 mm SL and 3 males 114-142 mm SL. Hubbs (1936) mentioned 10 more paratypes (3 females, 131-151 mm SL and 7 males 97-125 mm SL).

RANGE.—This species is known from Progreso, Sisal, and Rio Lagartos, Yucatan, and Chiquila, Quintana Roo, in the Yucatan Peninsula of Mexico (Fig. 6).

DISCUSSION.—The most notable meristic features of *F. grandissimus* are given in the Diagnosis. Especially noteworthy is the total number of mandibular pores (12), a feature that readily distinguishes *F. grandissimus* from the closely related *F. grandis*. Body proportions are similar to *F. grandis*.

Hubbs (1936:159) stated that *F. grandissimus* apparently resembles *F. grandis* from the Florida Keys (interpreted here as *F. g. saguanus*). My data show that *F. grandissimus* and *F. g. saguanus* represent opposite extremes of divergence within the *F. grandis* population complex. Meristic counts are high for *F. grandissimus*, with marked, statistically significant differen-

ces in means when compared to *F. grandis* for lateral scales, predorsal scales, caudal peduncle circumferential scales, and total mandibular pores. Meristic counts are low for *F. g. saguanus*, which has the number of mandibular pores (10) typical of *F. grandis*.

ECOLOGY

Fundulus grandis and *F. heteroclitus* inhabit bays and tidal marshes, which usually have a mud or sand-mud substrate. The habitat of *F. grandissimus* is similar, but much less is known of that species. *Fundulus grandis* has been recorded from salinities ranging from freshwater (Tabb and Manning 1961) to 76⁰/₀₀ (Simpson and Gunter 1956). *Fundulus heteroclitus* is also extremely euryhaline, having been recorded from freshwater (Hildebrand and Schroeder 1928; Massmann, 1954), and is common in brackish situations.

Chichester (1920) observed spring migrations of *F. heteroclitus* in the Raritan River, New Jersey, from the mouth of the river to more brackish and freshwater areas, where they spend the summer and breed. In colder weather they leave the river and adjacent marshes and go into the deeper waters of the bays. If trapped in cold waters, they burrow in mud to a depth of 6-8 inches. Bigelow and Schroeder (1953) and Hildebrand and Schroeder (1928) also observed this burrowing behavior. Because of the more southerly distribution of *F. grandis*, it is doubtful that this species undergoes such a behavior pattern, and I have not noted *F. grandis* to burrow even when alarmed. It is my impression that many individuals of *F. heteroclitus* remain active throughout the winter months in northeastern Florida; whether any individuals burrow there is unknown.

Burger (1939) and Matthews (1938, 1939), working at Woods Hole, demonstrated that water temperature, not photoperiod, affects gonadal development in *F. heteroclitus*, and the same is probably true for *F. grandis*. Joseph and Yerger (1956) reported a spawning period of March through September for *F. grandis* on the Gulf coast, and Simpson and Gunter (1956:130-131) collected spawning individuals in Texas in October. Springer and Woodburn (1960) felt that *F. grandis* spawned from late fall through early spring in Tampa Bay, while Kilby (1955:197-198) suggested a continuous breeding season at Cedar Keys and Bayport. I have collected spawning fish through November on the northern Gulf coast. Apparently, southern populations of *F. heteroclitus* also spawn throughout warm months of the year (personal observation, Duval County, Florida).

Fundulus heteroclitus in the Gulf of Maine spawn from June to August (Bigelow and Schroeder 1953:163). In Chesapeake Bay the spawning period is somewhat longer, April through August (Hildebrand and Schroeder 1928:139), and becomes still longer southward (Brummett 1966:616-620).

Newman (1907) gave an account of the spawning behavior of *F. heteroclitus*. The male clasps the female with his dorsal and anal fins, and the pelvic fins of both individuals are forced against a rock or the substrate. The clasping posture lasts for about two seconds, during which time the gametes are released. Eggs are placed against rocks, oysters, debris, or at the base of *Spartina* or *Juncus*. Taylor et al. (1979) demonstrated a lunar periodicity of oviposition in which eggs are placed at the base of *Spartina* on the highest monthly tide and left stranded above the high tide mark until the next new or full moon. I have watched *F. grandis* spawning at Lanark Beach, Franklin County, Florida. The male forces the female into coves, clumps of debris, or among oysters and assumes a clasping posture similar to that of *F. heteroclitus*. For further information on killifish reproduction see Foster (1967a,b).

The small eggs of *F. heteroclitus* and *F. grandis* are demersal and adherent. Hubbs and Drewery (1959) and Newman (1908) have successfully obtained artificial hybrids between *F. heteroclitus* and *F. grandis* females and *F. majalis* males. Natural hybrids are known between *F. diaphanus* and *F. heteroclitus* (Hubbs, Walker, and Johnson 1943).

Members of this species complex form schools, but not to the extent of *F. majalis*. Feeding groups of 12-20 individuals are frequently encountered. Food consists primarily of molluscs, crustaceans, and small fishes. I have removed the following fishes from the oral cavity of *F. grandis*: *F. majalis*, *F. grandis*, *Cyprinodon variegatus*, *Gambusia affinis*, and *Gobiosoma* sp. Radiographs show fish remains in the gut of many specimens of both *F. grandis* and *F. heteroclitus*. *Fundulus grandis* in aquaria readily eat *Gambusia affinis*. *Fundulus heteroclitus* is known to feed on gammarid amphipods (van Dolah 1978).

Seine hauls that yield *Fundulus heteroclitus* or *F. grandis* also often yield *F. majalis*. *Fundulus majalis* is a bottom feeder and does not generally eat other fishes, whereas *F. heteroclitus* and *F. grandis* are middle-level feeders, or top feeders, and do prey on fishes. The perplexing problem is that where *F. heteroclitus* and *F. grandis* are sympatric, they appear to be fully syntopic, even to the point of forming mutual schools. I, and others, have collected both species in the same short haul of a seine. No habitat difference is detectable between them. As the breeding seasons of both species are extensive, there seems to be no temporal separation, and yet I have seen no hybrids. Perhaps sexual recognition is well developed in each species, and interspecific mating is therefore rare. This implies a situation similar to that in *F. notatus* and *F. olivaceus*, in which the species are quite similar superficially (to the human eye), but which hybridize very infrequently (Thomerson 1966). It is also possible that interspecific matings occur in nature, but zygotes are inviable.

REMARKS

The patterns of geographic variation in this species complex are: (1) possible racial differentiation of *Fundulus heteroclitus* north and south of Cape Lookout; (2) isolation of two species, *F. bermudae* and *F. rhizophorae* from a *F. heteroclitus* stock on Bermuda; (3) differentiation of *F. heteroclitus* and *F. grandis* as full species (sympatry in northeastern Florida; diagnostic features are length of anal sheath of females and number of mandibular pores); (4) differentiation of an extreme south Florida population (and Cuba) which is referred to *F. grandis saguanus*; (5) possible racial differentiation of *F. grandis* in the western Gulf of Mexico and on the Florida east coast; and (6) differentiation of *F. grandissimus* in Yucatan.

THE *FUNDULUS MAJALIS* SPECIES COMPLEX

Fundulus majalis (WALBAUM) AND THE NOMINAL
Fundulus similis BAIRD AND GIRARD

FIGURES 9-12
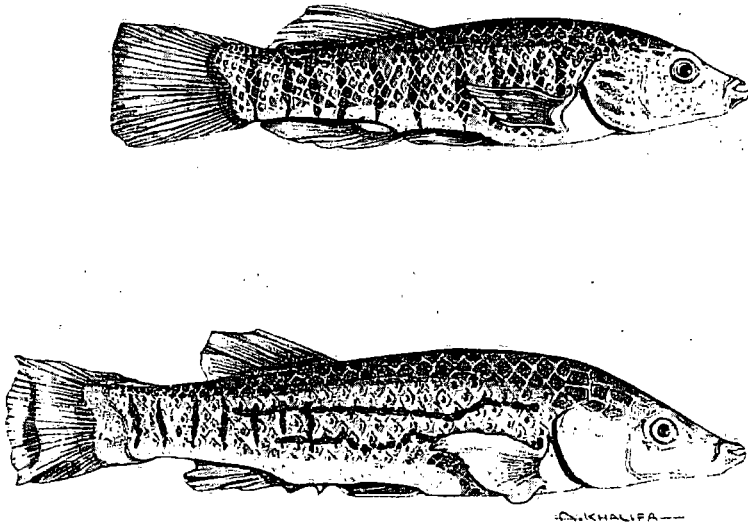
FIGURE 9. *Fundulus majalis* (JU 805), St. Johns County, Florida. Upper: male 61 mm SL; Lower: female 77 mm SL. This is the typical *"majalis"* pigmentary pattern.

Cobitis majalis Walbaum 1792:12 (original description; Long Island, New York; types not examined); Jordan and Evermann 1896:639 (placed in *Fundulus*).
Esox flavulus Mitchill 1815:439 (original description, New York); Jordan and Evermann 1896:639 (synonymy).
Esox zonatus Mitchill 1815:440 (original description, New York); Jordan and Evermann 1896:639 (synonymy).
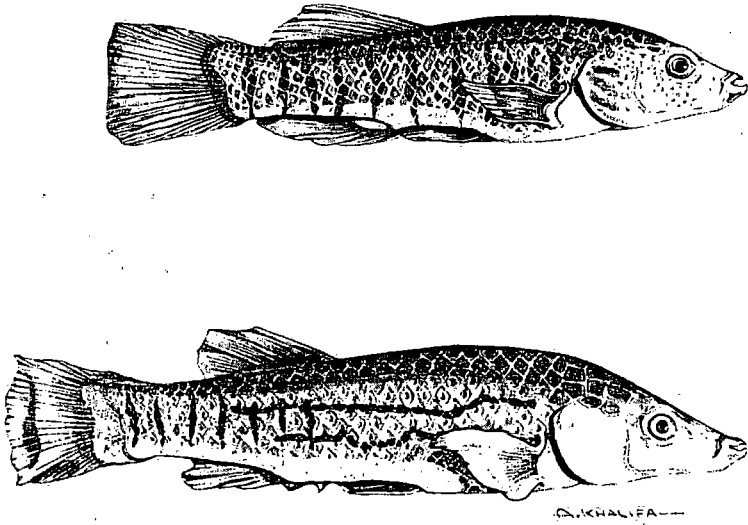
FIGURE 10. *Fundulus majalis* (JU 995), Brevard County, Florida. Upper: male 87 mm SL; Lower: female 75 mm SL. This represents the classical "*similis*" pigmentary pattern.
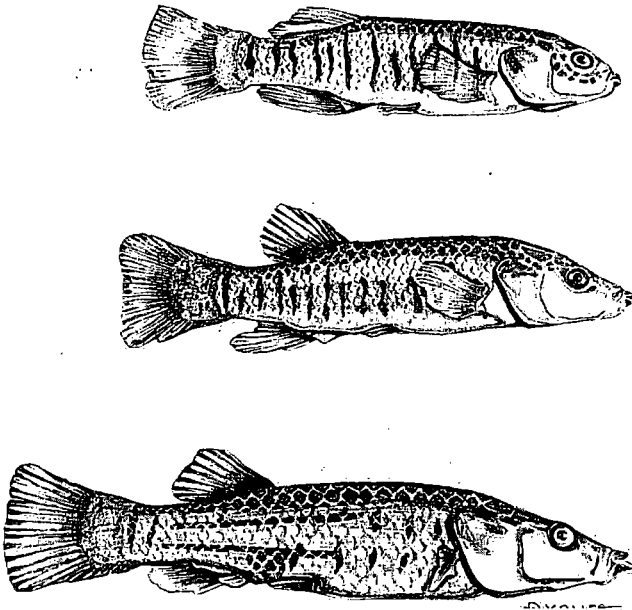
FIGURE 11. *Fundulus majalis* (intergrade pattern) (JU 768), Flagler County, Florida. Upper: male 66 mm SL; Middle: female 71 mm SL; Lower: female 88 mm SL.
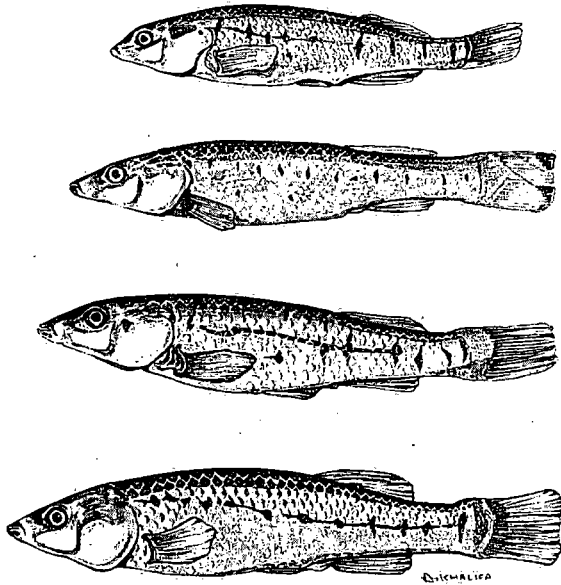
FIGURE 12. *Fundulus majalis* (JU 693), St. Johns County, Florida. Juveniles (from top to bottom) 47, 51, 53, and 57 mm SL.

Hydrargyra trifasciata Storer 1837:417 (original description, Massachusetts); Jordan and Evermann 1896:639 (synonymy).

Hydrargyra majalis Cuvier and Valenciennes 1846:207 (South Carolina); Uhler and Lugger 1876:128 (Maryland); Yarrow 1877:214 (North Carolina); Goode 1879:118 (St. Johns R., Florida); Jordan and Evermann 1896:639 (synonymy).

Hydrargyra vernalis Cuvier and Valenciennes 1846:206 (original description, South Carolina); Jordan and Evermann 1896:639 (synonymy).

Hydrargyra similis Baird and Girard 1853:389 (original description, Indianola, Texas; types not examined); Jordan and Everman 1896:638-639 (synonymy).

Fundulus similis Günther 1866:323 (removed *F. similis* from genus *Hydrargyra* and placed it in *Fundulus*)..

Fundulus majalis Günther 1866:322 (removed *F. majalis* from genus *Hydrargyra* and placed it in genus *Fundulus*); Garman 1895:104-105 (description; distribution); Jordan and Evermann 1896:639 (description; distribution; synonymy); Miller 1955:9 (distribution); Brown 1957:72-73 (identified in key; distribution).

MATERIAL EXAMINED.—The number of specimens follows catalogue number in parentheses. NEW HAMPSHIRE: UMMZ 145275(1). MASSACHUSETTS: ANSP 7050-51(2), 7118(10); UMMZ 158794(50). NEW YORK: UMMZ 103799(50), 104029(50). NEW JERSEY: ANSP 7102-17(16), 88226(2), 30987(1); UMMZ 114372(50), 109847(50). MARYLAND: ANSP 45631(2); TU uncat. (15); UMMZ 97817(40), 66865(50). VIRGINIA: UMMZ 99400(14), 99399(13), 99398(2), 102347(1), 171291(3). NORTH CAROLINA: ANSP 80733(18); TU 16510(11); UMMZ 132805(14); USNM 58975(3), 58977(3), 51854(4). SOUTH CAROLINA: UMMZ 136059(58). GEORGIA: ANSP 80735(4), 80736(16); TU 21235(101), 21351(1); UMMZ 88584(3). FLORIDA: ANSP 89772(1), 74884(10), 30613-16(4); FSU uncat. (15), uncat. (4), 1579(17), 6518(12), 12418(30), 6526(69), 8892(3), 10385(1), 4639(6); JU 46, 74, 88, 114, 708, 697,

733, 685, 693, 679, 552, 474, 497, 504, 165, 147, 791, 643, 787, 776, 768, 805, 795, 793, 860, 841, 840, 892, 877, 906, 1285, 1337, 1468, 1571, 1617; TU 20474(6), 5902(118), 37444(203), 20596(122), 18165(5), 18207(11), 20385(212), 41204(310), 41591(99), 2274(59), 20337(42), 21260(26), 41063(140), 40571(3), 27786(47), 9745(18), 18306(5), 18413(258), 20952(67), 20578(11), 18357(106), 20425(8), 18223(1), 41080(13), 41572(50), 41563(63), 20303(61), 16703(16), 41582(20), 41847(1), 20992(51), Uncat. (KR-Fla.-34) (13), 36160(2); UF 4011(2), 6611(30), 5227(28), 5201(1), 2987(2), 3303(3), 3117(5), 3298(79), 3137(2); UMIM 2603(12), 5314(2), 3151(2); UMML 3321(1); UMMZ 55989(3), 65242(2), 139341(33), 177472(53), 139390(1), 136587(2), 138388(96), 139369(77); USNM 18052(2), 104955(2), 62636(2). ALABAMA: TU 19837(36), 14519(1). MISSISSIPPI: TU 10873(3), 28139(11), 9858(1). LOUISIANA: TU 19508(19), 5881(85), 23209(26), 23635(259), 18760(1), 19162(30), 15337(148), 8267(26). TEXAS: JU 1640, 1649, 1654, 1667, 1674, 1687; TU 12864(1), 1831(9), 39874(1), 21952(1), 21551(390), 41101(8). MEXICO: Tamaulipas: UMMZ 157322(3), 35 mi. N of Tampico.

DIAGNOSIS.—Members of the *Fundulus majalis-F. similis* species complex may be distinguished from all other members of the genus by the scaled preorbital region. Other diagnostic features include: dorsal rays 11-16, (usually 12-15), anal rays 9-13 (usually 10-12), lateral scales 30-37 (usually 33-35), gill rakers 6-10 (usually 7-8), pectoral rays 16-21 (usually 18-19), mandibular pores 8 (occasionally 7), branchiostegal rays 6, and vertebrae 31-38 (usually 34-36).

DESCRIPTION.—In addition to the meristic features presented in the Diagnosis and in Tables 8-12, there are 6 rays in each pelvic fin, 13-20 (usually 15-18) branched caudal fin rays, 13-17 (usually 14-15) predorsal scales, and 15-22 caudal peduncle circumferential scales (usually 20-21 north of Cape Lookout and 17-19 southward).

There are 4 preopercular and 3 preorbital scale rows. Opercular scales are irregularly arranged. There is an enlarged interorbital scale surrounded by a rosette of 7 smaller scales. Contrary to Cooke's (1965) statement, the interorbital scale arrangement will not distinguish this species from *F. heteroclitus* (or *F. grandis*). Preorbital scalation extends dorsally beyond the second preorbital pore, except in extreme south Florida populations. This latter exception seems to be related to the elongation of the head southward in this species complex (see morphometrics). Curiously, the area immediately dorsal to the fourth (most ventral) preorbital pore, approximately the size of one preorbital scale, is naked.

Of 183 specimens examined, 181 had 14 preopercular pores, and 2 specimens had 15 pores. Of 320 specimens examined, 251 had a total of 8 mandibular pores, 13 had 6, 53 had 7, and 3 had 9. There are typically 4 preorbital pores. Cephalic sensory pore arrangement was described in detail for this species by Gosline (1949), and does not differ markedly from the arrangement for the *F. heteroclitus-F. grandis* species complex.

The upper pharyngeal plates are separated into anterior and posterior regions by a distinct groove and are about as wide as long. The anterior portion is large (nearly as large as the posterior portion), but in the *F.*

heteroclitus-F. grandis species complex the anterior portion is small. Pharyngeal plate structure is the object of continuing research by the author. On the anterior portion of the upper plate are two vaguely defined transverse rows of teeth, and 4 or 5 transverse rows on the posterior portion. Pharyngeal teeth are small, numerous, and conical. The lower pharyngeal plates are fused to form a broad triangular plate. The overall morphological structure of the pharyngeal plates of *F. majalis-F. similis* resembles that of *F. diaphanus* and *F. seminolis*.

Meristic characters and body markings vary considerably geographically. The dorsal fin ocellus of males is prominent in northern populations, but is reduced in intensity or lacking in southern populations. Body markings of females, which range from vertical bars (*F. similis* type) to longitudinal stripes (*F. majalis*), are discussed in another section. Juvenile pigmentation is like that of females (see Figs. 9-12).

Males in breeding color are a dark steel blue, especially dorsally. The ventral region of the head and body are bright yellow anteriorly, shading to white posteriorly, and an intense dark blotch occurs in the middle of the operculum. The tip of the snout to the occiput is green. The median fins are dark, and the caudal fin has a dark margin. The pectoral and pelvic fins are bright yellow. An orange predorsal stripe extends from the dorsal fin origin to the interorbital region (this stripe may be absent in extreme south Florida specimens). Contact organs occur on the head, dorsal, and anal fins and on body scales. In northern populations, 7 or 8 contact organs appear on the posterior rim of each body scale and 4-6 in southern populations.

Members of the *Fundulus majalis-F. similis* population complex are large species, attaining a maximum standard length of about 130 mm.

RANGE.—*Fundulus majalis* ranges continuously along the Atlantic coast from New Hampshire, Great Bay, mouth of Lamprey River (Jackson 1953:192), southward to Lake Worth, Palm Beach County, Florida (JU 1337), and disjunctly in the Gulf of Mexico from Collier County, southwestern Florida (UMIM 3151, FSU 1579) continuously northward and westward along the coast to near Tampico, Mexico (Miller 1955:9) (Fig. 13). An allopatric population occurs in the Florida Keys. Within this overall range, the nominal *F. majalis* occurs, according to Miller (1955), from New Hampshire southward to the Matanzas River, and the nominal *F. similis* from the Matanzas River southward through the Florida Keys and westward in the Gulf of Mexico to Mexico. I find (in several JU collections) the "*majalis*" pigmentary features farther south than the Matanzas River, to Flagler County. The "*similis*" form occurs southward from there. In all Tables in this paper, therefore, the designation Flagler County includes specimens that are "*majalis*" in appearance.

MERISTIC VARIATION.—Along the Atlantic coast the modal number of dorsal rays (Table 8) is 14 in northern populations and 13 in southern
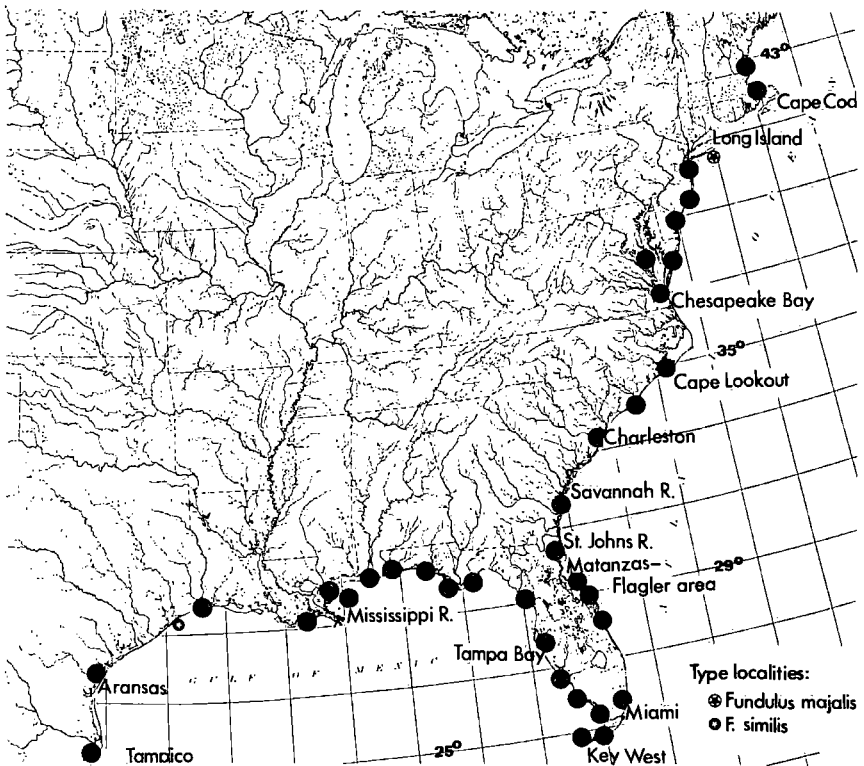
FIGURE 13. Map of the geographic distribution of *Fundulus majalis*. Mexican localities in the Tampico area actually farther south than indicated.

populations, the shift occurring between the Matanzas River and Flagler County populations (both "*majalis*" types). The means for these two populations are statistically different, and the trend is clearly clinal. In the Florida Keys the mode is 12, and the mean is significantly different from populations adjacent in the Gulf and on the Atlantic coast. Dorsal rays show a slight increase from north to south in the Gulf of Mexico. Of note is that 87% of the specimens examined from Cape Lookout to the Matanzas River had 14 or fewer dorsal rays, while 98% from Chesapeake Bay northward had 14 or more. A strong north-south cline is indicated, including gradation from "*majalis*" to "*similis*." It is not altogether clear whether low counts in Florida Keys population represent a southerly terminus of the cline or a separate distinct population.

The modal number of anal rays is 11 in all populations, and any statistical differences between means is marginal.

The mean number of branched caudal rays (Table 9) for the lower Florida east coast population (15.87), and for the Flagler County population (16.20) differs significantly from the mean for the Matanzas River

population (16.99). A clinal pattern is evident. The mode for caudal rays shifts from 16 west of the Mississippi River to 15 eastward and back to 16 on the Florida east coast from Mosquito Lagoon southward.

The modal number of lateral scales (Table 10) is 34 in all populations from Cape Lookout southward on the Atlantic coast and throughout the Gulf of Mexico, but is 32 in the Florida Keys. Populations from Chesapeake Bay northward show an increase in the number of lateral scales, but means are not significantly different from those of southern populations. The mean for the Florida Keys population is significantly lower than means for adjacent populations.

Predorsal scales do not differ markedly between populations, except that the mean for predorsal scales in the lower Florida east coast race (15.24) differs significantly from the Flagler County population mean (14.62). The modal number of predorsal scales for the Florida Keys population does not distinguish this population from Gulf of Mexico populations (nor does the mean), but the Florida Keys mean (14.76) is statistically different from the mean (15.24) for the lower Florida east coast population.

The modal number of gill rakers is 7 in all populations except those west of the Mississippi River (mode = 8). The mean for this latter population is also significantly different from populations in the Gulf east of the Mississippi River.

Populations north and south of Cape Lookout are sharply delineated by the number of caudal peduncle circumferential scales (Table 11). The Chesapeake Bay mean (19.91) is significantly different from the Cape Lookout-Charleston Bay mean (18.80), but there seems to be a general clinal decrease southward along the Atlantic coast. In the Gulf of Mexico the number of circumferential scales increases west of the Mississippi River (mean is significantly different). Lower Florida east coast populations resemble the Matanzas River population more closely than they do Gulf of Mexico populations, which would either indicate gene flow from *F. majalis* to the nominal *F. similis* or convergence in the Atlantic coast environment. The mean for Florida Keys populations differs significantly from the mean for Florida east coast populations, but not from the mean for the southward Florida population in the Gulf.

The modal number of pectoral fin rays is 19 in all populations, except for the Florida Keys and lower Florida east coast populations which have 18. The means (18.16 and 18.39, respectively) for these latter populations are marginally statistically different from the Flagler County population mean (18.73). Flagler County specimens are close, with regard to this character, to Matanzas River specimens (mean = 18.79). The Florida Keys' population mean (18.16) differs significantly from the mean (18.85) for the southwest Florida population, but not from the Florida lower east coast mean (18.39).

The number of vertebrae (Table 12) shows little variation throughout the population complex, except for the Florida Keys. No statistical difference exists between the Matanzas River, Flagler County, and lower Florida east coast populations with this character, but the mean for the Florida Keys population is markedly different from adjacent population means. The mode is 36 from Chesapeake Bay northward, 35 southward on the Atlantic coast, 34 or 35 in Gulf populations and 33 in the Florida Keys.

MORPHOMETRIC VARIATION.—Little noteworthy variation occurs in body proportions throughout the population complex, but head length data (Table 13) are presented, as Brown (1957:72-73) suggested that this character will serve to distinguish between *F. majalis* and *F. similis*, which my data do not support. Southern populations on the Atlantic coast (both males and females) have longer heads than northern populations, but this character shows broad overlap in range. Gradation from *F. majalis* to *F. similis* seems evident. Florida Keys and Gulf of Mexico specimens (especially in southwest Florida) have the longest heads. Preliminary data not presented here indicate that elongation of pharyngeal plates accompanies this southward increase in head length.

BODY MARKINGS.—The body markings of males (Figures 9-10; also see excellent illustration in Garman 1895) do not vary greatly geographically. Males typically have a well defined dorsal fin ocellus, which is formed by a concentration of pigment on the last four dorsal rays and surrounded by a cream-colored area. This mark is well defined southward along the Atlantic coast to the Matanzas River. Farther south along the east coast of Florida and in the Keys and Gulf of Mexico, the intensity of the ocellus decreases. Miller (1955) did not note the ocellus in *Fundulus persimilis* from Yucatan. In addition, the ocellus is usually lacking in the western Gulf of Mexico population (from which *F. persimilis* was derived?).

The body markings of females show considerable geographic variation. Northern females (Fig. 9; also see Garman 1895) have two or three longitudinal stripes, which begin just behind the pectoral fin and extend well onto the caudal peduncle. One to four vertical bars appear on the caudal peduncle. The stripes all lie on the ventral half of the sides. Juveniles have from 7 to 14 vertical bars. The barred juvenile pattern breaks up by the flattening of the dorsal region of each bar to form a "T." This process begins anteriorly and proceeds posteriorly, leaving the last one or two bars on the caudal peduncle unaffected (Newman 1907). The next step in the process is the formation of a short longitudinal slash about midway on each vertical bar. Occasionally a third slash appears farther ventrally (Fig. 12).

As this process continues, the longitudinal slashes coalesce to form stripes, and the bars are completely disrupted. In northern populations this process is usually completed by the time an individual attains 20 mm standard length, whereas in southern populations the process is not com-

plete until about 40-50 mm SL.

On the lower east coast of Florida, in the Gulf of Mexico, and in the Florida Keys, the vertical bars are retained throughout the life of the individual (Fig. 10). Adult female specimens from Flagler County, Florida (between Matanzas River and Mosquito Lagoon), have a pattern in which several bars are broken up into spots (Fig. 11). This north-south trend enhances the idea that *F. majalis* and *F. similis* are conspecific.

Several females from the Chandeleur Islands in Mississippi Sound have a distinct tendency toward the development of longitudinal stripes. In this same collection (TU 8267) are several males with a well-defined ocellus in the dorsal fin, showing that these body markings may appear in various localities. In addition, I have examined adult *F. majalis* (up to about 70 mm SL) from New York and South Carolina that have not completely developed the typical stripes. Juveniles from South Carolina, Georgia, Florida, and throughout the Gulf of Mexico are indistinguishable, whereas northern *F. majalis* juveniles generally show the adult female striped pattern early. This probably accounts for the erroneous records of *F. similis* from South Carolina by True (1883:255) and Jordan and Gilbert (1883:585). I believe that it may also account for the record of *F. similis* from the Matanzas River by Miller (1955).

Water temperature may be a factor involved in the ontogenetic pigmentary changes in this species and should be more thoroughly investigated. Specimens hatched at different times of the year may develop the characteristic adult pattern at different rates. The single presumed *F. similis* from the Matanzas River (UMMZ 139390; a 73 mm female) was collected on 19 August 1936. Another female (74 mm SL; JU 88) collected in September near St. Augustine has *"similis*-like" bars, but two of the bars on one side are flattened dorsally to form a short stripe. These fish would be about one year old. By contrast, numerous 30-40 mm juveniles that I collected in the Matanzas River in August, which are presumably from a spring spawning of the same year, had nearly completed the pigmentary changes. Specimens about 30-40 mm SL collected in the same area in March (presumably from a fall spawning) show only the very beginnings of pigmentary changes and perhaps would not attain the adult pattern until the next fall. Such specimens collected in the spring or early summer would still have vertical bars and would attain adult markings at a later age and greater size than individuals from a spring spawn. The two *"similis*-like" specimens from the Matanzas River have, in my opinion, retained the juvenile barred pattern, and can be allocated to *F. majalis*.

Females of the southern races typically have from 8 to 11 dark vertical bars on each side, but the range is from 7 to 14, the character being very variable (Fig. 10). The last vertical bar on the caudal peduncle may be reduced to one, or often two spots, but this feature is changeable on any one

fish in a matter of minutes (personal aquarium observation). The same is probably true of the number of vertical bars, although there appears to be some genetic fixation of this character. One specimen from Fort Walton, Florida, had only five vertical bars on each side on the posterior half of the body when taken alive. During several months in an aquarium it never developed more than five bars on each side.

The vertical bars found on adult females from southern populations appear to be a retained juvenile character. Presumably the populations in the Gulf of Mexico and on the lower Florida east coast are derived from a population that differentiated in isolation from a F. majalis stock during the Pleistocene (see Zoogeography). One manifestation of this isolation was apparently the retention of juvenile body markings.

From the previous accounts of geographic variation of meristic and morphometric characters and body markings, it is evident that *Fundulus majalis* and *F. similis* are conspecific. No character affords specific separation, and the supposed sympatry of the two forms, based on a single "*similis*-like" specimen collected in the Matanzas River, is untenable.

Differences between Atlantic and Gulf of Mexico populations of *Fundulus majalis* are obvious, and the lower Florida east coast populations vary with respect to meristic characters in the direction of *F. majalis* from the Matanzas River, and yet body markings of the former clearly resemble those of Gulf of Mexico populations.

The Flagler County specimens are certainly transitional between Matanzas River and Mosquito Lagoon specimens. Some taxonomists would consider the Flagler County material to represent intergrades between two subspecies, but the only characters that would afford slight separation of such subspecies are dorsal rays and body markings. The clinal nature of these characters has been discussed previously. Admittedly there is a definite transition from one form to another along the east coast of Florida, but this is merely sharp clinal gradation. I find no compelling evidence for the awarding of subspecific designations, although other investigators might.

Griffith (1974) has concurred with this position, and Chen's (1971) comparative chromosome analysis demonstrated no differences between *Fundulus majalis* and *F. similis*. These forms should be considered conspecific.

Florida Keys populations are allopatric (or appear to be), much like *Fundulus g. saguanus*. In some respects these Keys specimens resemble Atlantic coast populations, and in others Gulf populations. In other respects (i.e. vertebral number), they differ markedly from other populations. Any possible gene flow between the populations in the Florida Keys and adjacent populations remains to be demonstrated. In some ways (lateral scales) the Keys' population seems to be the southern end of a cline. My original

inclination (Relyea 1967) was to describe the Florida Keys population as a distinct species equivalent to *F. g. saguanus*. This may yet prove to be the correct interpretation, but I think that the characters exemplified in the Keys may be expected in southernmost populations. Yucatan populations of both species complexes being considered do not show the low meristic counts expected of southernmost populations (some meristic features increase from north to south in *F. grandis*).

This all may be evidence of, as I suspect, a lack of close genetic affinity of Florida Keys and Yucatan populations, or it could reflect different developmental environments. One might also be suspicious of the influence of genetic drift in an isolated small population such as in Yucatan. *Fundulus majalis* (and *F. g. saguanus*) exists throughout the Florida Keys, however, and genetic drift should probably not play a major part in determining the observed frequencies of the characters studied; natural selection and environmental influences, perhaps temperature, on development must be assumed to be more significant. The structure of populations in the Florida Keys and Yucatan is different. In addition, the possibility of recent or continuing gene flow to the Florida Keys population from peninsular Florida populations must be considered possible; such gene flow to Yucatan populations would probably not have been possible for a long time. Yucatan and Florida Keys populations should not be expected to vary in the same way from other populations. Perhaps it is most significant that Yucatan *F. grandissimus* and *F. persimilis* differ from other populations in similar ways, and so do Keys populations of *F. grandis* and *F. majalis*, and yet Keys and Yucatan populations represent different extremes of morphology in their respective species complexes.

It should also be noted here that the divergence of populations west of the Mississippi River is not sufficient, in my opinion, to warrant recognition of eastern and western Gulf of Mexico subspecies.

If subspecies are to be recognized in this population complex, then Gulf of Mexico, Florida Keys, and lower Florida east coast (Mosquito Lagoon southward) populations should be considered *F. majalis similis;* populations from the Matanzas River northward should be *F. m. majalis;* and the Flagler County material should be intergrades.

Fundulus persimilis Miller

Fundulus persimilis Miller 1955:13-25 (original description, Rio Lagartos, Yucatan, Mexico; holotype UMMZ 163094, male 75 mm SL; paratypes UMMZ 163095 [30 spec.], UMMZ 162303 [2 spec.]; Brown 1957:69 (Yucatan).

DIAGNOSIS.—A species of *Fundulus* most closely related to *F. majalis* ("*similis*-type"), from which it may be distinguished by the smaller dorsal and anal fins, the numbers of dorsal fin rays (9-11, usually 10), anal-fin rays

(9-10, usually 10), vertebrae (35-37, usually 36), and lateral scales (34-37, usually 35-36) (see Miller 1955:13, Tables I, II, and III).

RANGE.—This species is known only from the Yucatan Peninsula of Mexico.

DISCUSSION.—*Fundulus persimilis* has fewer dorsal and anal fin rays and more vertebrae and lateral scales than *F. majalis*. These features and the marked disjunction in its distribution relative to *F. majalis* leave little doubt as to its specific validity. It is interesting to note that *F. persimilis* does not resemble *F. majalis* from the Florida Keys, and as with the *F. heteroclitus-F. grandis* species complex, the Yucatan population and Florida Keys population seem to represent opposite morphological extremes.

ECOLOGY

Members of the *Fundulus majalis* population complex are euryhaline and inhabit estauries, salt marshes and lagoons. Specimens have been collected from a salinity range of $3.2^0/_{00}$ (Springer and Woodburn 1960) to $76.1^0/_{00}$ (Simpson and Gunter 1956). Although *F. majalis* congregates around the mouths of creeks (Hildebrand and Schroeder 1928; personal observation), it apparently does not swim upstream much beyond tidal level. Gunter (1956) included this species in his list of euryhaline fishes, but it is less euryhaline than either *F. heteroclitus* or *F. grandis* (see Griffith 1974 for extensive data).

There is a definite preference for a soft-mud, or sand-mud, substrate, although *F. majalis* is extremely common along sandy shore lines (Springer and Woodburn 1960:27; Hildebrand and Schroeder 1928:141; Bigelow and Schroder 1953:165). My field observations indicate that the limiting factors of dispersal are the degree of surf action in a given area and the availability of shallow water zones. On the east coast of Florida the species is encountered in tidal marshes and estuaries off the major inlets. At Destin Inlet, in the northern Gulf, the species is encountered in the inlet along shallow, sandy shore margins, but not near the mouth of the inlet where the wave action is intense. In Franklin County, Florida, *F. majalis* is common along the sand-mud shorelines of the area, where wave action is minimal because of the several offshore barrier islands and Alligator Peninsula to the east. When strong south winds prevail, often in conjunction with an incoming tide, the fishes retire to protected coves and creek outlets. On Dog Island (Franklin County), the fishes are abundant on the bay side where surf action is slight, but they are absent on the Gulf side. The same is true on Alligator Peninsula. I have seen specimens in tide pools and low surf near the mouth of the St. Johns River, Duval County, Florida.

Inlets on the east coast of Florida are often quite deep, and present only a narrow shallow water zone or none at all. *Fundulus majalis* is rarely encountered at depths of more than 2 feet, and consequently this species is

restricted to limited areas on the Atlantic coast of Florida. This results in small isolated populations wherever suitable conditions exist, severely limits dispersal, and may, in part, explain the marked transitions from one population to the next on Florida's Atlantic coast.

The Gulf coast presents nearly continuous shallow water zones, with little wave action and extensive tidal marshes. Consequently, the species is continuously distributed, shows less variation, and is abundant in the Gulf. Numerous mangrove islands and mud flats provide the necessary habitat in the Florida Keys.

Fundulus majalis forms larger schools (up to about 20 individuals) than most species in the genus, with the exception of *F. seminolis*. Most ecological studies including these forms have noted school formation.

Joseph and Yerger (1956) and Kilby (1955) stated that this species (as *F. similis*) spawns from spring through fall. Burger (1939) and Matthews (1938, 1939) showed that water temperature, not photoperiod, stimulates gonadal development in *F. heteroclitus*. Harrington (1959) demonstrated the same for *F. confluentus*, and this probably prevails in *F. majalis*. The length of the spawning period consequently decreases northward. *Fundulus majalis* spawns in Chesapeake Bay from April to September (Hildebrand and Schroeder 1928) and in the Gulf of Maine in late spring and summer (Bigelow and Schroeder 1953).

Spawning occurs in shallow cup-like depressions in shallow water (Simpson and Gunter 1956; Martin and Finucane 1969). The large demersal eggs are forced into the sand or mud during oviposition. The failure of artificial hybrids (between female *F. majalis* and male *F. heteroclitus* and *F. grandis*) to survive has been attributed to the large size of the egg (2 mm diameter), and to the inability of the hybrid embryo to absorb all of the yolk (Hubbs and Drewery 1959).

Newman (1909) stated that *F. majalis* spawns in small groups of several males and females which my field observations support. In general protected waters with some debris or silt on the bottom are preferred, although spawning also takes place along shallow, sandy shorelines. The spawners may eat their own eggs. This is apparently related to general feeding behavior, as schools of *F. majalis* constantly poke into the substrate for food. Individuals will also burrow into the substrate when alarmed. *Fundulus seminolis* exhibits a similar spawning behavior.

Small crustaceans and molluscs are primary dietary items. Numerous X-ray radiographs show that most individuals ingest great quantities of sand while feeding. Hildebrand and Schroeder (1928:141) and Bigelow and Schroeder (1953:163) stated that small fish are eaten. I have found no fish remains in the alimentary tracts of the many specimens I have examined, nor have I any evidence that *F. majalis* eats other fishes. Specimens that I have kept in aquaria refused to eat small *Gambusia affinis*.

COMPARISON OF THE SPECIES COMPLEXES

The similar distribution of the *Fundulus heteroclitus-F. grandis* and *F. majalis* species complexes affords a unique opportunity of comparing geographic variation and population differentiation between them. A point of interest is the fact that in both species complexes a distinct species occurs on the Yucatan Peninsula of Mexico, separated by a distance of several hundred miles of coastline from related Gulf of Mexico forms.

The pattern of geographic variation within *F. grandis* and southern populations of *F. majalis* are strikingly similar: (1) racial differentiation east and west of the Mississippi River; (2) isolation on the east coast of Florida; and (3) allopatry in the Florida Keys. A major notable difference is that *F. grandis* had dispersed to Cuba and the Tortugas, whereas *F. majalis* has not.

Fundulus grandis does not hybridize with its northern cogener, *F. heteroclitus,* while a transition between races of *F. majalis* is apparent. The area of sympatry of *F. grandis* and *F. heteroclitus* is about the same as the area of transition between races of *F. majalis.*

Fundulus majalis and *F. heteroclitus* both show racial differences north and south of Cape Lookout, North Carolina. *Fundulus heteroclitus* has dispersed farther northward (to Canada) on the Atlantic coast than *F. majalis,* and has populated Bermuda (perhaps several times).

The *Fundulus heteroclitus-F. grandis* complex has been more successful in reaching more isolated, or harsher, regions than *F. majalis.* This probably reflects both dispersal ability and ability to exploit new regions once they are attained. Williams (1960) showed that *F. heteroclitus* does not move very much from a given place, even across tidal creeks with moderate tidal currents. Nevertheless, this species has dispersed to Bermuda, and *F. grandis* to Cuba and the Tortugas.

Racial differentiation in *F. majalis* north and south of Cape Lookout would be the direct influence of temperature, with more northern populations exhibiting higher counts for meristic features. This is not obvious in *F. heteroclitus,* as the northern race tends to have lower meristic features. Gabriel (1944) demonstrated that *F. heteroclitus* reared in colder waters tended to have more vertebrae than those raised in warmer waters. Fahy (1972) came to the same conclusion for *F. majalis.* Gabriel (1944) also demonstrated genetic control of vertebral number, but other characters should not necessarily respond to water temperature during developmental stages in the same way, or at all, as do vertebrae, and for pectoral rays, gill rakers, and caudal peduncle circumferential scales, the northern race has fewer than the southern race. The length of the anal sheath of females also increases southward, but how this could be influenced by water temperature is unclear. Moreover along the Gulf coast these same characters increase from north to south in *F. grandis.*

Racial differentiation in *F. heteroclitus* and *F. majalis* is surely a combination of genetic and environmental influence. Populations of these forms are continuous along the Atlantic coast, and there is no valid basis for recognizing the geographic races nomenclaturally.

Racial differentiation in *F. majalis* and *F. grandis* in the Gulf of Mexico is not marked. The strong outflow of freshwater from the Mississippi River probably serves to keep eastern and western Gulf races at least partially separated, showing a parallel to William's (1960) work on a magnified scale.

Florida east coast populations are geographically isolated from Gulf populations, and gene flow from Atlantic to Gulf is nonexistent. This results in disjunct populations of *F. grandis* and *F. majalis*, with an intervening, closely related form in the Florida Keys. That the differences between Atlantic and Gulf races are in part genetic is plausible. As pointed out previously, lower Florida east coast *F. majalis* show the genetic influence of the Matanzas River population, and thus differ from Gulf populations in that respect.

ZOOGEOGRAPHY

The present distributions of *F. heteroclitus* and *F. grandis* reflect population movements (in a long term sense) during and since the Wisconsin glaciation. Walters and Robins (1961) pointed out that Pleistocene sea levels may have been as much as 450 feet lower than present sea levels, and Emiliani (1958) demonstrated that Wisconsin glacial period sea temperatures in Florida may have been as much as 6° C lower than present temperatures. Such lowered temperatures would have forced the temperate fauna southward into south Florida and the Caribbean. For a discussion of this Trans-Florida faunal group see Walters and Robins (1961). A fine discussion of Gulf-Atlantic disjunct distribution can also be found in Dahlberg (1970). Hedgepeth (1953) discussed disjunct invertebrate distributions. The reader is also referred to Miller (1966) and Myers (1966) for discussions of Caribbean distribution.

As water temperatures have warmed since the last glaciation, populations have moved northward. Separation into temperate Atlantic and Gulf of Mexico populations (disjunct Carolinian fauna) was inevitable for temperate forms incapable of existing in tropical south Florida environmental conditions.

Fundulus grandis would appear to be a Gulf derivative of an *F. heteroclitus* population (or a common precursor of both) isolated during some earlier glacial-interglacial sequence. The mandibular pore number of 8 in *Fundulus heteroclitus* is shared with most other *Fundulus*. The 10 mandibular pores of *F. grandis* is presumably a derived state. The current disjunct *F. g. grandis* populations in the Gulf and Atlantic (Keys' populations [= *F. g.*

saguanus] considered later) reflect the most recent northward movement on each side of the Florida peninsula of southerly populations. This disjunction could be a repetition of the mechanism that earlier isolated *F. grandis* and *F. heteroclitus*. The situation with *F. majalis* is similar, except that reproductive isolation had not been achieved between the early Gulf and Atlantic disjuncts, so that intergradation occurs along the northeastern Florida coast in the region of contact between Gulf and Atlantic forms.

In this regard, the distributions of several fishes are worth noting:

1) *Menidia beryllina, M. peninsulae,* and *M. menidia* present a strikingly similar pattern of distribution to the *Fundulus* considered here. *Menidia beryllina* and *M. peninsulae* appear to have disjunct Gulf and Atlantic populations (same gaps in southeastern Florida and southwestern Florida as for *Fundulus,* although the exact distribution in south Florida and the northern Florida Keys is as yet unclear). Isolated populations also occur in Yucatan (*M. colei* and *Menidia* species) and the Florida Keys (*M. conchorum;* considered later). *Menidia menidia* is an Atlantic coast form that ranges from Canada to northeastern Florida (range nearly identical to *F. heteroclitus*). *Menidia beryllina* occurs throughout the Gulf of Mexico and ranges northward to Massachusetts on the Atlantic coast. *Menidia beryllina* (or *M. peninsulae*) and *M. menidia* may hybridize in the Matanzas River in northeastern Florida (Gosline 1948). The reader is referred to Gosline (1948), Robbins (1969), Johnson (1975) and Duggins (1980) for further discussion of *Menidia* systematics.

2) The zone of overlap between *Chasmodes bosquianus* (disjunct Gulf and Atlantic populations) and *C. saburrae* (intervening peninsular Florida form) is near Marineland in northeastern Florida, the area of contact between Gulf and Atlantic populations of *Menidia* and *Fundulus* discussed above (Springer 1959; Williams 1983).

3) The region of sympatry of the temperate Atlantic puffer *Sphoeroides maculatus* and the southern puffer, *S. nephelus* (essentially a Gulf form) is in the same northeastern Florida area noted above (Shipp and Yerger 1969).

4) *Floridichthys carpio* ranges from Cape San Blas, near Port St. Joe, Florida (Kaill 1967), southward along Florida's Gulf coast through the Florida Keys and northward on the Atlantic coast to Lake Worth, Palm Beach County, Florida (JU 1338). It then occurs disjunctly (?) on the Atlantic coast from the waters around Fort Pierce northward to the southern end on Mosquito Lagoon, Volusia County, Florida, just to the north of the Cape Canaveral area (JU 1298) (the same northeast Florida area noted above). This presently known distribution suggests separation of the two populations in South Florida. Two subspecies of *F. carpio* are recognized from Yucatan (Hubbs 1936); but Duggins (1980) challenged that view.

Another related factor worth noting is that *Floridichthys carpio* is not common north of the Cedar Key area of Florida's Gulf Coast (about 29° N

Lat.). In addition, the disjunct northeastern Florida population is concentrated near the same latitude. This also marks the zone of transition between previously mentioned species and is approximately the northern distributional limit of mangroves. Parr (1933) emphasized a winter thermal barrier to the dispersal of marine organisms along the Atlantic coast, and pointed out the abrupt change of average winter temperatures of about 60° F north of Cape Canaveral to 70° F to the south (due to the Gulf Stream). This marked temperature change between the southern and temperate parts of Florida (Carolinian Province) is not evident on the Gulf coast, and, with the exception of *Floridichthys carpio*, is not reflected by fish distributions.

The distributional limits of killifishes in the western Gulf of Mexico are also near the northern limits of mangrove growth (northern limit is about 20°N Lat., Tamaulipas, Mexico; Thorne 1954). Currently accepted southern limits of some cyprinodontids in the western Gulf area: *Fundulus grandis*, Laguna de Tamiahua, Veracruz, Mexico (Miller 1955); *F. majalis*, near Tampico, Mexico, (Miller 1955); *E. confluentus*, Laguna Madre, Texas (Breuer 1962); *Adinia xenica*, San Patricio County, Texas (Hastings and Yerger 1971); *Cyprinodon variegatus*, into northeastern Mexico (Kaill 1967); *Lucania parva*, Tampico, Mexico (Hubbs and Miller 1965). These distributions range slightly north or south of 25° N Lat., the latitude of the Florida Keys in the eastern Gulf, and the southern limit in the east for all species listed above (*Fundulus grandis* and *F. majalis* actually extend south to about 22° N Lat.). *Menidia beryllina* and *M. peninsulae* are similarly distributed.

Allopatry in the Florida Keys is also demonstrated by *Menidia conchorum*, and may be equivalent to the Keys *Fundulus* populations. *Syngnathus floridae mckay;* is a Florida Keys endemic isolated from its disjunct Gulf-Atlantic relatives *S. f. floridae* (Cape Sable, Florida to Corpus Christi, Texas) and *S. f. hubbsi* (Chesapeake Bay to South Carolina) (Herald 1965). I believe *Lucania parva* in the Florida Keys may also be an allopatric population. Hubbs and Miller (1965) did not examine specimens from south of the St. Johns River on the Atlantic coast. I have specimens southward to the Ft. Pierce area, but none are known between there and the Florida Keys (Duggins 1976, 1980). The relationship of *Cubanichthys cubensis* of Cuba to *L. parva* should be investigated as well (see Rosen 1975). *Cyprinodon variegatus* may be isolated in the Keys, too. Jordan (1884) described *Cyprinodon* in the Florida Keys and Cuba as *C. v. riverendi*. All of these Keys' forms probably constitute glacial relicts, in the sense of Walters and Robins (1961). Other populations of *Cyprinodon* in the Bahamas and West Indies (see Hubbs and Miller 1942) may likewise be glacial relicts.

I believe that based on my data, *Fundulus grandissimus* and *F. persimilis* and possibly *Cyprinodon variegatus artifrons, Floridichthys* popula-

tions, and *Menidia colei* represent glacial relicts (originating from western Gulf of Mexico populations) that have become isolated in Yucatan. *Floridichthys carpio* does not now occur in the western Gulf of Mexico, but may have in the past and did not survive the last glaciation except as a relict in Yucatan and South Florida. I do not believe that Florida Keys and Yucatan populations of these are very closely related, nor that a direct, overwater Keys-Yucatan dispersal has been involved. Rather dispersal on a north-south basis in the western Gulf or following interglacial-glacial events has occurred.

The reader is referred to a recent paper on this problem by Rosen (1975). Rosen's vicariance (allopatric speciation) model of Caribbean zoogeography suggests a North American-Caribbean distributional track (among others) that is the result of tectonic movement that fragmented an ancestral biota. With respect to my study, the relationship of Cuban (Antillean) and south Florida populations to Yucatan populations is at issue. Rosen presented an excellent summary (1975: 457, Fig. 21) of cladistic interpretation of vicariance versus dispersal for Caribbean distributions, and convincing arguments. My data support Rosen's suggestion that the distribution and cladistic relationships of populations in *Fundulus heteroclitus-F. grandis* species complex do not fit the vicariance model, and that dispersal over long periods of time (Pleistocene glacial-interglacial events) best accounts for observed distribution and relationships. These data do not support Rosen's suggestion of overwater dispersal from Florida to Yucatan. Cuban and Floridian populations are more closely related to one another than either is to *F. grandissimus* of Yucatan. This suggests Florida-Cuba dispersal, but not dispersal from Florida (or Cuba) to Yucatan. Other cases of Cuba-Florida or Keys-peninsula relationships may be cited: *Floridichthys carpio*, Yucatan and Florida, but not Cuba, with possibly disjunct Gulf-Atlantic populations; *Menidia beryllina* (or *M. peninsulae*) is probably more closely related to *M. conchorum* of the Florida Keys than either is to *M. colei* of Yucatan (personal communication, Dr. Robert R. Miller); *Cyprinodon* populations noted earlier; *Fundulus majalis* of the Florida peninsula and the Keys are more closely related than either is to Yucatan *F. persimilis*.

An intriguing "hybrid" pattern is suggested by *L. parva.* The seeming isolation of Florida Keys populations from very closely related peninsular populations, the close relationship of Gulf coast populations to *Lucania* from Mexico (personal communication, Dr. Robert R. Miller), and the isolation of the more distant sister species, *Cubanichthys cubensis* on Cuba, suggest both dispersal and vicariance. Indeed, this may be the critical point. Obviously, Pleistocene glacial-interglacial alternation occurred, as did the Caribbean tectonic events Rosen described. Any theory used to explain current distributions of American north temperate-subtropical

organisms must acknowledge both. Animals and plants exist in certain ecological regimes that have probably moved with glacial movements. These are not abrupt movements, but rather gradual shifts or ranges over tens of thousands of years. These are themselves vicariant events (as actually acknowledged by Rosen 1975:432). My collection data for Florida east coast killifish suggest seasonal and yearly distributional shifts. Perhaps some of the best examples of Pleistocene shifts involve isolation of subterranean populations of animals, notably fishes and crayfishes in North America, from epigean ancestral populations that were moved either northward or southward, or brought to extinction by glacial-interglacial events. Relyea (1976) discussed this situation for Florida cave crayfishes, and suggested a similar origin as a result of isolation in the springs of Florida during a glacial period, for the endemic killifish of the Florida peninsula: *Lucania goodei*, sister species of *L. parva; Fundulus seminolis*, sister species of *F. majalis* (?); *Jordanella floridae*, sister species of *Floridichthys carpio* (is *Garmanella* of Yucatan a close relative of *Jordanella*, or is it a species similar in appearance to *Jordanella* for ecological reasons, that has been independently derived from Yucatan or western Gulf of Mexico *Floridichthys carpio*?). Finally, the geminate species in the Gulf of Mexico and along Florida's Atlantic coast argue for a dispersal theory as well.

A critical point for further study involves the large gap between northeastern Mexico and Yucatan in killifish and silverside distributions. Is this the result, as I suggest, of north-south dispersal and extinction in the Gulf of Mexico of a fragmented Antillean-Yucatan biota or a result of tectonic events or of overwater dispersal from Florida to Yucatan?

The seeming lack of affinity between some greater Antillean and Yucatan fishes, exemplified best by the killifishes noted above, would suggest the former (dispersal) and is at odds with Rosen's North American-Caribbean track, but does not invalidate any of his other evidence or conclusions. My data, I believe, further the gradual elucidation of North American-Caribbean fish distributional patterns, and additional studies of complexes such as *Floridichthys-Jordanella-Garmanella* species group are needed.

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TABLE 1.—Frequency distribution of lateral scales in the *Fundulus heteroclitus-F. grandis* species complex. The *t* value between asterisked populations is 3.37. The *t* value following the Florida Keys population is for comparison with Southwest Florida.

Population	30	31	32	33	34	35	36	37	38	39	40	41	42	N	X̄	S	t
F. heteroclitus																	
North of Cape Cod				11	40	66	36	9	1					163	34.97	.98	
																	4.00
Delaware River-Long Island			3	13	42	46	13	2	1					120	34.53	.82	
																	2.69
Chesapeake Bay		1	5	16	35	32	4	2						95	34.18	1.03	
																	.64
Cape Lookout-Charleston area		2	3	24	49	33	7							118	34.09	1.10	
																	3.85
Savannah River-St. Johns River			3	22	50	61	25	5						166	34.59	1.06	
																	3.69
South of St. Johns River		1	2	6	22	16	1							48	34.11	.70	
																	2.36
F. grandis grandis																	
Florida east coast°			3	20	59	42	18							142	34.37	.66	
																	17.12
F. grandis saguanus																	
Florida Keys	4	12	29	45	18	1								109	32.59	.94	
																	9.26
Cuba	4	4	2	1										11	31.00	— —	
																	— —
F. grandis grandis																	
Southwest Florida°			1	3	38	46	14	2						104	34.72	.89	
																	.87
Tampa Bay-Apalachicola Bay			1	13	83	95	23	4						219	34.63	.84	
																	3.11
Cape San Blas-Mississippi River			2	10	57	61	46	10						186	34.91	.98	
																	1.20
West of Mississippi River		1	3	12	60	95	25	11	2					209	34.79	1.03	
																	15.98
F. grandissimus																	
Yucatan							2	2	8	4	4	7	2	29	39.21	1.64	

TABLE 2.—Frequency distribution of predorsal scales in the *Fundulus heteroclitus-F. grandis* species complex. The *t* value between asterisked populations is 3.73. The *t* value following the Florida Keys population is for comparison with Southwest Florida.

Population	13	14	15	16	17	18	19	20	21	22	23	24	25	N	X̄	S	t
F. heteroclitus																	
North of Cape Cod		2	17	44	43	38	8	0	1					153	16.83	1.18	
																	4.73
Delaware River-Long Island	1	12	23	41	27	10	3	2						119	16.12	1.28	
																	5.87
Chesapeake Bay	4	15	37	28	7	1								92	15.24	.98	
																	1.23
Cape Lookout-Charleston area	4	27	47	30	7									115	15.08	.91	
																	4.90
Savannah River-St. Johns River		25	52	56	25	9	1							168	15.67	1.05	
																	.56
South of St. Johns River	1	4	14	21	4	1								45	15.58	.91	
																	.50
F. grandis grandis																	
Florida east coast*	2	12	49	57	20	5								145	15.66	1.01	
																	4.85
F. grandis saguanus																	
Florida Keys	8	18	44	25	6									101	15.03	.99	
																	7.85
Cuba		4	7											11	14.64	— —	
																	— —
F. grandis grandis																	
Southwest Florida*		6	20	45	27	8	1							107	16.13	1.03	
																	2.38
Tampa Bay-Apalachicola Bay	1	12	67	100	41	7	1							229	15.83	1.13	
																	2.48
Cape San Blas-Mississippi River	5	30	51	65	27	7	1							186	15.56	1.14	
																	.60
West of Mississippi River	4	9	79	74	23	3	2							194	15.62	.93	
																	38.52
F. grandissimus																	
Yucatan								3	5	13	8	2		31	23.03	1.10	

TABLE 3.—Frequency distribution of gill rakers in the *Fundulus heteroclitus-F. grandis* species complex. The *t* value between asterisked populations is 1.22. The *t* value following the Florida Keys population is for comparison with Southwest Florida.

Population	7	8	9	10	11	12	13	14	15	16	17	N	X̄	S	t
F. heteroclitus															
North of Cape Cod		2	22	55	65	19	4					167	10.53	1.01	
															3.83
Delaware River-Long Island			8	24	56	25	7					120	10.99	.97	
															1.31
Chesapeake Bay			4	33	40	16	4					97	10.82	.96	
															11.00
Cape Lookout-Charleston area				3	23	53	38	4				121	12.14	.85	
															5.05
Savannah River-St. Johns River				1	21	44	84	16	6	0	1	173	12.67	1.01	
															1.85
South of St. Johns River				2	7	19	16	5	1			50	12.36	1.04	
															15.06
F. grandis grandis															
Florida east coast°		1	42	69	32	2						146	9.95	.71	
															9.77
F. grandis saguanus															
Florida Keys	1	25	52	31	2							111	9.07	.81	
															7.06
Cuba			9	2								11	9.18	— —	
															— —
F. grandis grandis															
Southwest Florida°	1	2	31	61	14	3						112	9.84	.79	
															2.56
Tampa Bay-Apalachicola Bay	1	13	87	110	20	1	1					233	9.61	.79	
															.63
Cape San Blas-Mississippi River		19	73	69	22	2	1					186	9.56	.89	
															1.50
West of Mississippi River		13	77	87	25	4	1					207	9.68	.83	
															3.38
F. grandissimus															
Yucatan		3	20	5	1							29	9.14	.61	

TABLE 4.—Frequency distribution of vertebrae number in the *Fundulus heteroclitus-F. grandis* species complex. The *t* value between asterisked populations is 2.30. The *t* value following the Florida Keys population is for comparison with Southwest Florida.

Population	31	32	33	34	35	36	37	38	N	X̄	S	t
F. heteroclitus												
North of Cape Cod			2	17	18	13			50	34.84	.85	
												3.22
Delaware River-Long Island			1	10	19	18	9		57	35.42	1.05	
												4.94
Chesapeake Bay			5	20	18	5	1		49	34.53	.83	
												.38
Cape Lookout-Charleston area			5	15	20	6			46	34.59	.73	
												5.06
Savannah River-St. Johns River		2	11	15	4	1			33	33.73	.77	
												2.10
South of St. Johns River	1	4	9	11	1				26	33.27	.89	
												9.13
F. grandis grandis												
Florida east coast°			1	7	16	14	3		41	35.27	.85	
												7.76
F. grandis saguanus												
Florida Keys		2	17	23	8	1			51	33.78	.99	
												5.15
Cuba	1	7	1						9	32.00	— —	— —
F. grandis grandis												
Southwest Florida°			1	4	14	2			21	34.81	.67	
												.42
Tampa Bay-Apalachicola Bay			1	16	29	12			58	34.89	1.00	
												2.65
Cape San Blas-Mississippi River			1	7	25	18	5		56	35.34	.85	
												2.00
West of Mississippi				7	14	6	1		28	35.04	.57	
F. grandissimus												
Yucatan						1	6	1	8	37.00	— —	

TABLE 5.—Frequency distribution data for total mandibular pores in the *Fundulus hetero-clitus-F. grandis* species complex. The *t* value between asterisked populations is 44.72.

Species	6	7	8	9	10	11	12	N	X̄	S	t
F. bermudae			30					30	8.00	—	
F. rhizophorae			30					30	8.00	—	
F. heteroclitus	2	1	100					103	7.95	.32	
											58.52
*F. grandis grandis**				17	203	1	1	222	9.94	.20	
F. grandis saguanus					20			20	10.00	—	
*F. grandissimus**						3	25	28	11.89	.32	

TABLE 6.—Anal sheath length, expressed as thousands of standard length, and standard length (in mm) of specimens, of females for the *Fundulus heteroclitus-F. grandis* species complex.

Population	Standard Length			Anal Sheath Length	
	N	Range	Mean	Range	Mean
F. bermudae	10	53-71	62.8	112-155	140.0
F. rhizophorae	10	46-58	52.0	103-164	143.2
F. heteroclitus					
North of Cape Cod	10	67-90	75.6	59-114	86.7
Long Island	10	56-84	66.9	107-145	125.1
Chesapeake Bay	10	58-79	67.6	155-200	173.5
Cape Lookout-Charleston area	10	54-83	63.6	180-233	200.1
South of Savannah River	10	55-89	76.0	166-194	178.8
F. grandis					
Florida east coat	10	62-77	69.7	52-80	69.0
Florida Keys	10	59-82	70.4	52-99	79.4
Southwest Florida	10	59-81	67.4	34-80	53.9
Northern Gulf of Mexico	10	57-80	65.4	67-100	85.6
Western Gulf of Mexico	10	58-70	62.9	67-103	77.7
F. grandissimus	3	111-134	124.7	54-75	64.0

TABLE 7.—Summary of meristic data for *Fundulus heteroclitus*, *F. bermudae*, and *F. rhizophorae*. The *t* value that follows *F. rhizophorae* compares the mean for that species and *F. heteroclitus*.

Dorsal Fin Rays	10	11	12	13	14	15	N	$\overline{X}$	S	t
F. heteroclitus	2	188	419	111	10	1	731	11.92	.71	
										19.20
F. bermudae		1	2	33	36	5	77	13.55	.73	
										22.78
F. rhizophorae	2	50	51	1			104	11.49	.57	
										.60

Anal Fin Rays	9	10	11	12	13	14	N	$\overline{X}$	S	t
F. heteroclitus	2	178	498	57			735	10.82	.72	
										17.80
F. bermudae			2	47	26	1	76	12.34	.60	
										17.91
F. rhizophorae	1	24	72	8			105	10.83	.53	
										.14

Branched Caudal Rays	13	14	15	16	17	18	19	20	21	N	$\overline{X}$	S	t
F. heteroclitus		5	28	105	170	231	126	39	4	708	17.62	1.29	
													.07
F. bermudae				3	30	34	7			74	17.61	.67	
													15.64
F. rhizophorae	2	8	42	40	10	3				105	15.54	.99	
													15.86

TABLE 7 Continued.

Lateral Scales	30	31	32	33	34	35	36	37	38	N	$\overline{X}$	S	t
F. heteroclitus		4	16	92	238	254	86	18	2	710	34.50	.92	
													4.93
F. bermudae		1	6	14	24	19	2			66	33.91	1.03	
													3.23
F. rhizophorae	1	3	14	35	37	12	1			103	33.40	.99	
													11.24

Predorsal Scales	11	12	13	14	15	16	17	18	19	20	21	N	$\overline{X}$	S	t
F. heteroclitus			10	85	190	220	113	59	12	2	1	692	15.84	1.28	
															9.99
F. bermudae		2	4	38	19	2						65	14.23	.76	
															3.05
F. rhizophorae	2	13	27	32	21	4	1					100	13.73	1.17	
															15.56

Gill Rakers	8	9	10	11	12	13	14	15	16	17	N	$\overline{X}$	S	t
F. heteroclitus	2	34	118	212	176	153	25	7	0	1	728	11.55	1.28	
														7.87
F. bermudae					27	34	9	1			71	12.77	.80	
														14.08
F. rhizophorae		1	31	50	20	2	1				105	10.94	.87	
														4.74

TABLE 7 Continued.

Caudal Peduncle Circumferential Scales	15	16	17	18	19	20	21	22	N	X̄	S	t
F. heteroclitus			5	37	147	270	29	4	492	19.60	.67	
												7.09
F. bermudae				18	24	16			58	18.97	.65	
												18.29
F. rhizophorae	4	43	36	20					103	16.70	.81	
												38.41

Pectoral Fin Rays	15	16	17	18	19	20	21	N	X̄	S	t
F. heteroclitus		7	91	307	240	50	2	697	18.34	.96	
											.79
F. bermudae			5	43	26	3		77	18.35	.68	
											21.75
F. rhizophorae	10	64	27	4				105	16.24	.62	
											21.65

Number of Vertebrae	31	32	33	34	35	36	37	38	N	X̄	S	t
F. heteroclitus	1	6	33	88	80	43	10		261	34.57	1.02	
												5.62
F. bermudae	1	2	14	11	3	1			32	33.50	.98	
												3.87
F. rhizophorae	1	16	22	4					43	32.67	.87	
												11.54

TABLE 8.—Frequency distribution of dorsal fin rays in the *Fundulus majalis* population complex. The *t* value between asterisked populations is .63

Population	11	12	13	14	15	16	N	X̄	S	t
F. majalis ("*majalis*-type")										
North of Cape Cod			1	12	15	2	30	14.60	.67	
										.44
Delaware River-Long Island			3	62	55	9	129	14.54	.71	
										2.33
Chesapeake Bay		1	8	53	38	3	103	14.33	.71	
										4.22
Cape Lookout-Charleston area		1	20	64	15	1	101	13.95	.66	
										3.00
Savannah River-St. Johns River		1	46	54	12		113	13.68	.70	
										1.56
Matanzas River, Florida		2	43	94	17	1	157	13.82	.85	
										4.95
Flagler County, Florida		8	48	29	2		87	13.28	.80	
										.09
F. majalis ("*similis*-type")										
Cape Canaveral area, Florida, and south*		11	40	24	4		79	13.27	.69	
										8.00
Florida Keys	8	56	52	7			123	12.47	.73	
										8.92
Southwest Florida*		23	90	45	6		164	13.21	.67	
										3.52
Tampa Bay-Apalachicola Bay	3	60	160	55	1		279	12.96	.82	
										.36
Cape San Blas-Mississippi River		58	162	40	1		261	12.94	.60	
										2.00
West of Mississippi River	1	27	91	34	1		154	13.05	.57	

TABLE 9.—Frequency distribution of branched caudal fin rays in the *Fundulus majalis* population complex. The *t* value between asterisked populations is 3.89.

Population	13	14	15	16	17	18	19	20	N	X̄	S	t
F. majalis ("*majalis*-type")												
North of Cape Cod				5	17	8			30	17.10	.67	
												1.00
Delaware River-Long Island			7	18	78	18	3	1	125	16.96	.83	
												.71
Chesapeake Bay		1	2	26	40	21	7	1	98	17.05	1.03	
												4.00
Cape Lookout-Charleston area			7	42	36	9	1		95	16.53	.73	
												4.31
Savannah River-St. Johns River			1	33	43	31	2		110	17.00	.84	
												.09
Matanzas River, Florida		1	2	36	64	36	3		142	16.99	.91	
												7.90
Flagler County, Florida			8	55	21	2			86	16.20	.57	
												3.30
F. majalis ("*similis*-type")												
Cape Canaveral area, Florida, and south*		1	16	43	9				69	15.87	.63	
												2.32
Florida Keys		5	43	64	8	1			121	15.65	.57	
												1.88
Southwest Florida*		6	71	69	7				153	15.50	.73	
												.14
Tampa Bay-Apalachicola Bay		20	124	109	21	3			277	15.51	.69	
												3.82
Cape San Blas-Mississippi River	1	19	154	74	12				260	15.30	.60	
												5.23
West of Mississippi River		5	61	69	15				150	15.63	.63	

TABLE 10.—Frequency distribution of lateral scales in the *Fundulus majalis* population complex. The *t* value between asterisked populations is 2.50.

Population	30	31	32	33	34	35	36	37	N	X̄	S	t
F. majalis ("majalis-type")												
North of Cape Cod					11	16	2	1	30	34.77	.53	
												3.45
Delaware River-Long Island			1	11	60	46	8		126	34.39	.72	
												1.97
Chesapeake Bay				10	35	37	13	3	98	34.63	1.03	
												2.00
Cape Lookout-Charleston area			6	22	51	19	3		101	33.91	.91	
												.26
Savannah River-St. Johns River			4	31	49	24	4		112	33.94	.78	
												.48
Matanzas River, Florida			3	38	63	39	2		145	33.99	.94	
												.95
Flagler County, Florida		1	2	8	38	21			70	34.09	.60	
												2.56
F. majalis ("similis-type")												
Cape Canaveral area, Florida, and south°			2	20	36	9	1		68	33.81	.70	
												15.41
Florida Keys	4	34	51	34					123	31.93	1.00	
												20.48
Southwest Florida°		2	4	27	83	42	4		162	34.06	.66	
												2.21
Tampa Bay-Apalachicola Bay			1	36	151	79	12		279	34.23	.87	
												1.31
Cape San Blas-Mississippi River			4	52	124	71	6	3	260	34.12	.96	
												.53
West of Mississippi River			1	34	73	41	3		152	34.07	.87	

TABLE 11.—Frequency distribution for caudal peduncle circumferential scales in the *Fundulus majalis* population complex. The *t* value between asterisked populations is 4.35.

Population	15	16	17	18	19	20	21	22	N	X̄	S	t
F. majalis ("majalis-type")												
North of Cape Cod						10	15	4	29	20.79	.78	
												2.91
Delaware River-Long Island					9	45	27	5	86	20.33	.60	
												4.72
Chesapeake Bay			1	21	51	11	2		86	19.91	.62	
												9.41
Cape Lookout-Charleston area		2	6	21	41	19	1		90	18.80	.96	
												2.97
Savannah River-St. Johns River			3	32	31	1			67	18.45	.54	
												1.62
Matanzas River, Florida		2	12	22	35	21			92	18.66	1.09	
												1.22
Flagler County, Florida			4	27	31	2			64	18.48	.77	
												.26
F. majalis ("similis-type")												
Cape Canaveral area, Florida, and south°		3	7	14	14	13			51	18.53	1.18	
												3.70
Florida Keys		6	31	36	20	3			96	17.82	.99	
												1.18
Southwest Florida°		7	23	22	6	4			62	17.63	1.00	
												2.70
Tampa Bay-Apalachicola Bay	1	44	67	48	20				180	17.23	1.02	
												2.54
Cape San Blas-Mississippi River	1	44	39	23	8				115	16.94	.93	
												8.99
West of Mississippi River		8	15	30	34	7			94	18.18	1.08	

TABLE 12.—Frequency distribution of number of vertebrae in the *Fundulus majalis* population complex. The *t* value between asterisked populations is 2.67.

Population	32	33	34	35	36	37	38	39	N	$\overline{X}$	S	t
F. majalis ("majalis-type")												
North of Cape Cod					8	12	6	1	27	37.00	.83	
												.71
Delaware River-Long Island				1	15	21	11		48	36.88	.46	
												3.78
Chesapeake Bay				2	17	20	2		41	36.54	.45	
												.55
Cape Lookout-Charleston area			5	20	22	5	2		54	35.61	.96	
												.48
Savannah River-St. Johns River			1	14	14	6			35	35.71	.97	
												.54
Matanzas River, Florida			5	21	43	15			84	35.81	.77	
												.56
Flagler County, Florida			2	12	24	6	3		47	35.91	1.08	
												.67
F. majalis ("similis-type")												
Cape Canaveral area, Florida, and south°			2	9	42	13	1		67	36.03	.71	
												13.42
Florida Keys	3	17	22	8	4				54	33.87	1.00	
												7.10
Southwest Florida°			5	14	11	4			34	35.41	.97	
												2.13
Tampa Bay-Apalachicola Bay				14	20	7			41	35.83	.67	
												2.57
Cape San Blas-Mississippi River		1	7	29	24	8			69	35.45	.86	
												3.60
West of Mississippi River		2	10	24	6	1			43	34.86	.83	

TABLE 13.—Head length, expressed as thousandths of standard length, and standard lengths (in mm) for *Fundulus majalis*.

Population	Females					Males				
	N	Standard Length		Head Length		N	Standard Length		Head Length	
		Range	Mean	Range	Mean		Range	Mean	Range	Mean
F. majalis ("*majalis*-type")										
North of Cape Code	10	72-84	78.0	316-333	323.4	10	62-70	66.7	323-339	330.0
Long Island	10	51-85	68.3	294-333	314.5	10	56-84	72.8	291-323	307.2
Chespeake Bay	10	55-87	68.6	301-341	316.4	10	63-85	72.5	286-350	304.0
Cape Lookout-Charleston area	10	62-94	80.7	315-350	334.0	10	60-95	74.4	316-343	329.4
Savannah River-Matanzas River	15	57-83	68.6	302-368	332.4	15	53-75	61.1	293-363	328.5
Flagler County, Florida	10	58-69	66.0	319-348	337.2	10	53-67	59.0	316-343	332.6
F. majalis ("*similis*-type")										
Cape Canaveral area, Florida, and south	15	60-97	72.5	297-358	330.2	15	51-66	58.7	306-339	321.1
Florida Keys	10	64-87	69.6	343-380	358.5	10	55-100	63.7	320-369	342.0
Southwest Florida	10	61-84	74.6	322-385	346.3	10	53-78	65.6	345-368	353.9
Northern Gulf of Mexico	10	59-72	63.4	308-346	323.2	10	55-70	61.2	301-333	323.2
West of Mississippi River	10	63-73	66.1	301-333	322.4	10	53-67	60.5	303-333	319.1

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