VARIATIONS IN THE NUMBER OF VERTEBRÆ AND OTHER MERISTIC CHARACTERS OF FISHES CORRELATED WITH THE TEMPERATURE OF WATER DURING DEVELOPMENT

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I

FOR several years I have been studying the correlations between altered environmental conditions and the number of vertebræ and other segmentally arranged structures in fishes. Johannes Schmidt, of the Carlsberg Laboratory in Copenhagen, has been carrying on a series of intensive investigations (see bibliography) which deal with the same problem, and which are for the greater part rather closely paralleled by my own studies. Both of us have obtained, independently, a rather large volume of experimental and observational evidence indicating that the meristic characters displayed by an individual fish are determined not alone by heredity, but in part also by the environmental conditions, particularly temperature, which prevail during some sensitive developmental period.

II

The present study is one of those comprising the series just mentioned. It deals with variations in the number of vertebræ, scale-rows and fin-rays within one year-class and between two successive year-classes of the lake "shiner," *Notropis atherinoides* (Cyprinidæ), and in comparison between the corresponding year-classes of the "blue-gill" sunfish, *Lepomis incisor* (Centrarchidæ). These variations appear to be correlated with differences in temperature prevailing during the several developmental periods involved.

The material of each species is probably a unit as regards " race." It was all obtained in a lagoon in Jackson Park, Chicago, during the third week of December, 1919. At this time what seemed to be the entire fish population of the lagoon was congregated in an opening, about five meters wide, in the ice along shore. These fishes showed symptoms of asphyxiation. They were so abundant that at times, while they were gyrating about, the mass of fishes below would force the almost solid upper layer a centimeter or two above the surface over an area of perhaps a square meter. A water bucket was filled with fishes, mostly *Notropis atherinoides,* by two or three sweeps of a small hand-net. More than one thou-

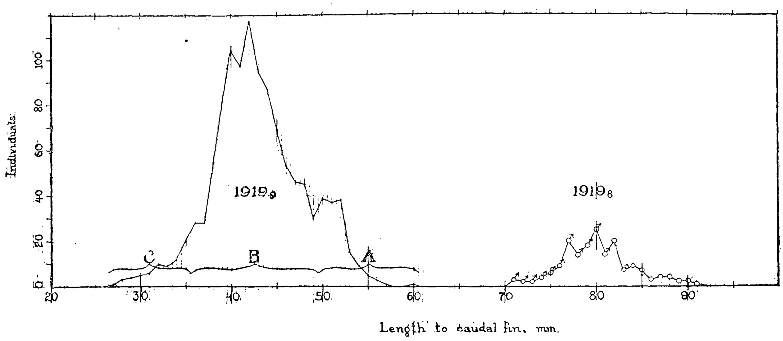

FIG. 1. Frequency graph, indicating the year-classes of *Notropis atherinoides.*

sand of the young of that year (1919) of the Notropis were saved after random selection, and preserved for study with all older fish of the same species. All of the sunfishes (*Lepomis incisor*) obtained at the same time and place were preserved and studied. Of the two species, the sunfishes belonged to a population practically confined to the lagoon, while the minnows had moved into the lagoon, late in the preceding autumn, from the more open waters of Lake Michigan.

The specimens thus obtained were grouped into year-classes. Age determinations were made by the usual methods of counting the annuli (winter lines) on the scales, and as a check the seasonal bands of the otoliths, and furthermore by the preparation of a frequency graph from the length measurements of the entire material. The young of the year (obtained in 1919) are referred to as the 1919_9 class; those of the previous year as the 1919_8 class, and so forth. The 1919_9 year-class of the *Notropis atherinoides* is further divided into three subclasses, A, B and C, named in the direct order of hatching, hence in

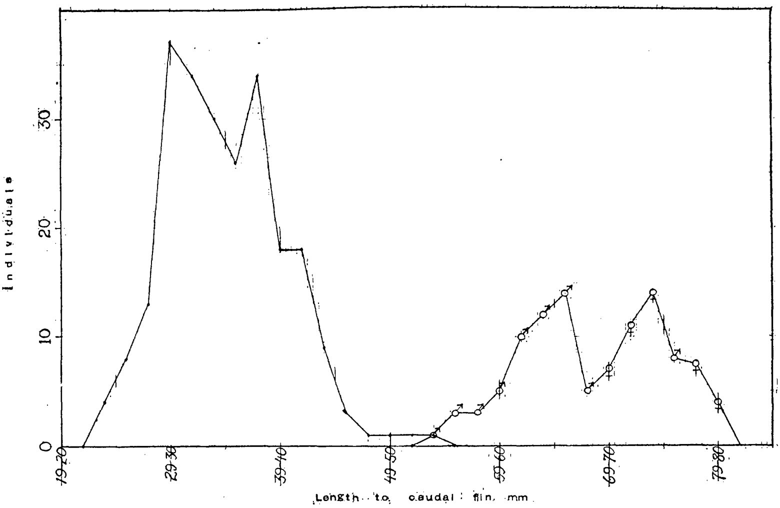

FIG. 2. Frequency graph illustrating the year-classes of *Lepomis incisor*.

the indirect order of size. The year-classes for both species are indicated on the graphs forming Figs. 1 and 2. The symbols on the curve for the 1919_8 class of each species indicate the sex predominant among the representatives of each size.

III

A series of water temperatures appear unavailable, but in the case of such a shallow, nearly enclosed lagoon the air temperatures of the region may safely be substituted. Hence the *Climatological Data* (Illinois Division, 1918 and 1919) for Chicago were used in constructing Fig. 3; the temperatures given for each week were obtained by averaging the daily means.

On the temperature chart there are indicated the periods of development for each of the two species as observed at the same locality in 1919. The data for *Lepomis incisor* seem satisfactory (see Hubbs, 1919), but those for *Notropis atherinoides* are less complete and more circumstantial. In the case of the minnow, the developmental period is divided into three periods (A, B and C) corresponding with the three subclasses into which the 1919 year-class has been divided. Period A followed an inshore spawning migration of the mature individuals, coincident with the rapid rise in temperature during March; period C preceded the withdrawal of the breeding stock from the shore waters of the lake; the intervening period is termed B.

The limited field observations on the spawning and developmental period for *Notropis atherinoides* during 1919 are, fortunately, strongly confirmed by a study of

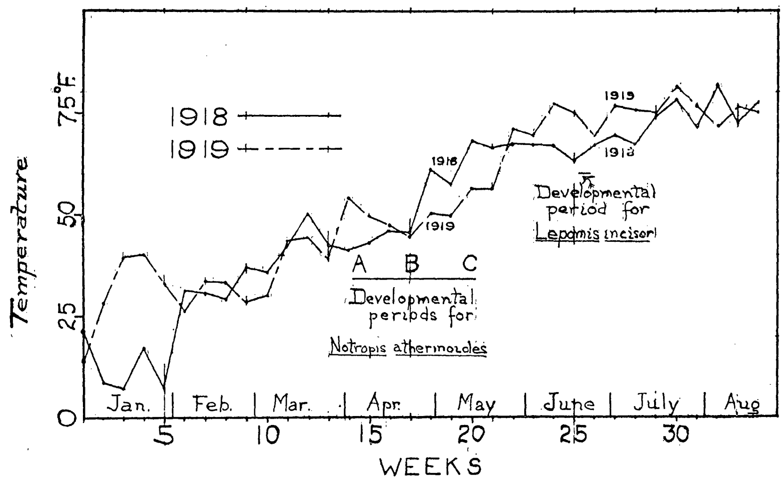

FIG. 3. Air temperature at Chicago, 1918–1919.

the scales. The scales of the largest specimens taken in December, namely those comprising subclass 1919_9A, and forming a distinct mode in the frequency graph (Fig. 1), show a well marked nuclear area of weak concentrated circuli indicative of retarded growth, followed by the coarser, more regular circuli indicative of normal summer growth. This initial period of retarded growth presumably corresponds with the cold period in April (see Fig. 3). The scales of the medium-sized specimens (subclass B) show on the average a narrower nuclear area suggesting slackened growth. It is presumed that these individuals passed through their early development toward the end of this cold period. The scales of the smallest specimens, those of subclass C, show no such nuclear area of weak concentrated circuli. These fishes supposedly developed during the warm weather of May.

The data on the developmental period of these two species for the preceding breeding season (1918) are less complete than those for 1919, yet not wholly lacking. *Lepomis incisor,* at least, bred during the corresponding weeks in both years (but in less abundance in 1918 than in 1919).

A comparison of the available observational data with the temperature chart (Fig. 3) indicates that, on the average, the developmental period for *Notropis atherinoides* was colder in 1919 than in 1918, whereas these temperature relations were distinctly reversed in the case of *Lepomis incisor,* and furthermore, that the temperature was distinctly higher at the beginning and toward the close of the 1919 breeding season for the Notropis, than during the middle of this period.

IV

These differences in the developmental temperature appear to be correlated with variations in the number of segments in the case of both fishes. Comparisons will firs+ be made between the two year groups of *Notropis atherinoides,* then between the same year groups of *Lepomis incisor,* and finally between the three subclasses into which the 1919 brood of the Notropis has been divided.

The vertebræ in the 1919_9 class of *Notropis atherinoides* are sufficiently more numerous on the average than those of the 1919_8 class to shift the modal number from 41 to 42, the average from 41.41 ($\pm$ 0.04)[1] to 41.74 ($\pm$ 0.015).

[1] The probable error of the average.

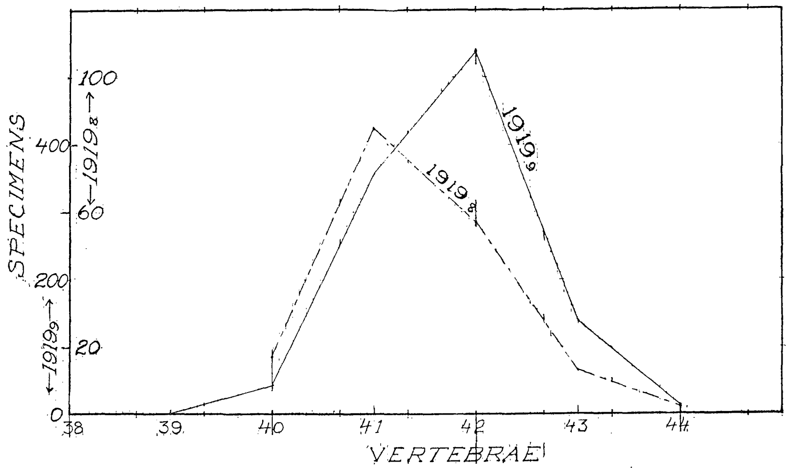

FIG. 4. Comparison of number of vertebræ in successive year-classes of *Notropis atherinoides.*

The portion of the vertebral column affected is the caudal, not the precaudal (abdominal) division: the averages for the precaudal vertebræ are 22.82 ($\pm$ 0.02) for 1919_8 and 22.85 ($\pm$ 0.01) for 1919_9 for the caudal vertebræ, 18.60 ($\pm$ 0.035) for 1919_8, and 18.87 ($\pm$ 0.01) for 1919_9. Similarly, the number of scales in the lateral line averages higher in the 1919_9 lot: the modal number is 40 rather than 39 as it is in 1919_8 class; the average number is 40.05 ($\pm$ 0.04) rather than 39.65 ($\pm$ 0.04). The modal number

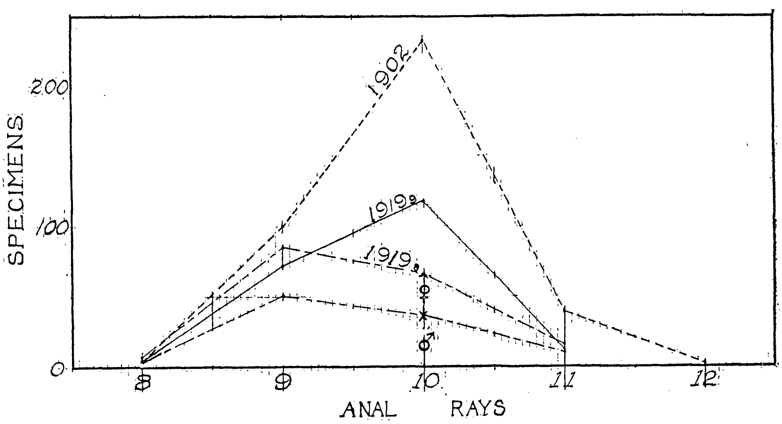

FIG. 5. Comparison of variations in number of branched and anal rays in different year-classes of *Notropis atherinoides.*

of branched anal rays[2] is 10 in the 1919_9 series, 9 in the 1919_8 class; the averages are 9.52 (± 0.05) for 1919_8 males,

FREQUENCY TABLE I

COMPARISON OF THE MERISTIC FEATURES OF THE 1918 AND 1919 BROODS OF *Notropis atherinoides*

Year-class	Total Number of Vertebræ								
	39	40	41	42	43	44			
1919_8	—	17	85	57	13	2			
1919_9	1	43	356	539	137	12			
	Number of Precaudal Vertebræ								
	21	22	23	24	25				
1919_8	3	38	121	13	—				
1919_9	2	240	766	78	1				
	Number of Caudal Vertebræ								
	17	18	19	20	21				
1919_8	6	74	80	16	—				
1919_9	6	269	661	142	10				
	Number of Scales in Lateral Line								
	37	38	39	40	41	42	43	44	45
1919_8	2	26	95	92	34	11	2	—	—
1919_9	—	22	90	164	66	21	9	2	1
	Number of Branched Anal Rays								
	8	9	10	11	12				
1902	4	100	232	39	2				
1919_8 ♂	4	51	37	10	—				
1919_8 ♀	3	34	29	6	—				
1919_9	4	72	118	12	1				

2 The last ray as usual was counted as double, *i.e.*, as divided to the base. Occasionally the posterior half of this divided ray is again divided well toward the base. In fact a complete transition can be traced between fins having a given number of rays with those having one more ray. It is highly improbable, however, that this transition is sufficiently frequent as to permit a serious modification of the average number of rays, through a personal error in counting.

9.53 ($\pm$ 0.06) for 1919_8 females, and 9.69 ($\pm$ 0.03) for both sexes of the 1919_9 class; in material collected in 1902 in the same lagoon the average is still higher, 9.83 ($\pm$ 0.02). The data on which these figures are based is given in Frequency Table I. In all three characters, namely the number of vertebræ, of scales along the lateral line, and of branched anal rays, the year-class developed in the cooler season displays a significantly higher average.

A highly similar yet exactly reverse condition is displayed in the analysis of the counts on the *Lepomis incisor* material. In this case the total number of vertebræ, and the number of caudal, but not precaudal, vertebræ; the number of dorsal spines, dorsal soft-rays, anal soft-rays, and hence the total number of vertical fin-rays, all

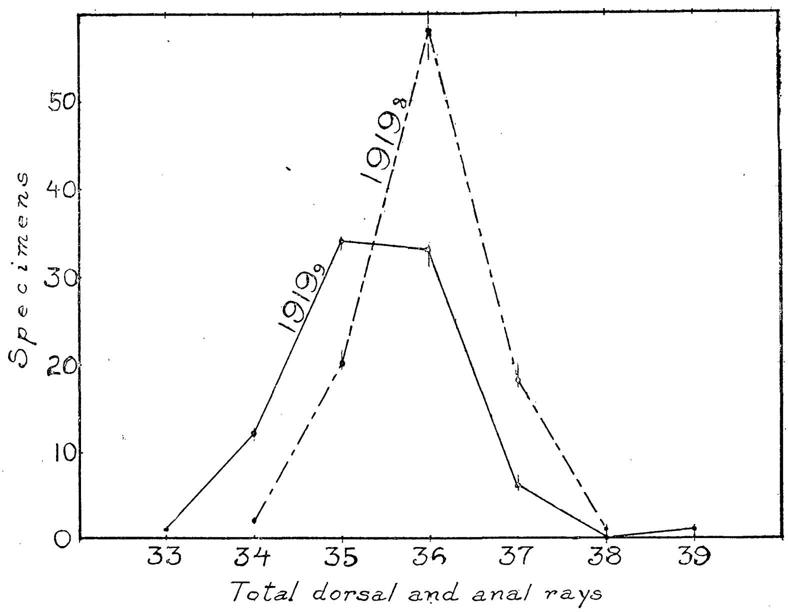

FIG. 6. Comparison of number of dorsal and anal fin rays in successive year-classes of *Lepomis incisor*.

average higher in the class born in 1918 than in that of 1919. But we noted above that the temperature relations during the developmental periods of the two years were likewise reversed. In both *Notropis atherinoides* and

FREQUENCY TABLE II

COMPARISON OF THE NUMBER OF VERTEBRÆ IN THE 1918 AND 1919 BROODS OF *Lepomis incisor*

Year-class	Character			Average	Probable Error
	Total Number of Vertebræ				
	28	29	30		
1919_8	—	95	9	29.10	0.02
1919_9	7	219	8	29.00	0.00
	Number of Precaudal Vertebræ				
	11	12	13		
1919_8	2	100	2	12.00	0.01
1919_9	2	230	2	12.00	0.00
	Number of Caudal Vertebræ				
	16	17	18		
1919_8	—	95	9	17.09	0.02
1919_9	7	219	8	17.00	0.01

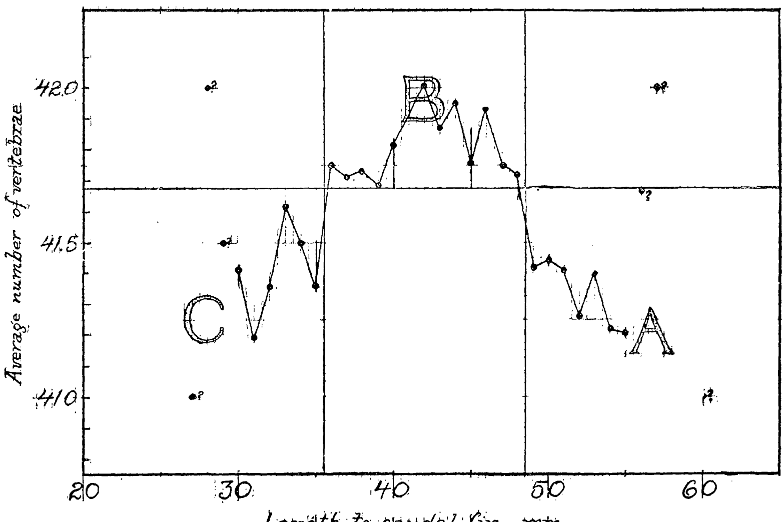

FIG. 7. Illustrating seasonal variation in number of vertebræ in *Notropis atherinoides*.

Lepomis incisor, therefore, a higher number of segments was developed in the year class developed at the lower temperature. The detailed data are given in Frequency Tables II and III.

Evidence has already been given indicating that the 1919 year-class of *Notropis atherinoides* is divisible into three subclasses, of which the middle (B) developed during colder weather than either the first (A) or the last (C). The data given in Frequency Table IV and in figure 6 demonstrate that this subclass B possesses a decidedly higher number of vertebræ than either of the other two. The averages are as follows: for the 146 specimens of subclass A, 41.38 (± 0.04); for the 845 comprising subclass B, 41.84 (± 0.02); for the 97 individuals of subclass C, 41.42 (± 0.05).

FREQUENCY TABLE III

COMPARISON OF THE NUMBER OF FIN-RAYS IN THE 1918 AND 1919 BROODS OF *Lepomis incisor*

Year-class	Character							Average	Probable Error
	Number of Dorsal Spines								
	IX	X	XI	XII					
1919_8	1	79	22	—				10.21	0.03
1919_9	2	74	11	1				10.125	0.03
	Number of Dorsal Soft-rays								
	10	11	12	13					
1919_8	1	37	63	—				11.61	0.03
1919_9	3	51	32	2				11.375	0.04
	Number of Anal Soft-rays								
	9	10	11	12					
1919_8	—	2	80	19				11.17	0.03
1919_9	1	12	70	5				10.90	0.03
	Total Rays in Dorsal and Anal Fins								
	33	34	35	36	37	38	39		
1919_8	—	2	20	58	18	1	—	35.96	0.05
1919_9	1	12	34	33	6	—	1	35.40	0.07

FREQUENCY TABLE IV

VARIATION IN NUMBER OF VERTEBRÆ WITHIN ONE-YEAR CLASS OF *Notropis atherinoides*

Sub-class	Size Group	Number of Vertebræ						Average	Probable Error
		39	40	41	42	43	44		
1919_9 C....	27	—	—	1	—	—	—	(41.00)	—
	28	—	—	1	1	1	—	(42.00)	0.32
	29	—	—	2	2	—	—	(41.50)	0.29
	30	—	—	9	4	—	—	41.31	0.09
	31	—	1	5	3	—	—	41.22	0.16
	32	—	2	7	4	—	1	41.36	0.175
	33	—	1	4	7	1	—	41.62	0.145
	34	—	1	7	10	—	—	41.50	0.095
	35	—	1	13	7	1	—	41.36	0.09
1919_9 B....	36	—	—	11	13	4	—	41.75	0.09
	37	—	1	16	18	6	—	41.71	0.07
	38	—	5	10	36	5	—	41.73	0.05
	39	1	4	24	39	8	1	41.68	0.06
	40	—	3	28	44	17	—	41.82	0.05
	41	—	2	24	46	16	2	41.91	0.055
	42	—	1	21	67	18	3	42.01	0.045
	43	—	3	24	41	17	1	41.87	0.06
	44	—	1	18	43	14	1	41.95	0.05
	45	—	2	21	31	6	2	41.76	0.07
	46	—	—	13	23	10	—	41.93	0.07
	47	—	—	14	23	2	1	41.75	0.06
	48	—	1	16	16	7	—	41.72	0.08
1919_9 A....	49	—	4	6	14	—	—	41.42	0.10
	50	—	3	14	16	1	—	41.44	0.10
	51	—	2	14	9	2	—	41.41	0.095
	52	—	2	16	9	—	—	41.26	0.075
	53	—	2	6	6	1	—	41.40	0.14
	54	—	—	7	2	—	—	41.22	0.09
	55	—	1	2	2	—	—	41.20	0.225
	56	—	—	1	2	—	—	(41.67)	0.18
	57	—	—	—	1	—	—	(42.00)	—
	58	—	—	—	—	—	—	—	—
	59	—	—	—	—	—	—	—	—
	60	—	—	1	—	—	—	(41.00)	—

V

It has generally been taken for granted, as a basic assumption, that such differences as those here shown to hold between two successive year-classes, and between successive groups within a single year-class, are indicative of racial distinction. Obviously this assumption can not be maintained as wholly true. Moenkhaus (1895, 1898) indeed long ago demonstrated the occurrence of a significant annual variation within one race of fishes (in the case of the darters *Percina caprodes* and *Boleosoma* *nigrum*). Schmidt (1921) has lately studied such annual fluctuations in great detail in *Zoarces,* and has induced like changes by experimental control of temperature in *Lebistes* (1919*a,* 1919*b*) and *Salmo* (1921). I have obtained similar experimental results for coregonine fishes and for *Esox lucius* (data yet unpublished).

On the other hand it has been clearly demonstrated in a number of cases that fine "racial" differences are inherited. Thus Schmidt (1917*a,* 1917*b,* 1918, 1920, 1921) has determined by his "offspring analyses" that a high degree of positive correlation holds between the number of segments and other features of the maternal parent and the unborn embryos of *Zoarces.* Similar results were obtained by Punnett (1904) for the viviparous shark, *Etmopterus* [*Spinax*] *niger.* In *Salmo,* Schmidt (1919*c*) has lately demonstrated that the finer differences in the number of vertebræ of both parents are inherited, and in the viviparous teleost *Lebistes reticulatus,* the same author has found (1919*a,* 1919*b*) that minor variations in the parental number of dorsal fin-rays are inherited. In somewhat similar fashion Sumner (1918, etc.) has demonstrated that subspecific differences in color and size in the mouse genus *Peromyscus* are inherited, even under changed enviromental conditions. A considerable body of indirect observational evidence might be brought forward, if needed, in confirmation of the assumption that these fine racial differences are inherited.

Clearly the same sort of variations as are induced by altered environmental conditions do characterize genetically distinct local races of fishes. Furthermore, these two sets of correlations display certain striking similarities or analogies, the significance of which the writer is attempting to determine in the series of studies of which the one here reported is a part.

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