MASS HYBRIDIZATION BETWEEN TWO SPECIES OF CYPRINID FISHES NOTROPIS CAMURUS AND NOTROPIS WHIPPLEI

By

ORTY EDWIN ORR

Bachelor of Science

Kansas State College

Pittsburg, Kansas

1950

Submitted to the Faculty of the Graduate School of the Oklahoma Agricultural and Mechanical College in Partial Fulfillment of the Requirements for the Degree of MASTER OF SCIENCE

1952

MASS HYBRIDIZATION BETWEEN TWO SPECIES OF CYPRINID FISHES NOTROPIS CAMURUS AND NOTROPIS WHIPPLEI

ORTY EDWIN ORR

MASTER OF SCIENCE

1952

THESIS AND ABSTRACT APPROVED:

Geo. A. Moore
Thesis Adviser

L. E. Wallen
Faculty Representative

D. G. McIntosh
Dean of the Graduate School

ACKNOWLEDGMENTS

The writer especially wishes to express his gratitude to Dr. George A. Moore, who in his capacity as adviser, worked long hours with me on this paper giving freely of his time. Doctors William H. Irwin and Bryan P. Glass read the manuscript and offered helpful suggestions.

TABLE OF CONTENTS

MASS HYBRIDIZATION BETWEEN TWO SPECIES OF CYPRINID FISHES NOTROPIS CAMURUS AND NOTROPIS WHIPPLEI

INTRODUCTION

Hybridization in cyprinid fishes has received considerable attention from ichthyologists as indicated by Hubbs, Hubbs, and Johnson (1943) who listed the works of many writers in Eurasia and America. Interspecific and intergeneric hybrids have been described, discussed and analyzed. Mass hybridization between the cyprinid genera Gila and Siphateles was ably treated by Hubbs and Miller (1942) who attributed that phenomenon to a changing environment occasioned by natural ecological events. The writer is not aware of published works concerned with natural hybridization of cyprinid fishes attributable to the influence of environmental changes brought about by man's activities.

Notropis camurus (Jordan and Meek) and Notropis whipplei (Girard) are allopatric species, occuring together nowhere, to my knowledge, except in Big Greenleaf Creek and Bayou Manard, tributaries of the Arkansas River and located in Cherokee and Muskogee Counties, Oklahoma. Big Greenleaf Creek is about 30 miles in length and is a typical stream of the western edge of the Ozark uplift. Its waters flow rather rapidly over a bed replete with alternating pools and riffles. Greenleaf Lake, located four miles northeast of Braggs, Oklahoma, is an artificial impoundment of about 900 surface acres constructed as

a Resettlement Project during the years 1935-1937.

No hybridization has been noticed between the species in question in Bayou Manard, but in Big Greenleaf Creek above the lake collections indicate a high incidence of hybridization. The population of hybridizing minnows, Notropis (camurus X whipplei), was discovered during the summer of 1950 by an ichthyology class directed by Dr. G. A. Moore.

Notropis whipplei and Notropis camurus occupy adjacent to slightly overlapping ranges (Fig.I). Notropis whipplei occurs from Southeastern Oklahoma (type locality, Sugarloaf Creek, a tributary of the Poteau River) eastward to West Virginia, south to Alabama and northward to Indiana, Ohio and New York. Notropis camurus does not enjoy such a wide distribution but, as now known, is restricted to the Arkansas River System of Oklahoma, Colorado (type locality, Fort Lyon), Kansas, Missouri, and Arkansas.

An interesting distributional pattern of the two species exists in the area surrounding Big Greenleaf Creek. Notropis whipplei is known in Oklahoma from the Poteau River, Big Greenleaf Creek and Bayou Manard (tributaries of the Arkansas River) and some tributaries of the Red River in Southeastern Oklahoma. Notropis camurus is unknown in the Poteau and the Red River systems, but is common in some Arkansas River tributaries such as the Neosho (Grand), Illinois, and Chikaskia River systems. Both of the parental species were collected in Big Greenleaf Creek below the lake in the summer of 1950, where they remain clearly distinct from each other. Unfor-

tunately these specimens were discarded before their importance was realizes. The summer of 1951 was so wet that Big Greenleaf Creek below the dam was filled with Arkansas River backwater during most of the months of June and July. It has therefore been impossible to check further the two species in lower Big Greenleaf Creek. Both of the parental species were also collected in Bayou Manard, about ten miles west of Big Greenleaf Creek, in the summer of 1950. There is therefore some overlapping in the range of these species. The collection from above the lake was preserved and brought to Stillwater and has become the object of this study.

The manifestation of apparent natural hybridization lends evidence to the belief that closely related species are partly interfertile (Blair, 1951). Dr. G. A. Moore has informed me that collections of Notropis lutrensis (Baird and Girard) and Notropis venustus (Girard) (in Oklahoma, restricted to the Red River System) from the same localities show that interbreeding between these two otherwise distinct forms is common. The circular black spot of Notropis venustus, the intense black pigment in the posterior interradial membranes of the dorsal fin, and eight anal rays are characters that clearly separate that species from Notropis lutrensis which has nine anal rays and no black pigment either in the dorsal fin or at the caudal base. In all collections containing both of these species, troublesome specimens are encountered. These specimens have a poorly defined caudal spot, little

black interradial dorsal pigment and a count of either eight or nine anal rays. Dr. Clark Hubbs (personal communication with G. A. Moore) has mentioned having made the same observations in collections from Texas.

Notropis camurus and N. spilopterus (Cope) are also close relatives and yet the two species occur together in the Illinois River without interbreeding. Extensive collecting (Moore and Paden, 1950) yielded many specimens of both species, all of which were easily determined (except young). The Illinois flows into the Arkansas River less than ten river miles from the mouth of Big Greenleaf Creek, and yet N. whipplei does not occur in the Illinois.

METHODS

The hybrid specimens used were largely from the 1950 collection taken from Big Greenleaf Creek above Greenleaf Lake by Dr. G. A. Moore and class. Additional smaller specimens were collected from the same creek in the summer of 1951 by Dr. Edgar M. Leonard and class during a poisoning demonstration. Many of the latter had been dead for some time before they were fixed in formalin and were therefore less desirable for study.

The 1950 collection was made by means of various seines, fixed in 10% formalin, washed in water and stored in 65% isopropyl alcohol.

The methods employed in this investigation are similar to those of Hubbs, Hubbs and Johnson (1943) and Hubbs and Miller (1943). Specimens of the parental species used for comparison with the hybrids are: N. camurus, from the Illinois River in Oklahoma, and N. whipplei, from the Mountain Fork River of McCurtain County, Oklahoma. In order to establish the identity of the suspected hybrids, the method of calculating the hybrid index, as introduced by Hubbs and Kuronuma (1942:291), was employed. The method involves the use of the following formula:

$$\text{Position of the Hybrid (P)} = \frac{V_h - M_1}{M_2 - M_1}$$

in which V_h represents the value of the character of the hybrid, M_1 the mean value for one parent and M_2 that of the other parent.

The hybrid index (I) equals 100P. In a comparison of each individual an average index is expressed as a figure on a scale of 100, a value for one of the parental types is set at 0 and the value of the other parent at 100.

In a paper by Hubbs, Hubbs and Johnson (1943) relating to hybridization in suckers, M_1 was applied to the parent that seemed to be the most primitive. I have applied M_1 to N. whipplei and M_2 to N. camurus, since the range of N. camurus is on the periphery of that of N. whipplei. It seems that there is some basis for application of the theory

which was recently applied by Hubbs and Bailey (1950) to the basses of Florida, that most differentiation occurs at the periphery of ranges. N. whipplei may thus be regarded as the more primitive.

The suspected hybrids have been checked closely for all characters of structure, form, and color that might show relationship to Notropis whipplei and Notropis camurus, the presumed parental species. The procedure for counting and measuring anatomical features conform to those outlined by Hubbs and Lagler (1949). All measurements were made that were thought to be critical and obtainable with accuracy.. X-ray pictures were made, for the determination of skeletal differences, but failed to yield positive results.

A fruitless effort was made to use the arm protractor method of Hubbs (1946). Although angles are doubtless important, it is often difficult to precisely locate the three points necessary for accurate measurement. The results obtained were so inconsistent that the method was abandoned.

FREQUENCY OF HYBRIDIZATION

The Notropids of Big Greenleaf Creek are an interesting mixture of Great Plains and Ozarkian forms. In this creek the Great Plains Region is represented by N. lutrensis, N. u. umbratilis (Girard) and N. camurus whereas N. zonatus pilsbryi Fowler, N. rubellus (Agassiz), N. greenei Hubbs and

Ortenburger) and N. boops (Gilbert) represent the Ozark Upland. Notropis whipplei is neither a Great Plains nor an Ozarkian form, but rather belongs to the Ouachita fauna in Oklahoma, although it has found its way into the Poteau and a few other Arkansas River tributaries.

Interspecific hybrids in the genus Notropis are not numerous (except as herein discussed) in the above-mentioned regions in Oklahoma. However, Moore and Paden (1950) did recognize a hybrid, Notropis (rubellus X zonatus pilsbryi) and reported another unidentified specimen. Since both N. camurus and N. whipplei are known to occur below the Greenleaf Lake Dam, it may be assumed that the two species occur naturally in Big Greenleaf Creek. Since the construction of the dam the two species are unable to move freely up and down the stream to find spawning sites. It may, therefore, be assumed that some congestion and partial isolation from other populations exists.

Numerous attempts were made to observe acts of spawning but frequent rains during the months of June and July of 1951 created conditions quite inimical to success. Unsuccessful attempts were also made to secure eggs by setting a nylon net at the foot of riffles. It is assumed that both species spawn below riffles since the largest and most mature individuals were taken in such habitats.

Notropis whipplei differs from its very close relative, N. camurus, in having a sharper-pointed snout, a slenderer more compressed body, a lack of a creamy white basicaudal bar, a slightly larger eye (Fig. II-III) and a lower average

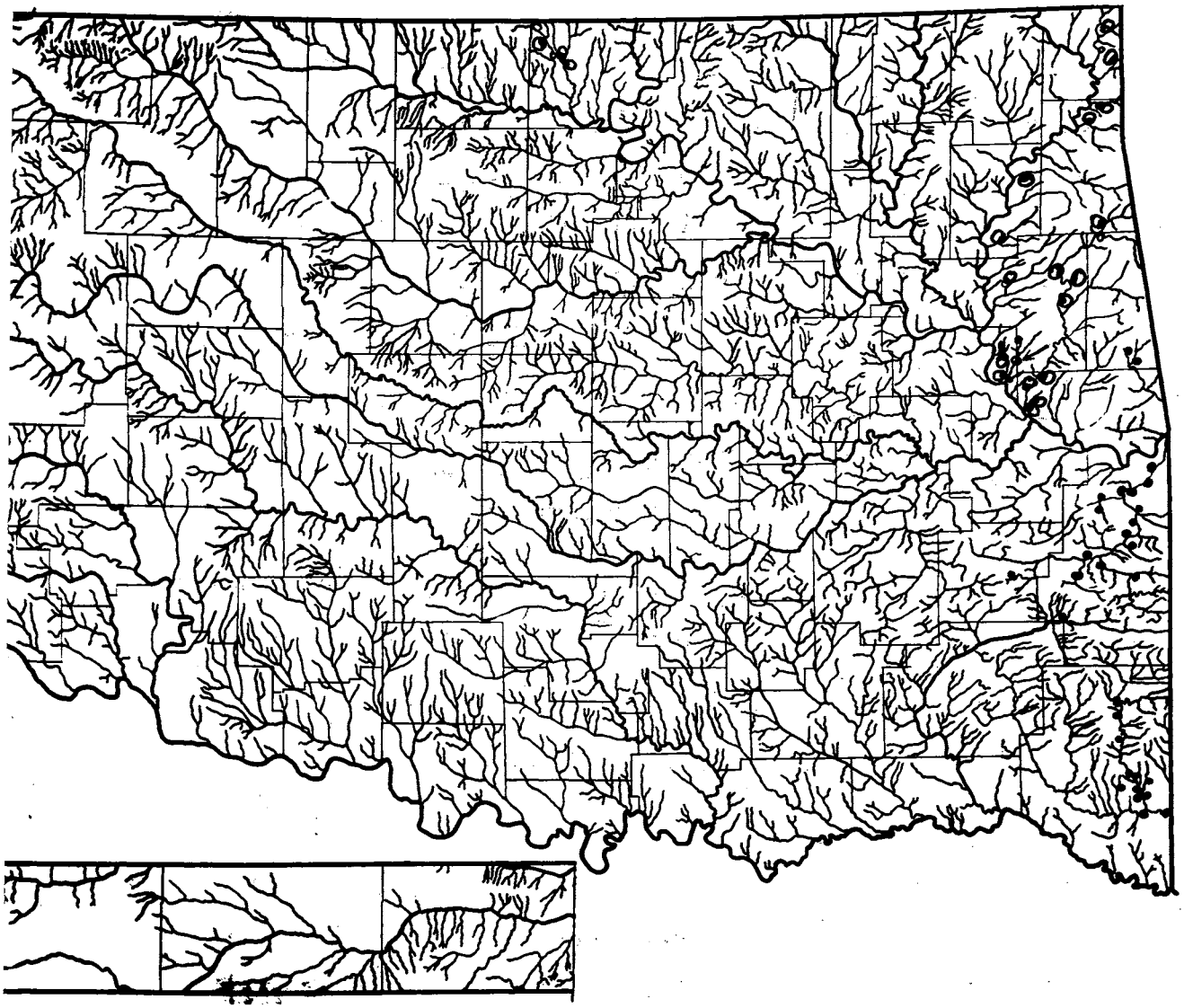

Figure I. Collection Stations.

Notropis camurus collections are indicated by half solid circle, Notropis whipplei by solid circle, hybrids by arrow.

number of scale radii. Of all characters studied only those concerned with head and body shape and the presence or absence of the creamy basicaudal bar are regarded as diagnostic. Therefore, those characters were used to arbitrarily separate representatives of the two species from the hybrids.

By inspection the collection was divided into three groups, one each for the parental species, Notropis whipplei and Notropis camurus, and one for the hybrids. From this division of adults ranging from about 50mm to slightly over 100mm, 15 percent were regarded as N. whipplei, 13 percent N. camurus, and 71 percent hybrids. Assuming that the arbitrary separation has not resulted in a considerable number of misidentifications, the above percentages would seem to indicate that the two species freely interbreed. It is also quite possible that the hybrids are partly fertile.

N. whipplei and N. camurus unquestionably have similar ecological requirements for both may be found in relatively clear or somewhat turbid water. For example, N. whipplei is abundant in the Poteau River (consistantly rather turbid) and has even been taken from roadside swamps in McCurtain County, Oklahoma. N. camurus is a common species in the clear Illinois and Grand Rivers, is less common in the muddier Chikaskia, and has been taken from Cedar Crest Lake in Mayes County, Okla.

EVIDENCE FOR HYBRID INTERPRETATION

Basis for the belief that Notropis whipplei and Notropis camurus hybridize in Big Greenleaf Creek is circumstantial. Similar evidence has been discussed and validated in papers such as Hubbs, Hubbs and Johnson (1943), Hubbs and Miller (1943) and others. In those publications there is much detailed explanation and discussion of the hybrid index and other analytical methods now being used in the interpretation of natural hybrids. Although the picture is not clear, in regard to the exact causes bringing about the breakdown of the isolating mechanisms between Notropis whipplei and N. camurus, in Big Greenleaf Creek, it is believed that ecological factors are responsible. Since hybrids have not been found below Greenleaf Lake, there exists the tempting suggestion that one of the causes of the breakdown of isolating mechanisms may be attributed to man's influences. The dam constitutes an effective barrier to free movement of both species to and from their former spawning sites and forces them to spawn in the more limited area above the lake.

The fact that adults of these species in breeding color are taken on riffles and at the foot of riffles, leads to the supposition that they are riffle spawners. Hybrid combinations have arisen from species that use ecologically contiguous spawning areas, such a situation was noted by Moore and Paden (1950). These writers believed that sperm cells from the riffle breeding Notropis zonatus drift into the

pools below the riffles to fertilize the eggs of Dionda nubila (Forbes). The adults of Notropis whipplei and Notropis camurus in breeding condition are most commonly taken on riffles and are believed to have ecologically similar requirements.

The breeding color of the adults is complimentary. The opercles and gill membranes are a light shade of pink, the anal, pelvic and pectoral fins having a more intensified shade. The dorsal and caudal fins have a pale shade of pink but have black punctulations on the interradial membranes. The body is pale bluish white, darker above and white beneath. It is believed that the species may not recognize their own kind and, therefore, breed indiscriminately when confined above Greenleaf Lake. "In some species, at least, males will court inanimate objects irrespective of their general appearance when they are manipulated somewhat to resemble the actions of a female ready to spawn," Blair (1951).

The main reason for considering this situation to be one of hybridization lies in the fact that many characters show intermediacy. In the pharyngeal teeth and gillrakers there is little or no evidence to indicate intermediacy, for these characters are quite similar in both parental species and the hybrids. At the beginning of the study there appeared to be a slight difference in the structure of the pharyngeal arches of the two forms, but this character was later abandoned, because difference was discernible in only a few examples. The pharyngeal tooth formula is occasionally 4-4,

generally 1,4-4,1 in the parental species as well as the hybrids. The number of gillrakers showed similar variation, usually 15 to 18 on the fourth arch.

Intermediacy in scale characters is displayed, a situation commonly encountered in hybrids of other scaled fishes. The differences in the features of the scales of the parental species Notropis whipplei and Notropis camurus are slight, scales of camurus are generally a little higher than long, the upper and lower edges somewhat more curved than those of whipplei. The scales of both species are shield-shaped, though not conspicuously so. The scales of camurus have a greater number of radii which extend more into the lateral fields than do the scales of whipplei. The scale radii of Notropis whipplei are fewer and weaker and also more regular than those of Notropis camurus. In the above mentioned characters the hybrids show quite consistant intermediacy. Counts of the radii of twenty adult specimens of each of the parental species and hybrids are shown in Table II.

In the various scale counts the differences between the parental species are not great. The average number of scales in the lateral line and above the lateral line is higher in Notropis whipplei. Below the lateral line and around the body the average numbers are greater for Notropis camurus. In these counts the hybrids are quite intermediate.

The fin rays showed very little variation, numbering for both species as follows: dorsal, 8; anal, 9; P_1, 12 to 14;

TABLE I

COMPARISON OF NOTROPIS WHIPPLEI, HYBRIDS AND NOTROPIS CAMURUS

Based on ten adults of each parent species and ten of the hybrids. The largest specimens of each were used.

	N. whipplei	Hybrid	Hybrid Index	N. camurus
	Range-mean	Range-mean		Range-mean
Standard length, mm.	98-64(76.58)	95-63(80.37)		103-51(74.51)
Predorsal length	459-530(509)	494-528(511)	29	505-529(516)
Prepelvic length	449-517(487)	471-506(491)	33	486-518(499)
Body depth	242-286(262)	272-304(285)	88	261-320(288)
Dorsal origin to lateral line	152-195(168)	186-214(194)	114	173-228(191)
Pelvic insertion to lat. line	91-108(98)	89-110(99)	50	88-115(100)
Body width	133-142(137)	150-182(163)	162	137-177(153)
Caudal peduncle depth	105-120(112)	116-143(129)	80	118-186(131)
Head length	225-247(238)	228-273(259)	80	254-276(264)
Head depth	149-166(157)	102-203(178)	65	172-205(189)
Snout length	64-87(74)	75-91(86)	133	69-94(83)
Eye length	48-63(55)	47-62(54)	-33	50-73(58)
Fleshy interarbital	78-94(89)	93-118(105)	123	91-110(102)
Upper jaw length	55-66(61)	62-78(68)	70	57-77(71)
Gape width	45-56(49)	51-78(63)	93	56-68(64)
Dorsal ray heigth	206-357(241)	267-325(295)	98	226-355(296)
Anal ray heigth	159-214(180)	169-188(179)	-14	186-231(203)
Anal base length	117-142(129)	126-143(134)	83	118-146(135)
Pectoral fin length	151-173(165)	173-189(181)	76	175-200(186)
Pelvic fin length	147-193(164)	162-183(175)	86	160-194(177)
Thousands of Head Length				
Head depth	606	685	60	737
Eye length	230	205	-227	219
Gape	201	242	-151	240
Scale Counts				
In lateral line	34-40(39.1)	37-40(38.9)	67	38-40(38.8)
Above lateral line	7-8(7.1)	7 (7)	50	6-7(6.9)
Below lateral line	4-5(4.8)	5-5(5)	40	5-6(5.3)
Around body	24-26(25.35)	24-27(25.4)	14	24-27(25.7)
		Total Average Index	68	

and P_2, 8. The fin rays of Notropis whipplei seem to be more fragile than those of either the hybrid or Notropis camurus, as shown by their condition after having been stored and subjected to handling. The fins of whipplei became more frayed and bent, principally the caudal fin, than either the hybrid or camurus. In other respects the hybrids seem to tend toward camurus, since the values for some characters exceed 100 and fewer are below 0 (Table I). The average hybrid index value (68) reflects a stronger influence of camurus.

Other measurements of the hybrids do not follow the general rule that interspecific fish hybrids are intermediate in their characters. Table I shows a hybrid index of 114 for the character of the distance from the lateral line to the origin of the dorsal fin, but for the distance from the pelvic insertion to the lateral line, the index is 50. This is possible because the hybrids have slightly wider bodies. The body width in thousandths of standard length of the hybrids was 10/1000 greater than Notropis camurus and 26/1000 greater than Notropis whipplei. This is only a slight amount, yet significant.

The position of the pelvic fins of the hybrid as indicated by the prepelvic length shows intermediacy, hybrid index, 33. As a diagnostic character there is such a slight difference between the parent forms that it is difficult to detect. In the original description (Jordan and Meek, 1884) the origin of the dorsal fin was noted to be slightly behind

the insertion of the pelvic fins. Notropis whipplei (Girard, 1856) was described as having the dorsal origin opposite the pelvic insertion. This character has not been used for identification in this study. The creamy white basicaudal bar of Notropis camurus was not mentioned by Jordan and Meek but is now regarded as a strong diagnostic character of camurus.

Also in the hybrid certain characters of the head show extreme development; that is, their indexes either rise above 100 or fall below 0. The average hybrid index values for snout length and fleshy interorbital distance are 133 and 123 respectively. The eye length yielded a minus average index value and is the only character, taken in thousandths of standard length, to do so.

The characters of head length, head depth and length of upper jaw gave indexes that are close to the average index for all characters. The depth of the caudal peduncle shows a tendency toward Notropis whipplei, whereas, body depth tends toward Notropis camurus in the same degree (Table I).

EXTREME CHARACTERS IN HYBRIDS

In the preceding paragraphs it has been noted that the Notropis whipplei X Notropis camurus hybrids tend to have some extreme characters. The body tends to be slightly wider and the eye length less than in either parent. Other writers (Hubbs and Miller, 1943; Hubbs and Kuronuma, 1942; and others),

TABLE II

FREQUENCIES OF COUNTS OF SCALE RADII

IN

NOTROPIS WHIPPLEI, HYBRIDS, AND NOTROPIS CAMURUS

Based on adults used in Table I. Only those radii reaching the scale margin were counted. The scale selected was the one in the next row above the lateral line, directly above the insertion of the pelvic fin.

	Number of scale radii							no.	range	ave.	hybrid index
	5 to 7	7 to 9	9 to 11	11 to 13	13 to 15	15 to 17	17 to 19				
N. whipplei	5	8	3	3		1		20	5-18	8.25	
Hybrid		4	5	5	5		1	20	7-17	10.85	67
N. camurus		1	4	5	6	2	1	19	8-18	12.10	

treating hybrid fishes involving characters with excessively high or low index values, consider heterosis as the explanation. This is believed to be the most plausible explanation of the greater body width in the hybrids under consideration.

The fact that the eye is small also may be explained as an expression of hybrid vigor. Analysis of some head characters, such as eye size, snout length and interorbital width, also may be explained on the basis of hybrid vigor. Large-eyed condition in species which normally have smaller eyes, is regarded as evidence of stunting and malnutrition. On the other hand, a fish that is well fed and vigorous never has excessively large eyes. The average hybrid index value for eye size is -33, indicating a tendency toward decrease in eye size beyond that of Notropis whipplei. Snout length and fleshy interorbital width yielded average hybrid index values of 133 and 123 respectively and therefore are beyond the range of Notropis camurus. The fact that some characters yield hybrid index values beyond the range of both parents supports the identification of the supposed hybrids.

In regard to the sex of the hybrids little can be reported from this study. All specimens of 40mm and up show considerable development of nuptial tubercles, indicating a high incidence of males. However, in both parent species the females have tubercles, but the tubercles are fewer in number and less highly developed than in the males. A considerable number of hybrid specimens were opened in a search for females

with eggs. None were found in the collection, but not all of the specimens were opened.

Interspecific hybrids are ordinarily considered infertile in at least one sex. Notropis camurus X Notropis whipplei males have highly developed secondary sexual characters, at least some individuals are probably fertile and, endowed with hybrid vigor, could compete strongly in spawning activity. Raney (1947) reported six large inter-generic hybrids, Nocomis leptocephalus (Girard) X Compostoma anomalum (Rafinesque) of which one male and two females appeared to be normally developed sexually. Hubbs and Hubbs (1931) stated that some sunfish crosses, endowed with hybrid vigor, more than hold their own in competition for food and spawning sites.

The fact that the hybrids approach Notropis camurus, a little more closely in proportional measurements, may have resulted from some back crossing. Notropis camurus grows to larger size than Notropis whipplei, but the hybrids are still larger than camurus. There seems to be no explanation for this fact other than heterosis. In a study of hybrid flounders, Hubbs and Kuronuma (1942) reported only a tendency toward the larger parent.

SUMMARY

The considerable amount of recent work on hybrids emphasizes the intermediacy between the parent forms and the hybrids as shown by the hybrid index (Hubbs, Hubbs and Johnson, 1931; Hubbs, 1940; Hubbs and Miller, 1943; Trautman, 1948; and others). Commonly the hybrid index total average is close to 50 in these hybrid studies, however in others it fluctuates considerably. Hubbs, Walker and Johnson (1943) show total averages for cyprinodont combinations that range from 42 to 66. The Notropis camurus X Notropis whipplei hybrids show a total average index of 68, indicating an inclination toward Notropis camurus.

In the years since the completion of Greenleaf Lake, these two minnow populations have been prevented from the free movement to some of their previously habitual breeding sites and are now forced to breed in a more congested location. It is believed that the impoundment of water on Big Greenleaf Creek may be largely responsible for the phenomenon of hybridization presented here. In so far as known at present hybridization between Notropis whipplei and Notropis camurus does not occur elsewhere, in spite of the fact that the two forms occasionally occur together in the Arkansas River System. Anderson (1949) stated: "The production of hybrid swarms is limited to times and places in which man or nature may have hybridized the habitat."

Figure II

Adult hybrid, Notropis whipplei X Notropis camurus, and the parent species.

Top: Notropis whipplei, 91 mm., standard length, from the Mountain Fork River, McCurtain County, Okla.

Center: Hybrid, 89mm., standard length, from Big Greenleaf Creek, Muskogee County, Okla.

Bottom: Notropis camurus, 94 mm., standard length, from the Illinois River, Sequoyah County, Okla.

Figure II

Figure III

Immature hybrid, Notropis whipplei X Notropis camurus, and parent species.

Top: Notropis whipplei, 51 mm., in standard length, from the Mountain Fork River, McCurtain County, Okla.

Center: Hybrid, 53 mm., in standard length, from Big Greenleaf Creek, Muskogee County, Okla.

Bottom: Notropis camurus, 55 mm., in standard length, from the Illinois River, Sequoyah County, Okla.

Figure III

BIBLIOGRAPHY

Anderson, Edgar 1949--Introgressive Hybridization. New York: Wiley, 1-109.

Bailey, Reeves M. and Carl L. Hubbs 1949--The black basses (Micropterus) of Florida, with description of a new species. Occas. Pap. Mus. Zool. Univ. Mich., 516:35-36.

Blair, Frank W. 1951--Interbreeding of natural populations of vertebrates. The Amer. Nat., 85(80):9-27.

Girard, Charles 1856--Researches upon the cyprinod fishes inhabiting the fresh waters of the United States of America, west of the Mississippi Valley, from specimens in the Museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Phila., 8:185-213.

Hubbs, Carl L. and Laura C. Hubbs 1931--Increased growth in hybrid sunfishes. Occas. Pap. Mich. Acad. Sci. Arts and Lett., 13:193.

------, Laura C. Hubbs and Raymond E. Johnson 1943--Hybridization in nature between species of catostomid fishes. Contr. Lab. Vert. Biol., 22:1-76.

------, and Katsuzo Kuronuma 1942--Hybridization in nature between two genera of flounders in Japan. Pap. Mich. Acad. Sci. Arts and Lett., 27:267-302.

------, 1946--An arm protractor for the precise measurement of angles in systematic ichthyology. Copeia, 1946 (2):79-80.

------, and Robert R. Miller 1943--Mass hybridization between two genera of cyprinid fishes in the Mohave Desert, California. Pap. Mich. Acad. Sci. Arts and Lett., 28: 343-377.

------, Boyd W. Walker and Raymond E. Johnson 1943--Hybridization in nature between species of American Cyprinodont Fishes. Cont. Lab. Vert. Biol., 23:1-20.

------ 1940--Speciation of fishes. Amer. Nat., 74:198-211.

Jordan, David S. and E. Seth Meek 1884--Description of four new species of cyprinidae in the United States National Museum. Proc. U. S. Nat. Mus., 7:474.

Moore, George A. and John M. Paden, 1950--The fishes of the Illinois River in Oklahoma and Arkansas. Amer. Midl. Nat., 44 (1):76-95.

Raney, Edward C., 1947--Nocomis nests used by other breeding cyprinid fishes in Virginia. Zoologica: N. Y. Zool. Soc. 32:15, 125-131.

Trautman, Milton B., 1948--A natural hybrid catfish, Schilbeodes miurus X S. mollis. Copeia, 1948(3):166-174.

THESIS TITLE: MASS HYBRIDIZATION BETWEEN TWO SPECIES OF CYPRINID FISHES, NOTROPIS CAMURUS AND NOTROPIS WHIPPLEI

NAME OF AUTHOR: Orty Edwin Orr

THESIS ADVISER: George A. Moore

The content and form have been checked and approved by the author and thesis adviser. "Instructions for Typing and Arranging the Thesis" are available in the Graduate School office. Changes or corrections in the thesis are not made by the Graduate School office or by any committee. The copies are sent to the bindery just as they are approved by the author and faculty adviser.

NAME OF TYPIST: Xava G. Orr

* * * * * * * * * *