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GROWTH OF BROOK TROUT (*SALVELINUS FONTINALIS*) AND BROWN TROUT (SALMO TRUTTA) IN THE PIGEON RIVER, OTSEGO COUNTY, MICHIGAN*

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INTRODUCTION

THE Pigeon River Trout Research Area was established in Otsego County, Michigan, in April, 1949, by the Michigan Department of Conservation. It includes 4.8 miles of trout stream and seven small lakes. The stream has been divided into four experimental sections, and fishing is allowed only on the basis of daily permits. This makes possible a creel census that assures examination and recording by trained fisheries workers of the total catch. Most of the scale samples upon which the present study is based are from fish taken in the portion of the stream in the research area. The fish were collected by two different methods: by hook and line, and by electric shocking. In all, scale samples were obtained from 4,439 brook trout (*Salvelinus fontinalis*) and 1,429 brown trout (Salmo trutta) older than one year; the collections were made between April 20, 1949, and November 30, 1951.

VALIDITY OF AGE DETERMINATION BY MEANS OF SCALES

Evidence in favor of the method of determining the age of brook trout by means of scales was presented in an earlier publication (Cooper, 1951). Further support for this method is given here because of the availability of fish of known age and also because the trout in the Pigeon River usually form quite distinct annuli, making the interpretation of age a relatively simple task (Pl. I). In all data for fish of known age there has been agreement between the age as determined by scales and the known calendar age of the fish.

For the brown trout, the validity of age assessment by means of

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scales seems to be well established (Dahl, 1918; and others). In the Pigeon River, formation of annuli on scales of this species is quite distinct, and comparisons of known age with the formation of annuli (up through the first two) have further validated the method (Pl. II). In this stream the resumption of feeding of the fish, growth, and the accompanying formation of annuli on the scales takes place during late April or early May, depending upon the temperature of the water.

LENGTH RELATIONSHIP OF BODY AND SCALES AND THE CALCULATION OF GROWTH

Calculation of the previous annual growth of fishes by means of scale measurements has been summarized by Ralph Hile (see Lagler, 1949). Of the various methods used by the early workers in this field, that of Monastyrsky (1930) seemed to be most applicable to both brook- and brown-trout populations in the Pigeon River. This assumption holds that the logarithms of scale length and fish length exhibit a straight-line relationship, that is, that

$$ASR = CL^n, \text{ or } \log ASR = \log C + n \log L,$$

where ASR is the anterior scale radius, L is the total fish length, and C and n are constants to be determined empirically. This assumption does not fit the data from very small fish satisfactorily since it assumes that scale growth and body growth begin at the same time. Actually, scales do not begin to form until the fish are about 40 mm. in total length. Scale growth then proceeds very rapidly, but at a diminishing rate. However, from the time the fish are one year old, Monastyrsky's method fits the data very well and yields quite accurate growth calculations for completed years of growth.

A determination of the length relationship for body and scales of the brook trout in the Pigeon River was made on 532 fish ranging in total length from 2.5 inches to 8.0 inches, as follows:

$$\log ASR = 0.99217 + 0.8723 \log L.$$

For the brown trout, 1,291 fish ranging in total length from 2.5 inches to 23.7 inches revealed the following relationship:

$$\log ASR = 1.25377 + 0.8968 \log L.$$

Nomographs patterned after the one described by Hile (1950) were constructed and used for all calculations presented here.

The length relationship of body and scales of the brook trout in the Pigeon River has been published earlier (Cooper, 1952a), along with data from four other populations of brook trout in Michigan. The length relationships of body and scales of all of these populations were best described by the Monastyrsky formulas, although minor variations did occur between different populations. The use of the direct-proportion method or of the direct-proportion method with a correction for the body length at the time of scale formation would result in errors of as much as 78 per cent in growth calculations of the brook- and the brown-trout populations described here.

AGE COMPOSITION OF THE PIGEON RIVER TROUT POPULATIONS

Sampling, either by hook and line or by electric shocking, indicates that there are very few old fish in either the brook-trout or the brown-trout population in the Pigeon River (Table I). Few of the

TABLE I

AGE COMPOSITION OF BROOK-TROUT AND BROWN-TROUT POPULATIONS IN THE PIGEON RIVER

Species and collection method	Age group					Total number of fish sampled
	I	II	III	IV	V	
Brook trout						
Hook and line	509	1,241	79	..		1,829
Electric shocker	2,006	562	41	1	..	2,610
Brown trout						
Hook and line	222	376	31	4	..	633
Electric shocker	547	210	33	4	2	796

trout live to be four years old, and over 95 per cent of the catch by anglers is composed of fish less than three years old. The Pigeon River population undoubtedly includes many more individuals of age group I than is suggested by the collections, since electric shockers are selective in that they capture a greater proportion of the larger fish. Collections taken by hook and line are also selective because of the 7-inch minimum-size limit. No information on the abundance of age group 0 is given because only the largest individuals of this class were collected.

A comparison of the brook-trout data with the data from collections made in Maine (Cooper and Fuller, 1945) and Manitoba (Doan, 1948) which, though rather small, contained brook trout in their fifth, sixth, seventh, and eighth summers indicates that the Pigeon River population is short-lived. This rapid disappearance of older brook trout in the population is associated with a high rate

TABLE II

COMPARISON OF CALCULATED TOTAL LENGTHS (IN INCHES) OF BROOK TROUT FROM GANGLE LAKE TAKEN BY DIFFERENT METHODS

Sampling method and date	Calculated lengths at end of successive years of life					
	1 year		2 years		3 years	
	Length	Number of fish	Length	Number of fish	Length	Number of fish
Hook and line						
1947	2.5	152	4.4	130	5.8	47
1948	2.5	226	4.5	206	5.8	83
Poison						
1948	2.3	416	3.8	209	5.0	50

of exploitation. Three brook trout are caught by anglers each year for every one of legal size left at the end of the season (Cooper, 1952b). Whether fishing alone is responsible for the difference in age composition between the population of Michigan waters and the populations of Maine and Manitoba waters is unknown because of the absence of any age-composition data on unfished or lightly fished populations in Michigan.

Brown-trout populations are not so easily exploited as are brook trout (Cooper, 1952b), and they contain greater numbers of old and large fish. There is also some evidence that the brown trout has a longer normal life span than the brook trout. Dahl (1918) says that brown trout in Norway reach an age of from twelve to fifteen years; the information on the maximum age of brook trout, though less complete, indicates a life span of about ten years.

EFFECT OF SELECTIVITY OF GEAR IN CALCULATIONS OF THE RATE OF GROWTH

In any discussion of the rate of growth of fish, the question of the selectivity of the gear used in collecting must be considered. Is the

TABLE III

COMPARISON OF CALCULATED TOTAL LENGTHS (IN INCHES) OF BROOK TROUT AND BROWN TROUT FROM THE PIGEON RIVER TAKEN BY DIFFERENT METHODS

Species and sampling method	Age group	Number of fish	Calculated lengths at end of successive years of life				
			1 year	2 years	3 years	4 years	5 years
Brook trout							
Hook and line	I	509	4.31	...	....	....	....
	II	1,241	3.30	6.26	....	....	....
	III	79	3.12	5.81	8.12	....	....
Electric shocker	I	2,006	3.58			....	....
	II	562	3.09	5.76	....	....	....
	III	41	2.90	5.33	7.69	....	....
	IV	1	2.80	5.90	7.50	8.90	....
Brown trout							
Hook and line	I	222	4.11	...		....	
	II	376	3.47	7.82	....	....	....
	III	31	3.68	8.15	10.66	....	....
	IV	4	4.40	8.58	11.63	13.55	....
Electric shocker	I	547	3.77	...	....	....	....
	II	210	3.63	7.90	....	....	....
	III	33	3.78	8.31	11.00	....	....
	IV	4	4.08	8.28	10.55	13.63	....
	V	2	3.80	8.75	13.30	16.45	19.10

sample taken representative of the population as a whole? An example of selectivity may be found in the data for hook-and-line fishing in Gangle Lake, Montmorency County, Michigan. In this lake, brook-trout collections were made by hook and line for a period of about two years. All fish caught, regardless of size, were scale-sampled. At the end of this period, the residual population was treated with rotenone and all of the fish then made available were sampled. An examination of the growth-rate data for the fish collected by these two methods indicates that hook-and-line fishing was apparently selective in capturing the faster-growing members of each age group, regardless of size (Table II).

The selective effect of angling was also noted for grayling (Gustafson, 1949). Studies of this fish in Lake Storsj6, Sweden, suggested a selection by angling that was effective up to the third year of life of the fish, with young grayling which exhibited a rapid growth rate being captured first.

Because of these indications that hook-and-line fishing might be selective, data from the two collecting methods, i.e., hook and line and shocking, were analyzed separately for the Pigeon River. They show that hook-and-line fishing for brook trout selects the faster growing individuals of each age group. But angling is not selective to the same degree for brown trout in this river. The calculated lengths of the brown trout caught with the electric shocker exceed slightly those of the brown trout taken by hook and line, but the differences probably are not significant (Table III).

LEE'S PHENOMENON

The phenomenon of the "apparent change in growth rate" was first described from studies of the scales of herring, haddock, and brown trout (Lee, 1912). It was noted that the calculated length for the first few years of growth tends to decrease as the age of the sample of fish increases, i.e., that the growth rate is apparently increasing each year. The most logical explanation for this phenomenon advanced by Lee was the greater mortality of fast-growing individuals of each year class. With the known high rate of exploitation for the brook trout in the Pigeon River, and also the selective effect of angling on faster-growing individuals, the growth data for this species might be expected to show Lee's phenomenon to a marked degree. That they do so is true not only for samples drawn from successively older age groups (Table III), but also for samples from the same year class taken at successive monthly periods (Table IV).

Brown trout in the Pigeon River do not show this phenomenon

TABLE IV

LEE'S PHENOMENON IN BROOK AND BROWN TROUT CAUGHT BY HOOK AND LINE IN THE PIGEON RIVER, 1949-51, WITH THE 1948 YEAR CLASS BEING COMPARED AS TO CALCULATED TOTAL LENGTHS (IN INCHES) AT THE END OF THE FIRST AND SECOND YEARS

Species and date of collection	Length at annuli		Number of fish sampled
	Annulus 1	Annulus 2	
Brook trout			
July, 1949	4.36		45
Aug.—Sept., 1949	4.27	. .	51
April—May, 1950	3.71	6.81	268
June, 1950	3.14	5.89	224
July, 1950	3.08	5.76	121
Aug.—Sept., 1950	3.08	5.68	99
Brown trout			
July, 1949	4.20		22
Aug.—Sept., 1949	4.09		43
April—May, 1950	3.58	7.76	67
June, 1950	3.30	7.33	65
July, 1950	3.48	7.43	36
Aug.—Sept., 1950	3.45	7.47	

to as great an extent as do brook trout. The fact is probably associated with the lesser exploitation of this species.

GROWTH COMPENSATION

In studies of the growth of fish involving calculated lengths based on scale measurements, many workers dealing with various species have found that initially slow-growing members of an age group grow faster in later years than do the initially fast-growing members of that same group. This phenomenon, referred to as the "law of growth compensation," was first described by Gilbert (1914) in relation to the sockeye salmon (*Oncorhynchus nerka).* Other workers have not found this compensation in growth to hold in different species to the same extent.

Growth compensation does occur in both the brook trout and the brown trout in the Pigeon River, according to the calculated lengths of two-year-old and three-year-old fish. Although growth increments of different-sized fish are similar, the relative growth of the fish that were the small yearlings is greater than that of the fish that were the large yearlings (Tables V and VI). This growth

TABLE V

GROWTH COMPENSATION OF BROOK TROUT AND BROWN TROUT OF AGE GROUP II FROM THE PIGEON RIVER (IN INCHES)

Size group at end of first year	Number of fish	Mean length at end of first year	Growth increment between first and second years
Brook trout			
1.6-2.0	42	1.90	2.90
2.1-2.5	202	2.35	2.88
2.6-3.0	437	2.81	2.87
3.1-3.5	458	3.29	2.84
3.6-4.0	314	3.78	2.90
4.1-4.5	142	4.27	2.92
4.6-5.0	50	4.73	2.67
5.1-5.5	8	5.30	2.44
Brown trout			
1.6-2.0	14	1.89	4.29
2.1-2.5	33	2.35	**4.44**
2.6-3.0	99	2.84	4.32
3.1-3.5	155	3.32	4.45
3.6-4.0	143	3.80	4.23
4.1-4.5	89	4.29	4.13
4.6-5.0	33	4.77	4.15
5.1-5.5	13	5.24	3.80

compensation is not sufficient, however, to overcome the original difference in growth exhibited during the first year, and the fish that were the large yearlings maintain their superiority in size throughout the first three years. The lack of old fish in the population prevents analysis of this phenomenon beyond the first three years.

TABLE VI

GROWTH COMPENSATION OF BROOK TROUT AND BROWN TROUT OF AGE GROUP III FROM THE PIGEON RIVER (IN INCHES)

Size group at end of first year	Number of fish	Mean length at end of first year	Growth increment between first and second years	Growth increment between second and third years
Brook trout				
1.5-2.9 ...	42	2.52	2.63	2.49
3.0-3.9 ...	50	3.40	2.71	1.96
4.0-5.0 ...	10	4.30	2.22	2.49
Brown trout				
1.5-2.9 ...	12	2.53	4.42	2.89
3.0-3.9 ...	27	3.54	4.52	2.37
4.0-5.0 ...	23	4.50	4.48	2.47

DISCUSSION

One of the principal advantages in the method using calculated lengths based on scale measurements to compare growth rates is the assumption that average growth rates thus obtained are directly comparable regardless of the time of collection because the calculated lengths of individual fish represent increments at completed seasons of growth. For a comparison of average growth rates the age groups sampled at different times should not have undergone any marked preferential mortality between collection dates. Furthermore, it is necessary that the collecting method ensure a random sample of the population.

It has already been shown for brook trout that angling selects the fast-growing individuals of each age group as soon as those individuals reach legal size, and that samples drawn from corresponding age groups show a decreasing trend in growth rate. Thus the main advantage of using scale measurements is nullified by a selective angling of high intensity. It follows that growth rates from different localities might reflect not only growing conditions per se, but also differences in the degree of exploitation of the stocks. Actual lengths of each age group offer no advantage in obtaining an unbiased index of growth rate, since selective angling would still operate to remove the larger individuals of each age group. For populations subjected to fishing there appears to be no way of obtaining an unbiased estimate of the growth rate of brook trout once the fish reach a size vulnerable to angling. In many of the populations exhibiting a fast rate of growth, calculations of growth to even the first annulus are greatly biased because of the 7-inch minimum-size limit in effect in Michigan. Mortality of sublegal-sized trout due to angling may also be a factor if any considerable number of fish are killed in this manner. Up to the present time in Michigan it has been impossible to obtain growth-rate information on wild brook-trout populations from which angling has been excluded.

Brown-trout growth-rate studies are apt to be less biased because of a smaller rate of exploitation. Information from the Pigeon River does not show any consistent differences in growth between brown trout from samples taken by angling and those taken by the electric shocker. An exception occurs in the few fish of age group I taken early in the season, when the fast-growing members of that group are first reaching the minimum legal size. However, the rate of exploitation is not high enough to deplete the number of these fast-growing members in the population, and later samples from this group show no serious decline in growth rate.

The marked difference in the rate of exploitation between brook trout and brown trout, along with the selective effect of angling on the brook trout, prevents a valid comparison of the growth rate of the two species. If we compare the calculated lengths at annulus 1 of the first individuals of an age group caught by fishermen (Table IV), the two species seem to be growing at similar rates. If two-year-old fish are used as a basis of comparison, however, it appears that the brown trout are growing much the faster. The greater part of this difference is probably to be explained by the selective harvesting of the fast-growing brook trout rather than by a difference in growth rate between the species.

The lack of sufficient growth compensation to offset initial slow growth, demonstrated for both the brook and the brown trout in the Pigeon River, has important implications for management. Under a low minimum-size limit, the fish with the best chances of becoming large, prize-winning individuals are sacrificed first, when they are small. Furthermore, a low minimum-size limit favors the survival of the slow-growing runts of each age group as spawning stock. If the effect of selective breeding applies to wild fish as it does to hatchery fish (Embody and Hayford, 1925; Hayford and Embody, 1930), the wild stock is being continually selected for slow growth under present laws, which permit excessive removal of the stock and at too small a size.

PIGEON RIVER TROUT RESEARCH AREA
MICHIGAN DEPARTMENT OF CONSERVATION
VANDERBILT, MICHIGAN

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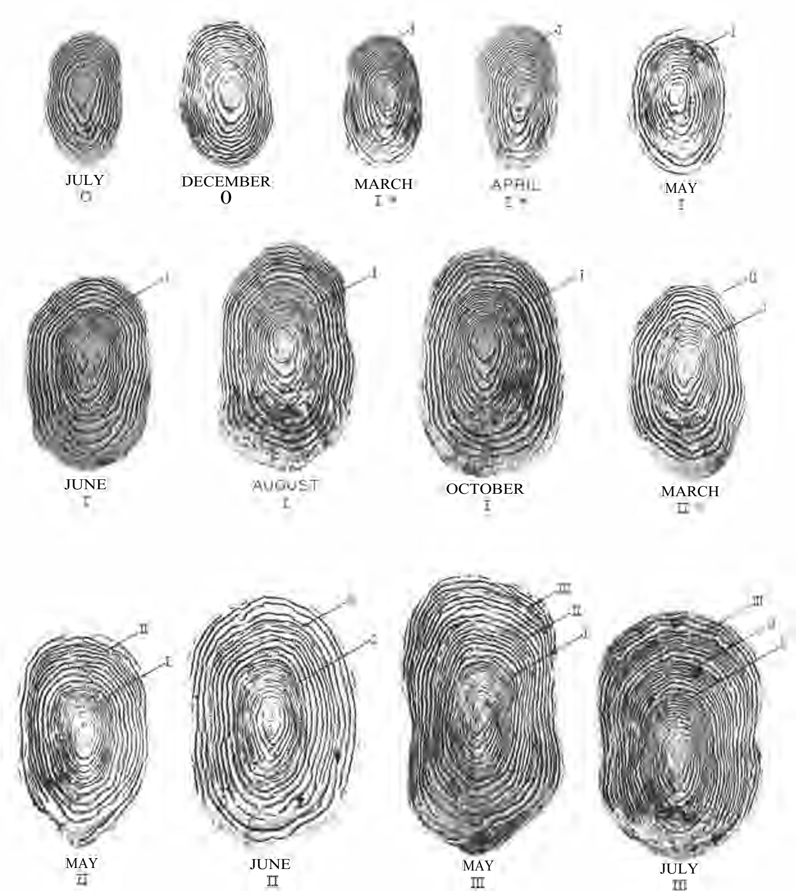
EXPLANATION OF PLATE I

Scales of brook trout from the Pigeon River, Otsego County, Michigan

(Actual body length of fish on dates specified is indicated below. The months are the months of catch; roman numerals indicate age groups and annuli; asterisks signify that the fish have completed another calendar year [established by agreement as January 1], but have not yet formed an annulus on their scales for this year of growth.)

July-0: 3.0 inches, July 9, 1949
December-0: 4.6 inches, December 28, 1949
March—I : 3.8 inches, March 13, 1950
April—I*: 4.5 inches, April 14, 1950
May—I: 3.9 inches, May 19, 1950
June—I: 5.0 inches, June 19, 1950
August—I: 5.6 inches, August 17, 1949
October—I: 6.0 inches, October 24, 1949
March—II*: 6.1 inches, March 13, 1950
May—II: 6.8 inches, May 19, 1950
June—II: 7.0 inches, June 19, 1950
May—III: 10.2 inches, May 30, 1949
July—III: 10.0 inches, July 3, 1949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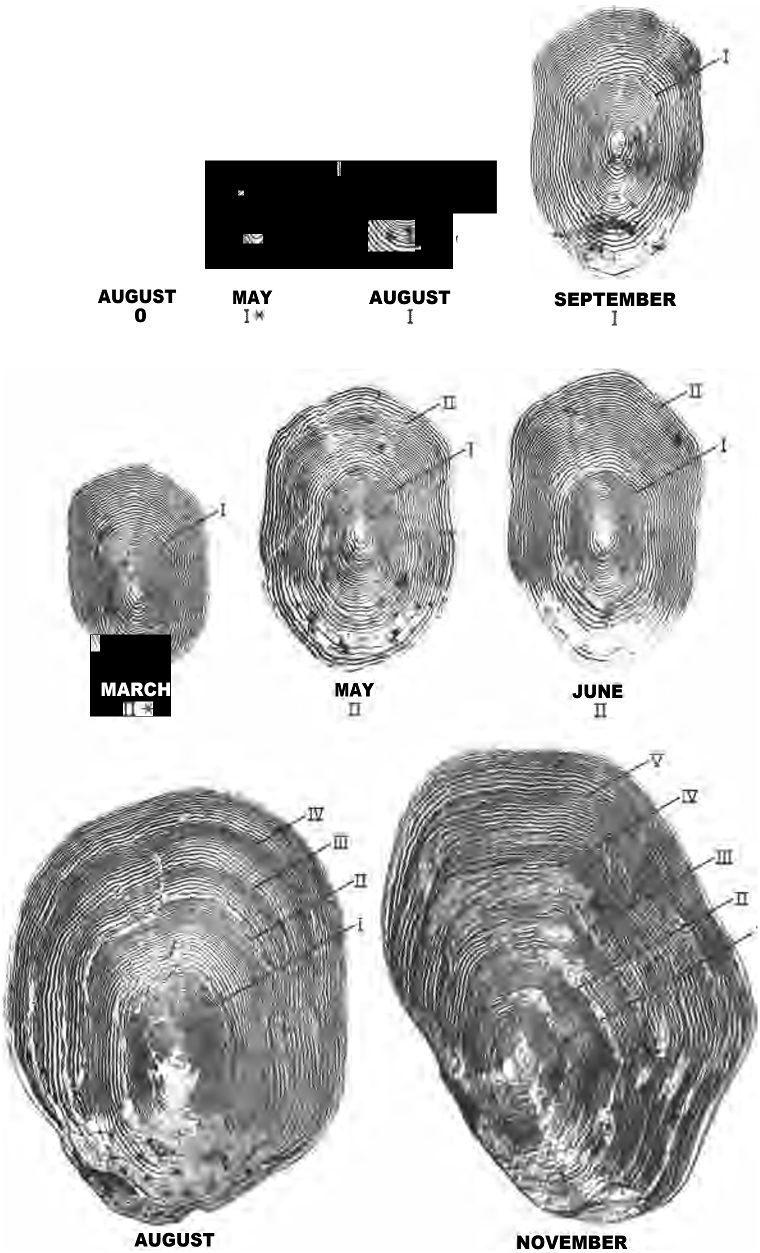
EXPLANATION OF PLATE II

Scales of brown trout from the Pigeon River, Otsego County, Michigan

(Actual body length of fish on dates specified is indicated below. The months are the months of catch; roman numerals indicate age groups and annuli; asterisks signify that the fish have completed another calendar year [established by agreement as January 1], but have not yet formed an annulus on their scales for this year of growth.)

August-0: 2.9 inches, August 10, 1949
May—I*: 3.3 inches, May 5, 1950
August—I: 5.9 inches, August 9, 1950
September—I: 7.7 inches, September 24, 1950
March—II*: 6.1 inches, March 27, 1951
May—II: 9.5 inches, May 21, 1951
June—II: 8.4 inches, June 20, 1951
August—IV: 19.5 inches, August 12, 1949
November—V: 21.4 inches, November 14, 1950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