

NUMBER 125

JULY 10, 1922

OCCASIONAL PAPERS OF THE MUSEUM OF  
ZOOLOGY

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UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN      PUBLISHED BY THE UNIVERSITY

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NOTES ON THE LIFE-HISTORY OF THE BROOK  
LAMPREY, *ICHTHYOMYZON UNICOLOR*<sup>1</sup>

BY PETER OKKELBERG

The brook lampreys live the greater part of their lives in a larval state, the period of adult existence being less than a year. As far as known, metamorphosis usually takes place in late summer or in the fall. At the time of metamorphosis the larvae have reached the adult size and no food is taken subsequent to transformation. After the spawning season, which is usually in April or in May, all the adults die, and consequently only larvae are found during the early summer months.

Due possibly to the difficulty of obtaining large collections of larvae from one locality at any one time, no one has yet tried to determine the rate of growth in the brook lampreys. Several attempts have been made, however, to determine the duration of the larval period, but so far no uniformity of results have been obtained. This may be due to the small number of specimens often used in making the calculations,

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<sup>1</sup> Mr. Carl L. Hubbs has kindly read and criticised the manuscript for this paper.

but it is also likely that different species vary with respect to the length of the life cycle and that the same species may vary in different localities.

Müller (1856), who is usually credited with the discovery that the ammocoetes are the larval forms of the lampreys, measured six larvae of the European brook lamprey, presumably *Lampetra planeri*, and found their lengths to be 5.8, 6.3, 6, 15.3, 15.4, and 14 centimeters, respectively. The first three he judged to be a little over a year old and the last three about two years. Two metamorphosed individuals measured 16.2 and 19.3 centimeters each, and he concluded that these must be at least over two years old and would be three years at the time of spawning.

In the same species, Lubosch (1903) found larvae of three different sizes. Those of the first few months measured from one to two centimeters in length. The average size of larvae of the first year was five centimeters, that of the second year larvae ten centimeters, and that of the third year larvae, or just before metamorphosis, fifteen to eighteen centimeters. He thus agrees with Müller regarding the length of the life cycle in this species.

Loman (1912), on the other hand, found larvae of four different sizes in single collections of this species, and he believed that these represented four different generations. No mention is made of the season when such collections were made, so it is not possible to tell whether he meant to imply that the life cycle is four or five years.

Larvae of the American brook lamprey, *Entosphenus appendix*,<sup>2</sup> collected near Ann Arbor, Michigan, were found by Schaffner (1902) to be of three different sizes just before the

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<sup>2</sup> The species commonly known as *Lampetra* or *Entosphenus wilderi*. See Creaser and Hubbs (1922).

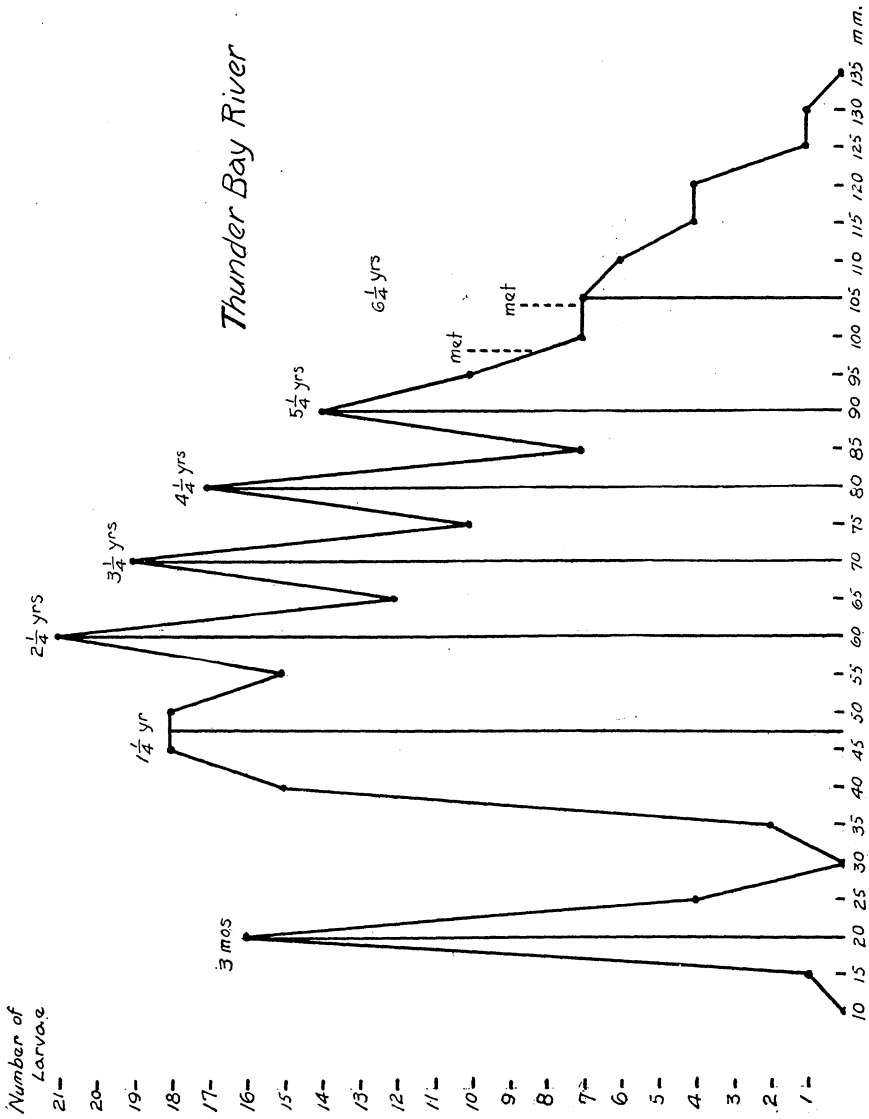


Fig. 1. Graph showing year groups of 229 larvae of *Ichthyomyzon unicolor* collected August 25, 1921, in Thunder Bay River, near Atlanta, Michigan

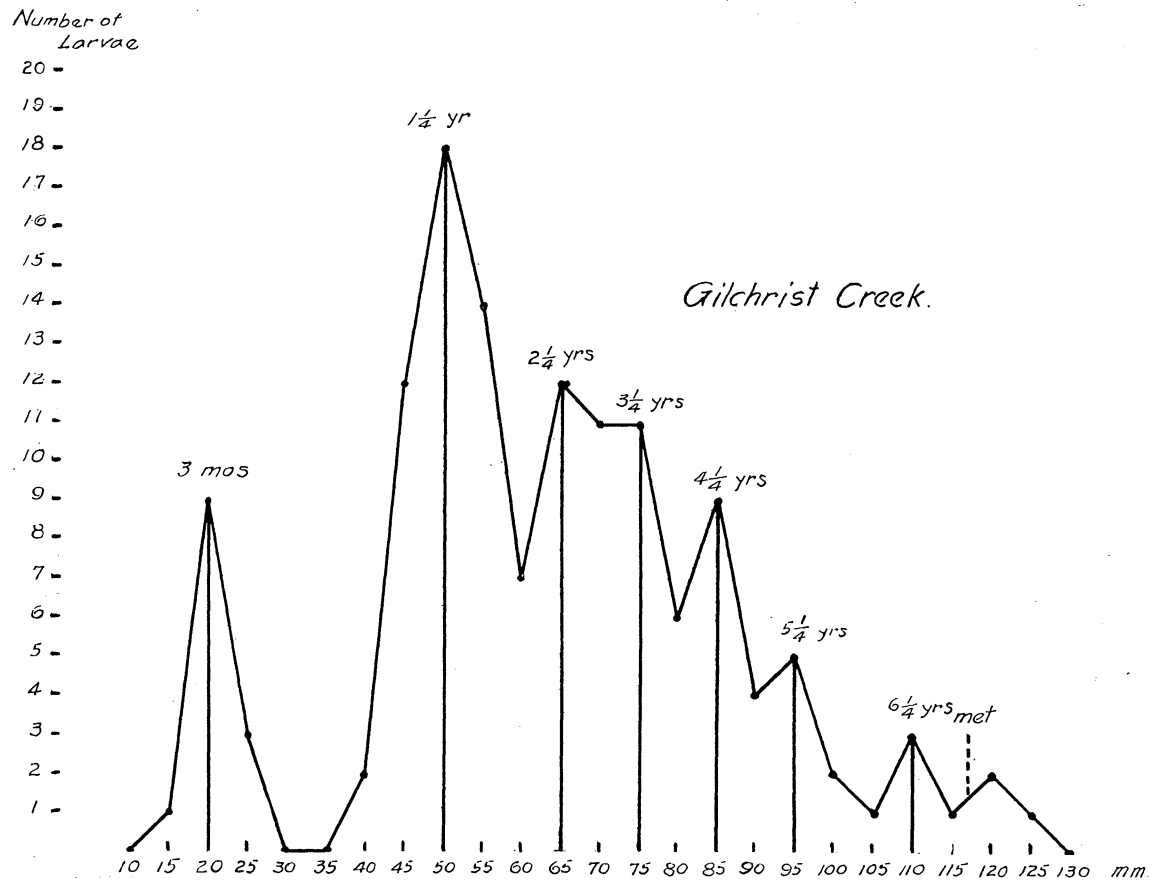


Fig. 2. Graph showing year groups of 134 larvae of *Ichthyomyzon unicolor* collected August 26, 1921, in Gilchrist Creek, a tributary of the Thunder Bay River.

spawning season in the spring, and he took this to mean that it required four years for the whole life cycle. The three groups were arranged by him as follows: larvae of the third year, 17 to 20 centimeters; those of the second year, 9 to 11 centimeters, and those of the first year, 3 to 6 centimeters.

In the same form and from the same locality, the writer (1921) found larvae of five different sizes during the month of August, indicating a life cycle of at least five years. This conclusion was based on measurements of 167 larvae. Similar results were obtained from collections made in February and during the months of April, May, and June.

*Nature of Material.*—In 1921 two collections of another species of brook lamprey, *Ichthyomyzon unicolor* (see Creaser and Hubbs, 1922), were obtained by Messrs. Carl L. Hubbs and Charles W. Creaser, one on August 25 in Thunder Bay River southeast of Atlanta, Michigan, consisting of 229 specimens, and another on August 26 in Gilchrist Creek, a tributary to Thunder Bay River, of 134 specimens. In the former collection there were two metamorphosing individuals and in the latter another one. These collections were kindly turned over to the writer for a determination of the rate of growth and of the length of the life cycle.

*Ichthyomyzon fossor*, a synonym of this species, was described by Professor Jacob E. Reighard and Mr. Harold Cummins in 1916 from specimens obtained in Mill Creek, near Dexter, Michigan. The adults which formed the basis for the description ranged in size from 112 to 149 millimeters and the larvae from 80 to 158 millimeters. The time of metamorphosis and the duration of the larval period were not determined.

*Length of the Life Cycle.*—The specimens of both collections were carefully measured and the measurements were

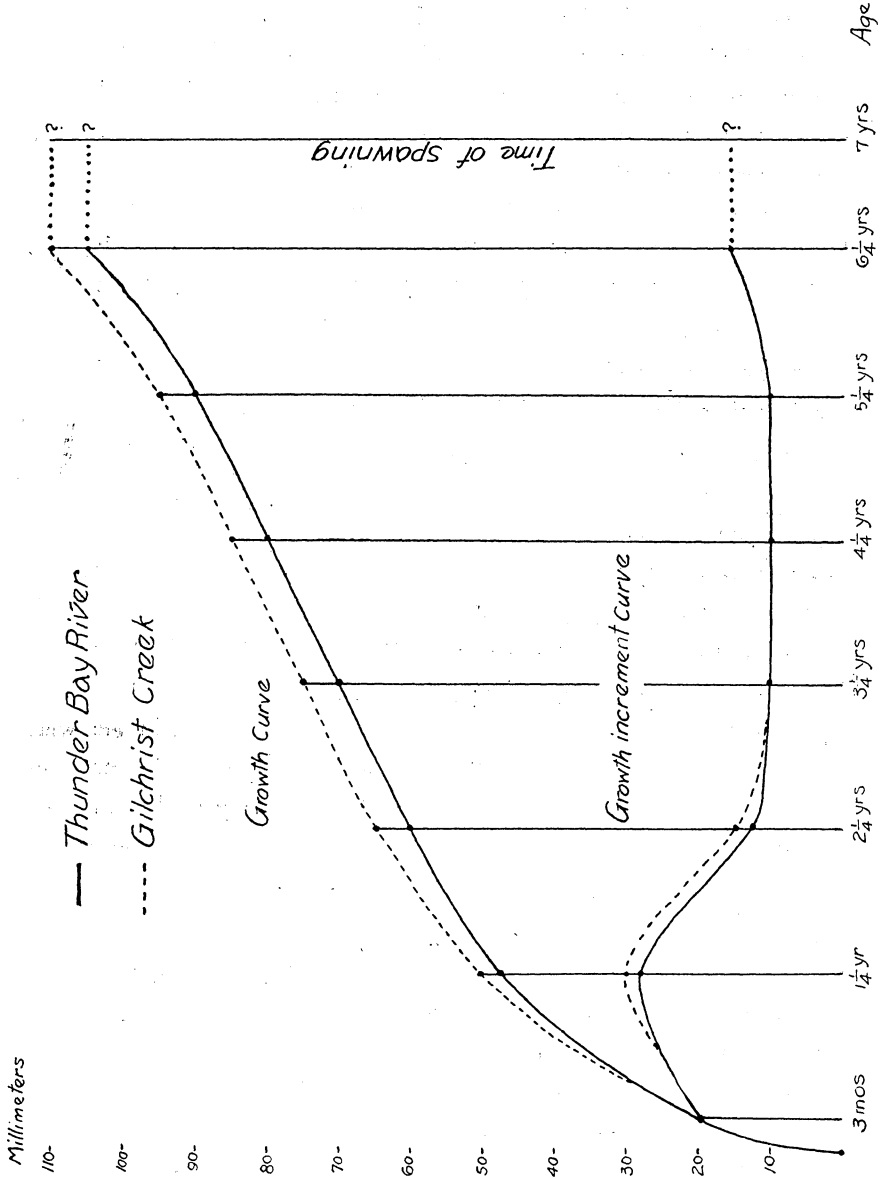


Fig. 3. Growth and growth increment curves of *Ichthyomyzon unicolor* collected in Thunder Bay River and Gilchrist Creek.

recorded separately. The larvae of the first collection were found to range from 16 to 128 millimeters in length and those of the latter from 17 to 126 millimeters. The measurements were plotted and used as the basis for the life cycle curves shown in Figs. 1 and 2, for the two collections respectively. The ordinates in the curves represent the number of individuals and the abscissae their lengths in millimeters.

A study of these graphs reveals the fact that they are made up of several distinct modes around which the larvae seem to be grouped. This can scarcely be a matter of chance, since both of the collections exhibit the same groups. The groups undoubtedly represent different generations of larvae, and the conclusion is reached that the length of the life cycle in this form and in this particular locality is seven years. This does not preclude the possibility, however, that some precocious individuals may metamorphose at an earlier stage than others and that some retarded individuals may even take more than seven years for their full development. The great amount of variation in the size of the larvae due to inequality of growth makes it impossible to determine with any degree of exactness the age of any single individual. The only part of the curve that stands out definitely in each case is that part which represents the youngest larvae in the collection, namely, those three months old. From this time on the year-group curves merge more or less with one another and it is only possible to arrange the larvae according to age around certain average sizes. The full-grown larvae are grouped around the last mode, which is at 105 millimeters, and although two transformed individuals were found to be shorter than this, it is likely that the adults would on the average be about 105 millimeters or more. Most of the larvae grouped around the last

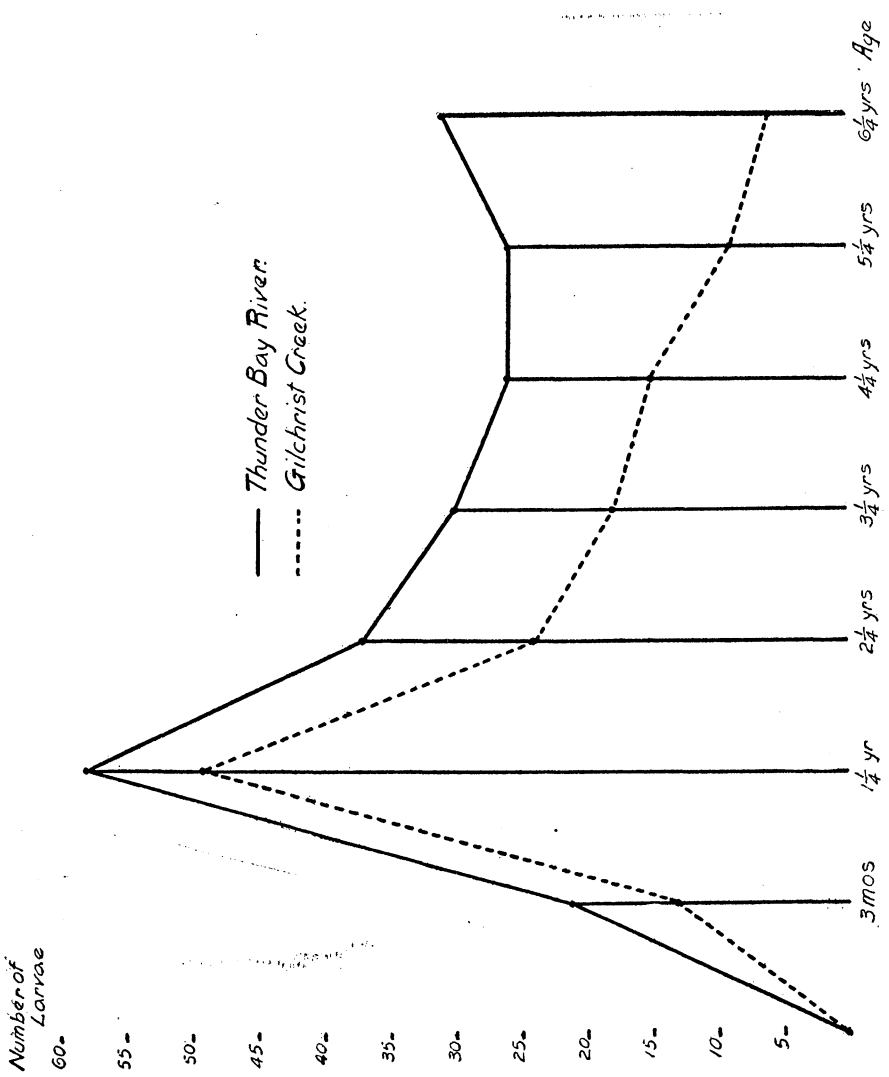


Fig. 4. Survival curves of *Ichthyomyzon unicolor* collected in Thunder Bay River and Gilchrist Creek.



mode would presumably transform before the next spawning season.

Summarizing the data contained in the curve, it is found that the annual groups may be arranged around the modes as follows:

<i>Age</i>	<i>Thunder Bay River</i>	<i>Gilchrist Creek</i>
3 months .....	20 millimeters	20 millimeters
1¼ years .....	47.5 "	50 "
2¼ " .....	60 "	65 "
3¼ " .....	70 "	75 "
4¼ " .....	80 "	85 "
5¼ " .....	90 "	95 "
6¼ " .....	105 "	110 "

At present there is not a sufficiently large collection of larvae from the type locality (Mill Creek, near Dexter, Michigan) on hand for the study of the life cycle. It is hoped that such a collection may be obtained so that a comparison may be made with the above more northern series. It is possible that temperature may have some influence on the length of the life cycle and that the northern form may pass through its development more slowly than the more southern forms. The difference in latitude between the two points is only about 185 miles, but the difference in the temperature of the water is greater than indicated by the difference in latitude.

*Rate of Growth.*—Taking the average size of the larvae of each year to be represented by the modes of the graphs 1 and 2, growth and growth increment curves may be constructed which will throw interesting light upon the rate of growth in the larvae during the successive years of their life cycle. Such curves are shown in Fig. 3.

It will be seen that the greatest increase in length takes place during the first year and a quarter of the animal's life. In fact, the larvae have attained to about half the adult length

at the end of this period. From this time on there is a sudden decrease in the growth rate up to the third year, when the rate becomes constant until between the fifth and sixth years, when there seems to be a slight increase again. This may accompany changes that eventually lead to metamorphosis. No data are available for a comparison of the size of the full-grown larva with that of the adult. Since the animal does not feed after metamorphosis, it is likely that there is no increase subsequent to this period. Neither is it likely that there is any decrease in size during or after metamorphosis, as Meek (1916) has suggested.

Reduced to percentages, the growth increments for the successive years of larval life are found to be as follows:

Age	Thunder Bay River	Gilchrist Creek
0 to 3 months.....	19.0%	18.1%
3 months to 1¼ years.....	26.1%	27.2%
1¼ years " 2¼ " .....	11.9%	13.6%
2¼ " " 3¼ " .....	9.5%	9.0%
3¼ " " 4¼ " .....	9.5%	9.0%
4¼ " " 5¼ " .....	9.5%	9.0%
5¼ " " 6¼ " .....	14.2%	13.6%

From the above table and from the graphs it will be seen that the rate of growth differs somewhat in the two collections. The rate is a little higher in the brook collection during the first and second years. This variation may, of course, be within the limits of error due to the small size of the series, but if any meaning can be attached to it, one might suggest the cause to lie in differences in food conditions, differences in temperature, or some other factor which might favor the brook-living individuals.

*Mortality Rate.*—By grouping the larvae that approximately belong to each year in the life cycle of the animal, it is possible to obtain some idea of the annual death rate. One can-

not be absolutely certain of the year to which a certain larva belongs, since there is a great deal of intergradation due to inequality of growth, but one should be quite nearly right by taking the larvae represented in each hump of the curve as the number of each year. These numbers and their equivalents in percentages are as follows:

Age	Thunder Bay River	Gilchrist Creek
3 months .....	21 indiv. or 9.1%	13 indiv. or 9.7%
1¼ years .....	58 " " 25.3%	49 " " 36.5%
2¼ " .....	37 " " 16.1%	24 " " 17.9%
3¼ " .....	30 " " 13.1%	18 " " 13.4%
4¼ " .....	26 " " 11.3%	15 " " 11.1%
5¼ " .....	26 " " 11.3%	9 " " 6.7%
6¼ " .....	31 " " 13.5%	6 " " 4.4%

On plotting these figures the curves represented in Fig. 4 are obtained. Theoretically, the largest number of individuals should have been obtained of larvae three months old, and yet the graphs show that relatively few were obtained of this age as compared with some of the older stages. There may be several reasons for this. For one thing, the young larvae are very small and some of those landed may have escaped observation. It may be also that the young larvae remain nearer the spawning grounds, among rocks and higher up the streams, during the first summer, due to the absence of conditions, such as floods, etc., which later would be operative in carrying them down stream and into more favorable collecting places.

The largest year-group of larvae obtained comprised those one year old. There is a sudden drop in number during the second year, and this is correlated with a sudden drop in the growth increment curve during the same period. This might indicate that this is a critical period in the life of the larvae, when vitality, perhaps, is low on account of some internal change of great importance. In another species of lamprey, *Entos-*

*phenus appendix*, this is the period when sex is being established in the larvae (see Okkelberg, 1921), and during which profound changes are taking place in the gonads. Since the germ cell history in *Ichthyomyzon unicolor* has not been studied, only the suggestion can be offered of correlation between the apparent low vitality of this period and the changes connected with the establishment of sex.

Another explanation of the sudden drop in the curve between the first and second years may be that the smaller larvae are more subject than the older ones to destruction by fish, for which they undoubtedly serve as food.

There is a gradual decrease in the number of larvae during the third and fourth years. After this there is no decrease in the series from Thunder Bay River and the curve even indicates an increase during the sixth year. In the tributary to the river, however, the decrease is quite gradual up to the last year. This discrepancy in the two curves may be correlated with a passive migration of the larvae down stream during heavy rains and spring thaws. Such transportation of larvae down stream has been suggested for *Entosphenus appendix* (Okkelberg, 1921). The larvae which during their early life period were found in the smaller streams might well have been carried into the river by the time of their fifth and sixth years, and thus there should be an increase of larger larvae in the collection from the river.

In the above discussion it has been assumed that spawning took place under identical conditions each year. It is conceivable that the crop of larvae of one year might be greatly reduced during or directly after the spawning season, through the agency of floods or other circumstances appearing at a time when the embryos or young larvae are least able to sur-

vive unusual conditions. Such catastrophes would, of course, influence the shape of the graphs.

SUMMARY

The length of the life cycle in *Ichthyomyzon unicolor* in the region of the Thunder Bay River, Michigan, appears to be seven years. This is a longer life cycle than has been recorded for any other lamprey.

The greatest increase in length takes place during the first year. At the end of the first year and a quarter the larvae have attained to about one-half their full-grown lengths. From this time on the increase is uniform from year to year except the last, when there is a slight increase over the normal. This may be correlated with changes leading to metamorphosis.

The mortality rate is greatest between the first and second years. A suggestion is made that this may be a period of low mortality correlated with internal changes leading to the establishment of sex.

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