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INDICATIONS OF COMPENSATORY GROWTH IN THE STRIPED BASS, *ROCCUS SAXATILIS* WALBAUM, AS REVEALED BY A STUDY OF THE SCALES *

Richard E. Tiller

ABSTRACT

Analysis of scale samples from 87 striped bass from the 1940 year class of the Chesapeake Bay, and 39 samples from the 1938 year class of the Hudson River, indicated that the smaller yearling individuals made a more rapid growth in their second year than the larger ones. Compensation was not complete, since the growth advantage of the larger individuals is maintained to a considerable degreee.

The study and analysis of striped bass scales is by no means new. Extensive studies have been made on age determinations, length frequencies, and the possibility of using variations in scale sculpture as an index of origin. But no study has been made of growth compensation between yearling and two-year-old fish. The purpose of this investigation was, therefore, to determine if such a compensation exists. Comparable data from widely separated areas were used.

Compensatory growth tends to reduce variation in size with increasing age, and involves a negative correlation between early growth and later growth. The length of the first and second years' growth zones, and of the total scale radius were measured. Using this data, and the body length of the fish, the length increments for both the first and second years can be calculated by the methods of Lea (1910). From these calculations, the existence of a positive or negative correlation between the first and second year's growth can be ascertained.

Van Oosten (1926), working on the lake herring or cisco, *Leucichthys artedi,* found definite compensation. Although the large yearlings remained large throughout life, the difference between relatively small and large individuals diminished each succeeding year. Later (1938) he determined from investigations on the common whitefish, *Coregonus clupeaformus,* that for two age groups studied, such a growth compensation did exist. His data showed that the advantage of size

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* The data used in this paper were presented in thesis form at the University of Maryland in partial fulfilment of the requirements for the degree of Master of Science in 1942.

reached in the first year was maintained throughout life, although the maximum difference between the smallest and largest individuals decreased progressively with age. The growth increments clearly indicated a compensation, that is, the smaller yearlings grew, on the average, more rapidly than the larger yearlings.

The first demonstration of compensatory growth was advanced by Gilbert (1913) in his work on the life history of the sockeye salmon, *Oncorhyncus nerka*. Using 100 samples grouped in ascending order of size, he observed a positive correlation in the first two years' growth—the large fish growing more rapidly—but in the third and fourth years a reversal occurred, and a negative correlation, indicative of compensatory growth, was observed. Following this work, Hubbs (1921), in tracing the life history of a fresh water fish, *Labidesthes sicculus,* concluded that the smallest individuals grow fastest, in relation to their final adult size, and the largest ones relatively slower. Working with Cooper (1934), Hubbs investigated the possibility of compensatory growth in the long-eared sun fish, *Xenotis megalotis,* in Michigan, and found no indication of a growth compensation in the first two years. Adequate data were not available for succeeding years, although he indicated that a tendency may be present. He suggested in support of his findings that a genetic difference in individuals, a physiological effect between the first and second years' growth, or a favorable ecological niche might account for the continued increased growth of the larger individuals. Hile (1940) supported Van Oosten's earlier work with the cisco in that he observed a compensation which reduced but did not obliterate the growth advantage of the larger individuals in succeeding years. According to McHugh (1942), Foerster in 1936 found that compensation might occur in some, but not necessarily in all year classes of young sockeye salmon. The most recent work is that of McHugh (1942), who studied the growth of the Rocky Mountain whitefish, *Prosopium williamsoni,* from which he found no indication of compensatory growth, all correlations between succeeding years being positive.

DESCRIPTION OF SCALES

The accompanying photomicrograph (Figure 1) shows a typical, symmetrical scale of the striped bass. It is roughly square or rectangular, with the anterior edge nearly straight, and the posterior edge broadly tapered. Only this broadly tapered posterior edge is visible *in situ,* the remaining portion being deeply imbedded in a dermal pocket. At the inner edge of the exposed portion, a marked differentiation is observed in the sculpture. The scales are ctenoid, having spines in the posterior field, and from the rough, spiny, radiation form seen in this portion, a sharp transition occurs to the regular, finely sculptured structure of the imbedded area. Close to this line of demarcation between the two areas, centrally located between the dorsal and ventral edges of the scale, and at the focal point of the radiating ridges or radii of the anterior portion, is the small, sharply defined focus. The focus may be of several forms: a spiral, a complete circle, or in the shape of two opposing semicircles of unequal

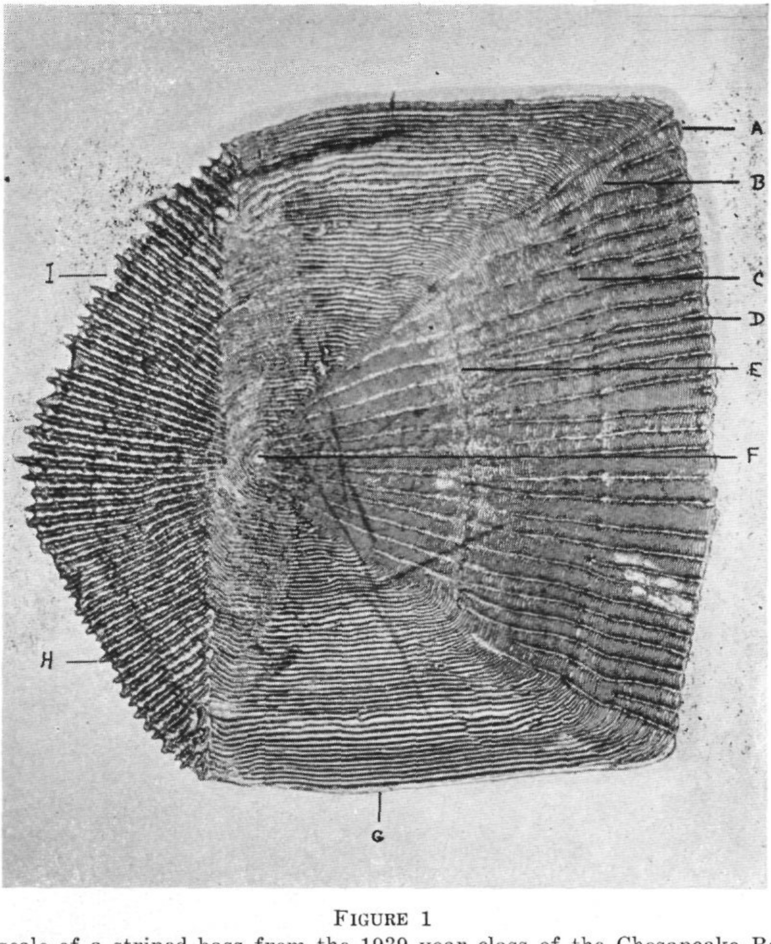

FIGURE 1

A scale of a striped bass from the 1939 year class of the Chesapeake Bay. (A) Anterior edge. (B) Circulus. (C) Annulus (end of second year's growth). (D) Radius. (E) Annulus (end of first year's growth). (F) Focus. (G) Lateral field. (H) Spine. (I) Posterior edge.

size. The imbedded anterior area is composed of a number of fine lines which run transversely across the radii and down the lateral fields. These are termed circuli, and may be considered the units of growth of the scale. As Merriman (1941) has pointed out, resumption of rapid growth in the spring, usually early in May, results in a disturbance of the continuity of the circulus pattern. This irregularity is termed an annulus, or annual ring (Figure 2). The annulus, seen as a continuous, markedly differentiated line, extends across the radii, and down the lateral fields. An annulus is formed each year, and, of course, the number of annuli of different scales of the same fish is constant.

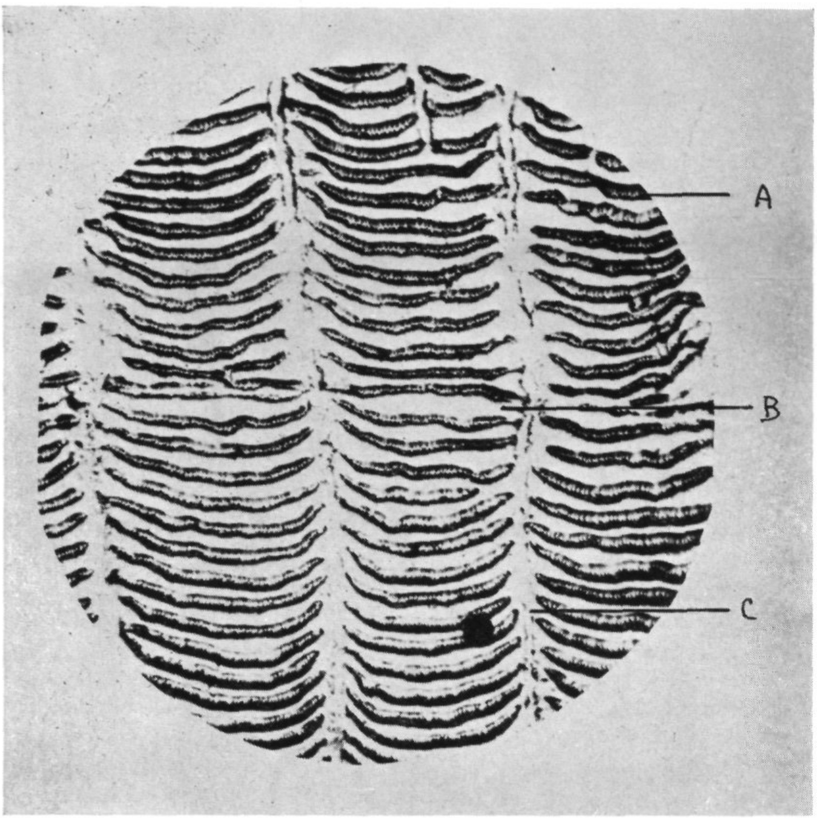

FIGURE 2

Enlarged portion of the scale shown in Figure 1, showing in detail the structure of an annulus and the adjoining circuli.
(A) Circulus (B) Annulus C. Radius

METHODS

Collection of Samples: To eliminate as far as possible variations due to environmental or physiological peculiarities, which might alter the scale sculpture of populations from different areas, all samples for a single series were taken from the same area on the same day, and from the same year class, thus minimizing the possibility of mixed populations.

Samples were taken in the field from the nets of commercial fishermen, the desired scales being removed and placed in small envelopes on which the necessary data were recorded. All fish were measured to the nearest half centimeter, lengths being taken from the nose to the fork of the tail.

Only regular, symmetrical scales from the area proposed by Merriman (1941) were used in this study. As will be shown later in the discussion of Lee's Phenomenon, the restriction of sampling to this body region, i. e., on the first and second white stripe above the lateral line, and between the spinous and soft dorsal fins, eliminated grossly inaccurate values for calculated length.

Chesapeake Bay samples were taken from a pound net off the mouth of Parker's Creek (about midway between Cove Point and Plum Point) on November 18, 1941. One hundred and fifteen samples were taken, of which one hundred were from fish of the 1940 year class. Of these, only 87 were usable because scales from the remaining samples were regenerated.

The Hudson River samples consisted of two-year old fish of the 1938 year class. Since fish showing one annulus and marginal growth are below the legal limit in the Hudson area, and are not taken with the standard gear of commercial fisherman, the data of necessity were limited.

Calculation of Growth Increments. The idea of using scales in determining body length and growth increments in successive years was first introduced by Einar Lea in 1910. Working with herring scales he determined annual rings and observed a ratio between scale and body growth. From his observations, Lea derived a formula which illustrated this ratio in a simple proportion that has become widely used for calculating length. This formula, subject to the introduction of correction factors by some investigators (Lee, 1912; Van Oosten, 1926), is as follows:

$$\frac{\text{Length of scale to annulus of year X}}{\text{Total scale length}} = \frac{\text{Body length at end of year X}}{\text{Body length when captured}}$$

The substitution of symbols which suggest the terms they represent, makes possible a more convenient expression of the formula, which then appears as:

$$\frac{s_1}{S} = \frac{l_1}{L};\ \frac{s_2}{S} = \frac{l_2}{L}$$

The length increments in each year may be indicated as i_1, i_2, etc., and $i_1 = l_1$; $i_2 = l_2 - l_1$; $i_3 = l_3 - l_2$; etc. These symbols will be used in subsequent tables and illustrations in this paper.

Rosa M. Lee (1912) observed, in comparing different year classes at corresponding periods of life, a decrease in calculated lengths with increasing age. This apparent change has been designated as "Lee's Phenomenon." Miss Lee advanced, in explanation of this change, the hypothesis that a contraction of the scale occurred with increasing age, while Lea (1913) proposed the idea that a relationship between sexual maturity and growth caused the variation.

Lee's Phenomenon can be disregarded in this study, since Merriman has shown that it does not occur in striped bass, at least when scales from the specified area are used for computation. It is apparent from his data showing the straight line relationship between scale growth and body growth that the phenomenon should not appear in length calculations, and in fact, his calculations, based on data from several age groups, do not show the progressive decrease in calculated values characteristic of the phenomenon.

ANALYSIS OF DATA

As may be seen from Table 1 and Figure 3, those individuals of the year class with the largest calculated values for i_1, were also the larger individuals at the end of the second summer. These larger fish, attaining a greater growth during the first season, retained enough of their advantage so that at the end of the second year, they were still the largest members of the year class. However, the advantage was not fully retained, for it may also be seen that both the absolute and relative second year increments are greater among the fish which were small at the end of the first year.

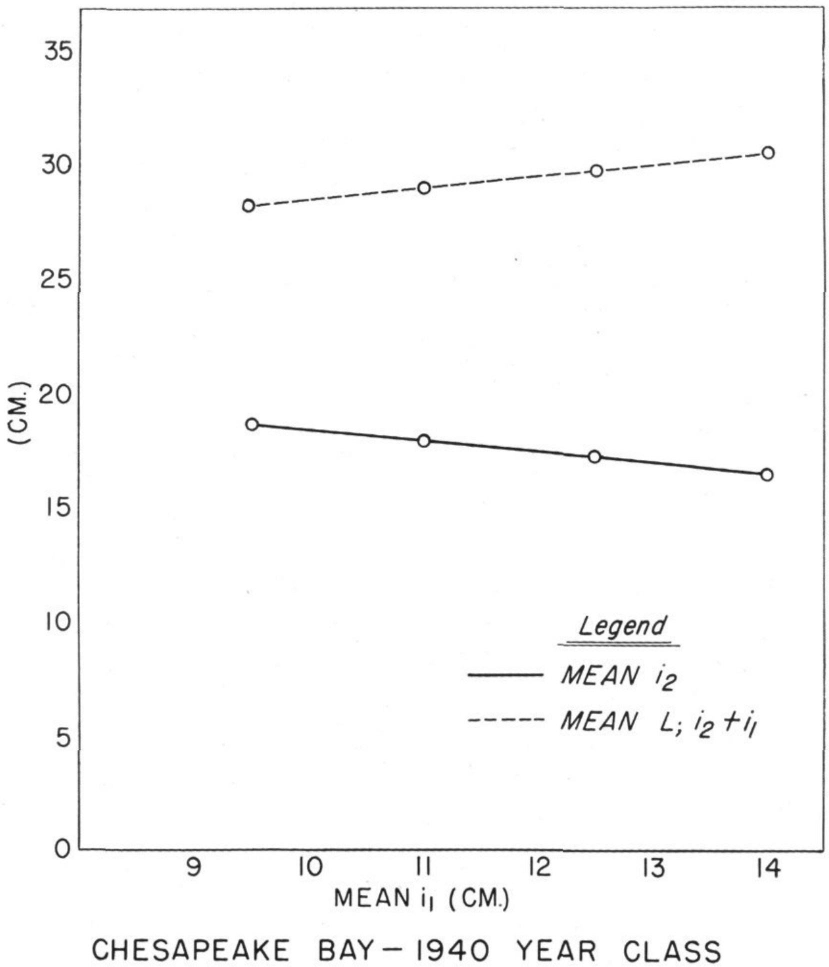

FIGURE 3

Total length and calculated second year growth increments of striped bass grouped according to the calculated first year's growth (Chesapeake Bay, 1940 year class).

TABLE 1

Total length and calculated second year growth increments of striped bass grouped according to the calculated first year's growth (Chesapeake Bay, 1940 year class).

	Calculated length Increments (cm.)		Body Length (cm.)
	$i_1 = l_1$	$i_2 = L\text{-}i_1$	L
	7.5	17.5	25.0
	7.5	17.5	25.0
	8.0	18.5	26.5
	8.0	19.5	27.5
	8.0	22.0	20.0
	8.0	17.0	25.0
	8.5	16.0	24.5
	9.0	17.5	26.5
	9.0	21.0	30.0
	9.5	17.0	26.5
	9.5	18.5	28.0
	9.5	19.0	28.5
	9.5	19.5	29.0
	9.5	20.0	29.5
	9.5	20.0	29.5
	9.5	20.5	30.0
	9.5	19.0	28.5
	10.0	16.0	26.0
	10.0	17.0	27.0
	10.0	10.0	28.0
	10.0	19.5	29.5
	10.0	20.5	30.5
	10.0	21.0	31.0
Mean Values	9.5	18.75	27.89
	10.5	15.5	26.0
	10.5	17.0	27.5
	10.5	17.5	28.0
	10.5	22.0	32.5
	11.0	14.0	24.0
	11.0	16.5	27.5
	11.0	18.5	29.5
	11.0	19.0	30.0
	11.0	19.0	30.0
	11.0	19.5	30.5
	11.0	20.0	31.0
	11.0	20.0	31.0
	11.0	20.5	31.5
	11.5	15.0	26.5
	11.5	15.0	26.5
	11.5	17.0	28.5
	11.5	17.0	28.5
	11.5	18.0	29.5
	11.5	18.0	29.5
	11.5	19.0	30.5
Mean Values	11.0	18.0	28.92

	Calculated length Increments (cm.)		Body Length (cm.)
	$i_1 = l_1$	$i_2 = L\text{-}i_1$	L
	12.0	16.0	28.0
	12.0	17.5	29.5
	12.0	17.5	29.5
	12.0	19.5	31.5
	12.0	21.5	33.5
	12.5	12.0	24.5
	12.5	13.5	26.0
	12.5	14.0	26.5
	12.5	15.5	28.0
	12.5	17.0	29.5
	12.5	18.0	30.5
	12.5	18.5	31.0
	12.5	18.5	31.0
	12.5	18.5	31.0
	12.5	19.0	31.5
	12.5	20.5	33.0
	13.0	14.5	27.5
	13.0	16.0	29.0
	13.0	18.0	31.0
	13.0	18.5	31.5
	13.0	19.0	32.0
Mean Values	12.5	17.25	29.78
	13.5	13.5	27.0
	13.5	13.5	27.0
	13.5	14.0	27.5
	13.5	15.0	28.5
	13.5	15.5	29.0
	13.5	17.5	31.0
	13.5	18.0	31.5
	13.5	18.5	32.0
	14.0	14.0	28.0
	14.0	19.0	33.0
	14.0	19.5	33.5
	14.5	17.5	32.0
	15.0	15.0	30.0
	15.0	17.0	32.0
	15.0	17.5	32.5
	15.0	18.0	33.0
	15.5	18.5	34.0
	16.0	18.5	34.5
	16.5	15.5	32.0
	16.5	18.0	34.5
	17.0	14.5	31.5
	17.0	15.5	32.5
	18.0	15.5	33.5
Mean Values	14.0	16.5	31.30

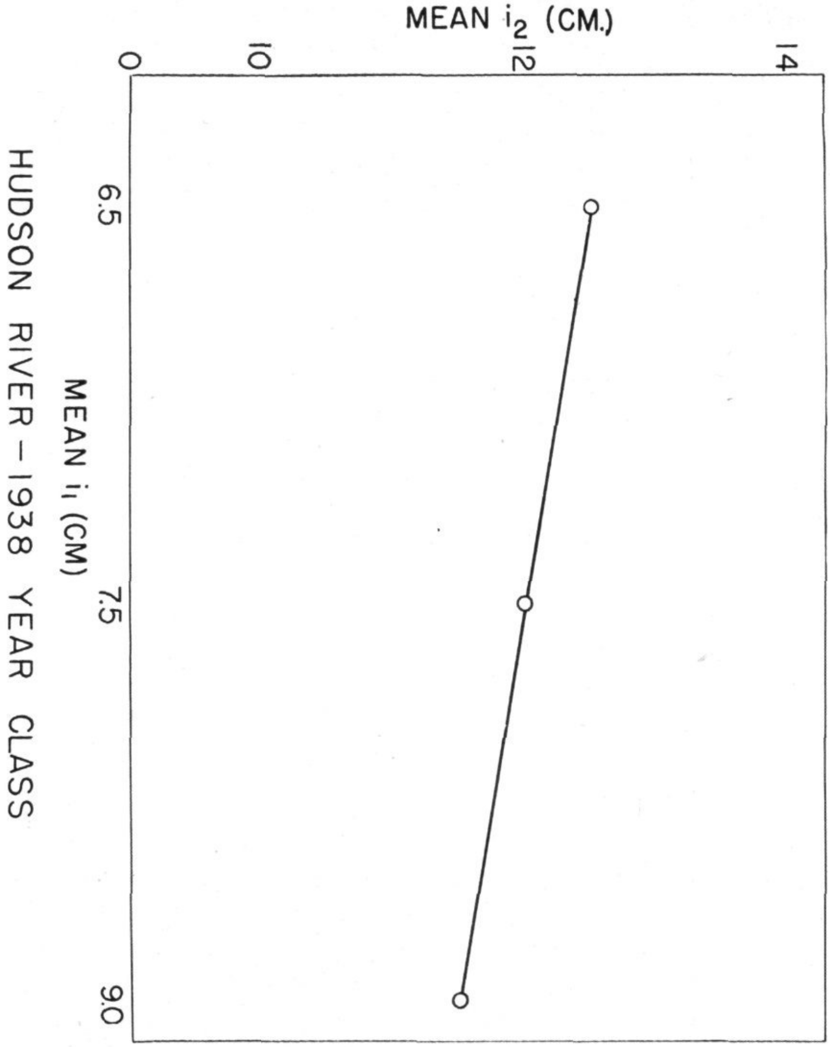

FIGURE 4

Calculated second year growth increments of striped bass grouped according to the calculated first year's growth (Hudson Bay, 1938 year class).

TABLE 2

Total length and calculated second year growth increments of striped bass grouped according to the calculated first year's growth (Hudson River, 1938 year class).

	Calculated length Increments (cm.)		Body Length (cm.)		Calculated length Increments (cm.)		Body Length (cm.)
	$i_1 = l_1$	$i_2 — L-i_1$	L		$i_1 = l_1$	$i_2 = L-i_1$	L
	6.0	10.0	28.0		8.5	13.0	29.5
	6.0	9.0	26.0		8.5	15.5	34.0
	6.0	15.5	31.5		8.5	12.5	31.0
	6.0	16.5	32.5		8.5	15.5	33.0
	6.5	14.0	28.5		8.5	8.5	29.0
	6.5	12.0	28.0		9.0	15.5	28.5
	6.5	11.0	25.5		9.0	8.0	27.0
	6.5	13.0	28.5		9.0	10.5	26.5
	6.5	14.0	29.0		9.5	12.5	27.0
	6.5	13.0	30.5		9.5	10.5	26.5
	6.5	12.0	26.5		9.5	12.5	27.0
	6.5	12.0	29.0		9.5	10.5	33.0
					9.5	12.5	27.5
Mean					10.0	12.5	33.0
Values	6.5	12.5	28.62		10.5	11.0	32.0
				Mean			
	7.0	10.0	26.0	Values	9.0	11.5	30.07
	7.0	14.0	26.5				
	7.0	12.0	27.0				
	7.0	12.5	27.0				
	7.0	12.0	29.0				
	7.5	9.5	29.5				
	7.5	13.5	31.0				
	8.0	11.5	27.5				
	8.0	13.0	30.5				
	8.0	13.0	26.5				
	8.0	10.0	27.0				
	8.0	10.5	25.5				
	8.0	11.0	26.5				
Mean	8.0	12.0	28.5				
Values	7.5	12.0	27.67				

DISCUSSION

The observation that older, larger animals grow more slowly than younger, smaller ones, suggests a possible explanation of the phenomenon of compensatory growth. Careful studies of the growth rate of populations and individuals of many species, such as those conducted by Pearl (1925), have presented considerable evidence of this decrease in rate with increased age. Precise biological knowledge, in the main, is lacking, but it seems logical and reasonable to assume that it is the result of independently operating factors in the environment or life history of the individual. Such factors exist in the case of the striped bass, the two of greatest importance being the time of spawning and the individual growth capacity. Spawning occurs from April through June, making possible a time advantage of three months for the earliest spawned individuals, in which they can establish themselves with little competition in the environment.

In consideration of the second factor, it is universally recognized that different individuals of the same species, subjected to similar environmental condition, will exhibit wide variation in growth. This can only be attributed to variability in what may be termed "the innate growth capacity." If these two factors, time of spawning and innate growth capacity, are considered to function independently, as do Mendelian unit characters, a number of combinations can be produced. An extreme simplification of this idea can present the wide number of variations possible in different individuals. If three degrees of growth capacity are established in this hypothetical representation, and are designated good, medium, and poor, and three periods are likewise selected in the spawning period, and designated as early, middle, and late, a total of nine possible groups are seen. When it is considered that this simplified picture discounts the effect of all other factors, the enormous possibility of groups showing different degrees of growth is seen.

The largest fish in the first year would, therefore, be those which were spawned early and had a good innate capacity for growth, the combination of the two factors giving them an advantage over the remainder of the year class. The fish of average size might be spawned later, and although their growth capacity might be good, the advantage of time held by the earlier fish, would restrict their growth. Perhaps they could be spawned earlier, but be restricted by their individual growth capacity. The smallest fish, or "runts" of the population, would probably be those which were spawned late, and had a poor growth capacity. Another factor of unquestionable importance, omitted to simplify the presentation, is the chance or luck of the individual in finding a favorable environmental niche.

The second year, however, may bring about a partial reversal of these conditions. Data accumlated from this study discloses that the largest fish maintain their growth advantage, and that a complete compensation between these largest individuals and the "runts" never occurs, but a significant increase does occur in the rate of growth of the smaller fish, accompanied by a decrease in the growth rate of the larger ones. The factor of time-of-spawning is, of course, eliminated in the second year, all fish starting theoretically on an even footing. Other important factors are introduced, however. In addition to chance in finding a favorable environmental niche, the change of food habits at different times of life is important. The "runts" may find their particular food supply abundant, while the larger fish, requiring, because of their greater size, a different diet, may have a struggle for food which retards the growth.

Only the body lengths for the first and second years were available in this study, and too, from the limited data, conclusions regarding the growth curve in later life are not made. Merriman, however, presented (1941) graphically body length increments for striped bass over a period of eight years, and a definitely decreasing slope was observed, indicating that as the fish increased in size the increments decreased.

CONCLUSIONS

A significant compensation in growth was observed in yearling fish of the 1940 year class from the Chesapeake Bay and the 1938 year class of the Hudson River. In both areas the smaller yearlings showed a decidedly greater increase in growth during their second year than the larger yearlings.

A complete compensation cannot be said to occur, since the growth advantage of the larger yearlings is maintained.

Only hypothetical considerations can be advanced in explanation of compensatory growth. The time of spawning, the growth capacity of the individual, that is to say, the efficiency of the individual's physiological adjustment, or the chance in finding a favorable environmental niche, may be presented as possible factors affecting this phenomenon.

Only pure populations from the same year classes were used in this investigation, and although this increased the accuracy and reliability of the data, conclusions should not be made concerning other year classes.

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