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LIFE HISTORY OF THE SEA LAMPREY OF CAYUGA LAKE, NEW YORK

By ROLAND L. WIGLEY

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ABSTRACT

A life history study of the sea lamprey, *Petromyzon marinus* Linnaeus, in Cayuga Lake, N.Y., was conducted during 1950, 1951, and 1952. One of the major objectives was to obtain biological data concerning this endemic stock of sea lampreys for comparison with the newly established stocks in the Great Lakes.

Sexually mature sea lampreys captured on their spawning migration in Cayuga Inlet were the basis of much of this study. Such items as meristic counts, body proportions, body color, sex ratios, lengths and weights, fecundity, rate of upstream travel, effect of dams in retarding upstream movement, nesting habits, parasites, predators, estimates of abundance, and morphological changes were based on mature upstream migrants. Sea lampreys were procured by weir and trap operations and captured by hand. Tagging and marking programs each spring made it possible to determine movements and morphological changes of individual lampreys, in addition to estimating the number of upstream migrants.

Growth of parasitic-phase sea lampreys was estimated from measurements of specimens captured in Cayuga Inlet and Cayuga Lake proper.

The incubation period of lamprey eggs and the habits of ammocoetes and transforming lampreys were ascertained from specimens kept in hatchery troughs and raceways. Length-frequency and weight-frequency distributions, together with the length-weight regression, of ammocoetes from Cayuga Inlet were utilized for estimating the duration of their larval life.

Lake trout, *Salvelinus n. namaycush* (Walbaum), from Cayuga Lake and Seneca Lake were the subject of an inquiry into the effects of sea lamprey attacks. Incidence of sea lamprey attacks on the white sucker, *Catostomus c. commersoni* (Lacépède), was investigated.

Three methods are suggested for reducing the number of sea lampreys in Cayuga Lake.

LIFE HISTORY OF THE SEA LAMPREY OF CAYUGA LAKE (N.Y.)

By Roland L. Wigley, *Fishery Research Biologist,* BUREAU OF COMMERCIAL FISHERIES

In recent years the sea lamprey, *Petromyzon marinus* Linnaeus, has attracted the attention of commercial fishermen, sportsmen, and fishery biologists because of the destruction of food and game fishes attributed to this parasite. It was the invasion and rapid multiplication of the sea lamprey in the upper Great Lakes, coincident with the drastic decline of food fishes, especially lake trout in Lake Huron and Lake Michigan, which stimulated interest in the life-history study of the sea lamprey. One phase of the Great Lakes sea lamprey investigation was to obtain detailed information on biological characteristics of an endemic sea lamprey population in order to make comparisons with the newly expanding Great Lakes population.

Cayuga Lake has been inhabited by a thriving sea lamprey population for centuries. In addition to offering a natural habitat of limited size, Cayuga Lake has only one tributary that is extensively used by the sea lamprey for spawning. Thus, a study of the Cayuga Lake sea lamprey was undertaken in order to obtain comparative data and basic information pertaining to the life cycle of the sea lamprey.

The year 1875 marks the beginning of scientific inquiry into the taxonomic status and life history of the Cayuga Lake sea lamprey. In the spring of that year, a large male lamprey was captured in Cascadilla Creek, a tributary of Cayuga Lake near Ithaca. This specimen was unusually large and its coloration and large ropelike dorsal ridge were greatly different from immature specimens previously taken from the lake. Wilder studied this specimen and, after he obtained others, named it *Petromyzon marinus dorsatus* (Jordan and Gilbert, 1883).

Meek (1889) summarized observations on spawning habits and gave some data on size composition and sex ratio of the 1886 spawning run in Cayuga Inlet. Surface (1898, 1899) reported considerable information on natural enemies, host species, and control methods. Gage (1893, 1928) contributed much to our knowledge of the sea lamprey of Cayuga Lake. His studies encompassed the anatomical and physiological aspects as well as its life history. His works have long been considered an authoritative source of information concerning the sea lamprey.

Profs. Edward C. Raney, Dwight A. Webster, and John C. Ayers, Department of Conservation, Cornell University, guided and assisted in the organization of this study. William F. Carbine, Dr. James W. Moffett, Dr. Ralph Hile, Dr. Vernon C. Applegate, and other members of the Great Lakes fishery investigations, the U.S. Fish and Wildlife Service, generously provided equipment, technical advice, and aid in preparing the manuscript. Members of the New York State Conservation Department, especially Dr. U. B. Stone, W. G. Bentley, and Dr. R. M. Roecker, aided in collecting lamprey data; C. W. Lyon, J. P. Galligan, Dr. R. D. Suttkus, Dr. R. M. Yerger, and many other associates assisted with the fieldwork; and Douglas S. Robson gave statistical advice.

ESTABLISHMENT OF THE SEA LAMPREY IN CAYUGA LAKE

Prior to 1921, the known range of the sea lamprey in North America extended from the Maritime Provinces of Canada southward along the Atlantic coast to northern Florida, and westward up the St. Lawrence drainage into Lake Ontario and four inland lakes in New York State. In recent times (1921 and later) this range has been extended westward throughout the Great Lakes. Detailed information on this invasion has been recorded by Hubbs and Pope (1937), Radforth (1944), MacKay and MacGillivray, (1949), Shetter (1949), Trautman (1949), Applegate (1950), and Loeb and Hall (1952).

Early accounts in the literature (Goode 1884) describe the capture of large numbers of sea lampreys in some New England rivers for utilization as food, and indicate that at one time they were abundant in that region. The sea lamprey is anadromous, and until several decades ago was considered to be primarily a marine species. In recent years it has been demonstrated that lampreys can adapt themselves successfully to a lake-stream habitat where conditions are suitable, as is evidenced by their recent success in the upper Great Lakes. Moreover, several lakes in New York, including Cayuga Lake, have supported landlocked populations of sea lampreys for centuries

During the Pleistocene period, when the glacial Great Lakes were forming, glacial Cayuga Lake was also passing through some profound alterations. Changes in the outlet drainage of glacial Cayuga Lake are of primary importance in this discussion of the sea lamprey's establishment in Cayuga Lake.

Marine-dwelling sea lampreys may have penetrated into Cayuga Lake through any one of three drainages.

1. The drainage of glacial Cayuga Lake southward into the Susquehanna River. This outlet opened up relatively early in the formative period of the Great Lakes, but was later cut off by a lower level drainage opened to the north and east through the Syracuse, Mohawk, and St. Lawrence outlets.

2. At a later date, the Syracuse outlet (via the Hudson River) may have permitted access to glacial Cayuga Lake.

3. A still later development was the final disappearance of the ice in the St. Lawrence Valley which permitted an arm of the sea to extend up the St. Lawrence into Lake Champlain. This situation would have permitted passage of the sea lamprey from the Átlantic Ocean, via the "Champlain Sea," into glacial Lake Iroquois and on into Cayuga Lake. Another alternative passage in existence during this same time was from the Atlantic Ocean to the Hudson-Champlain estuary, to the Mohawk outlet, into glacial Lake Iroquois, and into Cayuga Lake.

Because the first two routes mentioned above would have permitted the sea lamprey to establish itself in all the Great Lakes, which did not occur until approximately the present century, it would appear that the third route was the most probable path of entrance. The fact that Niagara Falls would have blocked their movement into Lake Erie, and the other upper Great Lakes, lends credence to the belief that the sea lamprey entered Cayuga Lake by way of the "Champlain Sea" or the Hudson-Champlain estuary and Mohawk outlet. Presumably, a sufficient supply of large host fishes in the lake made possible the establishment of a landlocked form of the sea lamprey.

To date, size is the only morphological difference recorded between the marine form and the landlocked form. The landlocked sea lamprey in Cayuga Lake attains approximately one-half to two-thirds the length of the marine form.

SIZE, GROWTH, AND MORPHOMETRY OF THE SEA LAMPREY

Length Composition

The sea lamprey of Cayuga Lake has often been termed the dwarf form of the species. A misconception of its relatively small size was one of the principal factors that prompted many authors to consider it a separate subspecies.

During the 3-year period 1950–52 the mean total length of 3,363 sea lampreys captured in Cayuga Inlet was 15.4 inches; extreme lengths were 8.4 and 21.4 inches. Only unspent, upstream migrants are considered in this discussion. A summary of length measurements, recorded in table 1, is listed according to sex and year of capture. To facilitate a comparison of mean values and their associated variation, these data are diagramed in figure 1. These diagrams are a modification of the type originally employed by Hubbs and Perlmutter (1942). The significance of differences between samples can be judged by com-

TABLE 1.—*Summary of length measurements of sea lampreys captured in Cayuga Inlet*

Year and sex	Number of specimens	Length (inches)			
		Mean	Range	Standard deviation	Standard error
1950					
Male	153	15.2	9.0–19.5	1.72	0.139
Female	92	14.8	10.7–18.7	1.54	.160
Total	508	15.0	8.4–20.7	1.84	.081
1951					
Male	961	15.3	11.0–20.8	1.61	.052
Female	591	15.2	11.3–20.2	1.54	.063
Total	1,917	15.3	11.0–20.8	1.56	.036
1952					
Male	519	15.9	11.1–21.0	1.24	.054
Female	419	15.8	11.5–21.4	1.86	.091
Total	938	15.9	11.1–21.4	1.75	.057

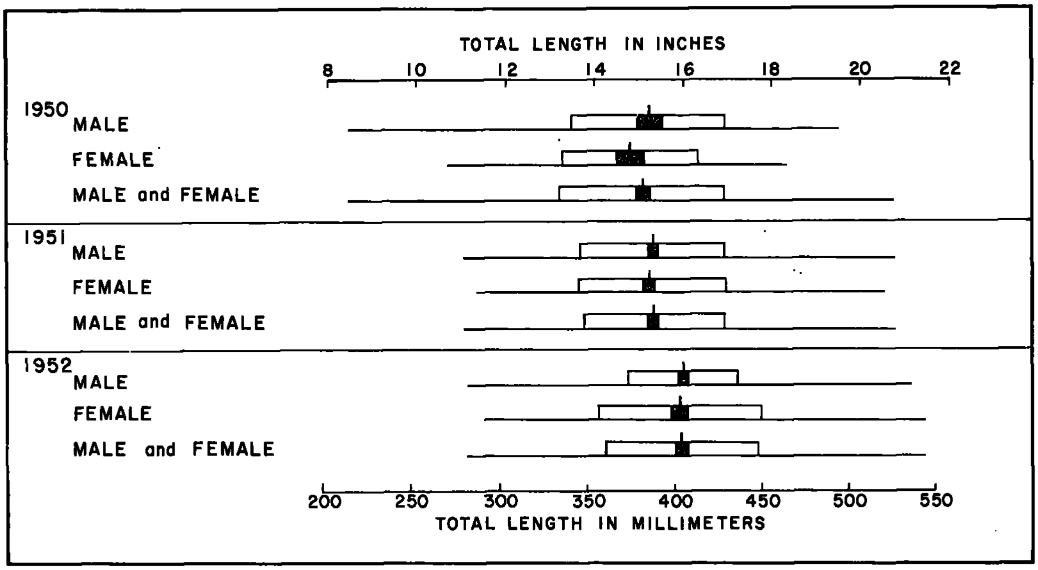

FIGURE 1.—Length composition of Cayuga Lake sea lampreys. The horizontal line represents the total range of variation; the mean is indicated by a vertical bar; the hollow rectangle on each side of the mean represents one standard deviation; the solid rectangle on each side of the mean represents twice the standard error.

paring the standard errors. If the solid rectangles, which represent twice the standard error, of the two samples are of nearly equal length and overlap one another by 10 percent or less, the difference between the means may be considered significant; that is, the probability that the two samples came from the same statistical population is 0.08 or less.

Annual mean lengths for the sexes combined, together with the estimated abundance of sea lampreys, were as follows:

Year	Total length (inches)	Estimated abundance [1]
1950	15.0	10-15,000
1951	15.3	9,390
1952	15.9	4,435

[1] Refer to p. 578 for details pertaining to population estimates.

For 1950, the mean length was calculated from measurements of 508 lampreys. These lampreys were taken relatively early in the migratory period and are thought to be biased in favor of large specimens. Mean lengths for 1951 and 1952 were determined from samples taken regularly throughout the entire migratory period. The 1,917 specimens measured in 1951 represent 20 percent of the estimated spawning population for that year. The 938 specimens measured in 1952 represent 21 percent of the total number in the run.

Mean length of Cayuga Lake sea lampreys increased slightly during the period 1950–52. The successive annual increases in length, 0.3 and 0.6 inch, were statistically significant. In these three years body length was inversely related to the total number of lampreys in each year class.

Total lengths of male lampreys consistently averaged longer than those of females. This difference was small, however, between 0.1 and 0.4 inch, and was not statistically significant.

The histogram of the length composition of adult Cayuga Lake sea lampreys (fig. 2) is based on length measurements of 1,917 specimens captured on their spawning migration in Cayuga Inlet during the spring of 1951.

Weight Composition

The average weight of 3,135 adult sea lampreys captured in Cayuga Inlet in 1950–52 was 4.5 ounces. Extreme weights were 1.4 and 12.1 ounces. A summary of weight measurements (table 2) is recorded according to the year of capture and sex. Diagrams of these data in figure 3 facilitate a comparison of the groups. Only unspent upstream migrants are included in this discussion.

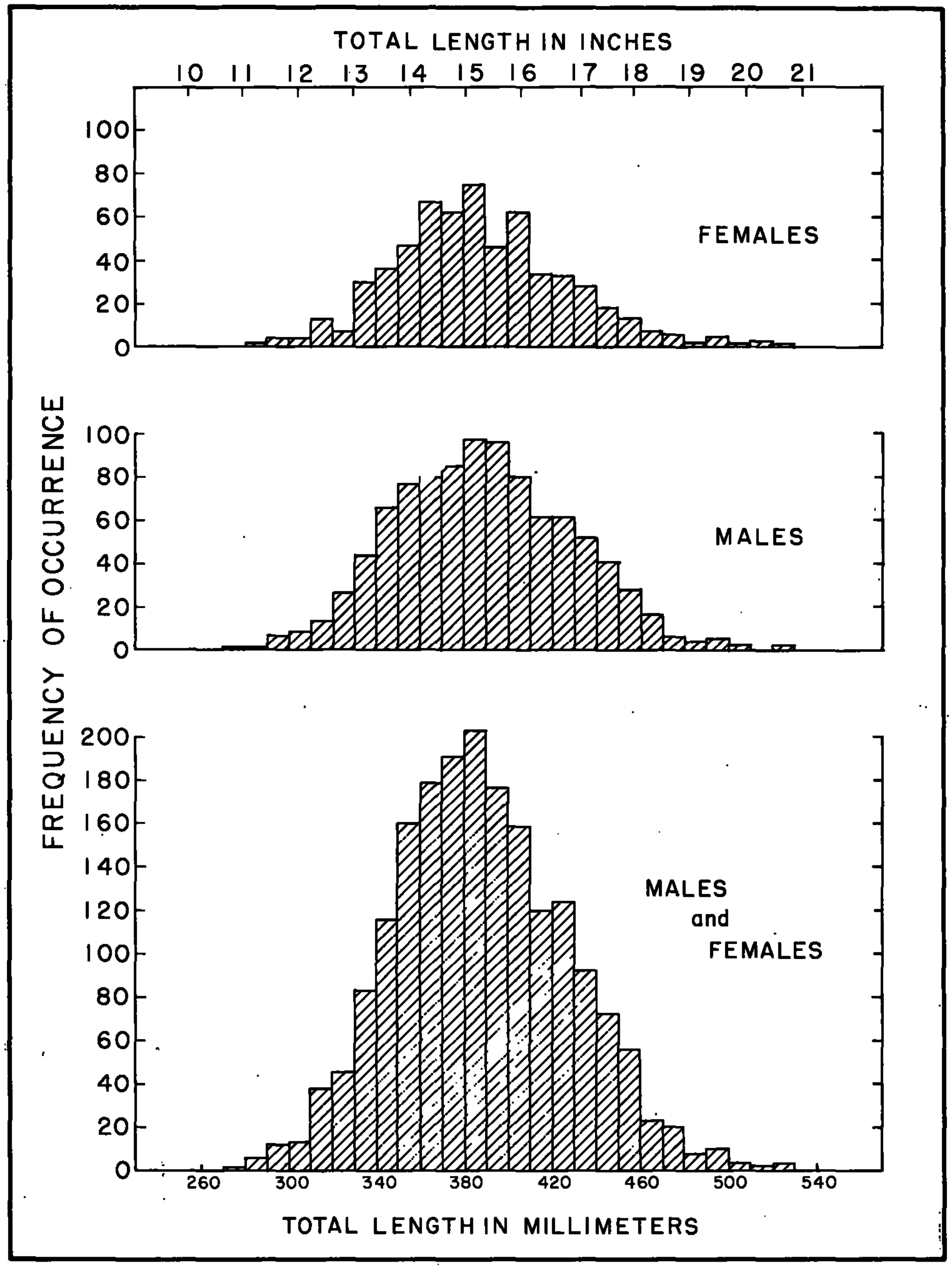

FIGURE 2.—Length-frequency distribution of adult sea lampreys taken in Cayuga Inlet, 1951.

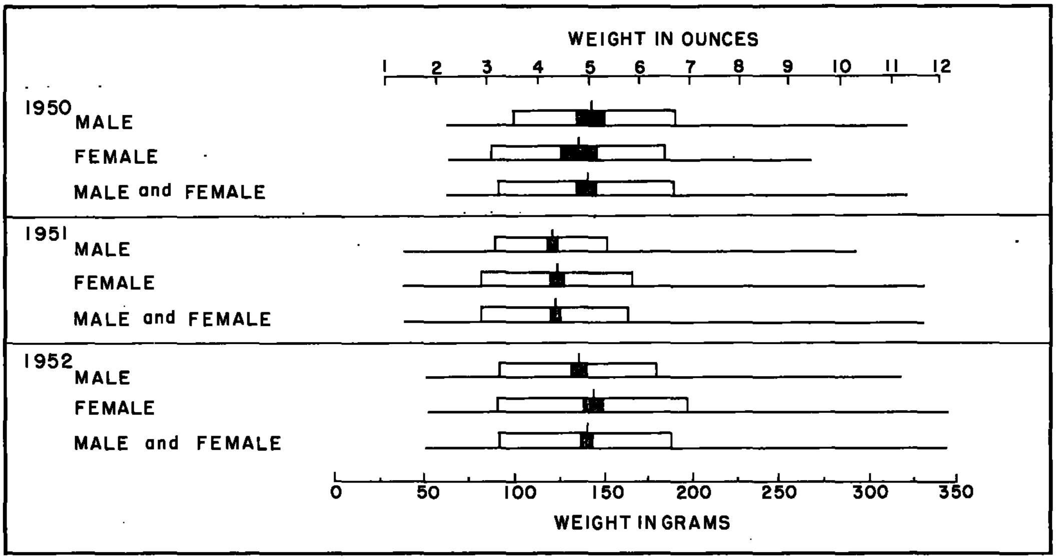

FIGURE 3.—Weight composition of Cayuga Lake sea lampreys. (Description of symbols is given in the caption of fig. 1.)

TABLE 2.—*Summary of weight measurements of sea lampreys captured in Cayuga Inlet*

Year and sex	Number of specimens	Weight (ounces)			
		Mean	Range	Standard deviation	Standard error
1950					
Male	153	4.8	2.2- 9.5	1.81	0.146
Female	92	5.1	2.2-11.3	1.91	.199
Total	245	5.0	2.2-11.3	1.95	.124
1951					
Male	961	4.4	1.4-11.7	1.22	.039
Female	604	4.3	1.4-10.3	1.65	.067
Total	1,968	4.3	1.4-11.7	1.63	.037
1952					
Male	507	5.1	1.8-12.1	1.73	.077
Female	416	4.8	1.8-11.2	2.08	.102
Total	922	4.9	1.8-12.1	1.90	.063

Annual mean body weights for the sexes combined, together with the estimated abundance of lampreys follow.

Year	Mean weight (ounces)	Estimated abundance [1]
1950	(5.0)	10-15,000
1951	4.3	9,390
1952	4.9	4,435

[1] Refer to p. 578 for details pertaining to population estimates.

Mean weight for the 1950 sample, shown in parentheses, was based on 245 specimens, which is approximately 2 percent of the estimated number in the spawning migration. Since they were taken during the early part of the migratory period, it is believed that this sample is biased in favor of unusually large specimens. Mean weights for 1951 and 1952 represent specimens taken throughout the migratory period, and each year 21 percent of the estimated total number were weighed.

The mean weight of sea lampreys differed significantly from year to year. Except for 1950, a biased value, these variations appear to be inversely related to their abundance.

No significant difference could be detected between weights of male and female specimens. In the seasons during which representative samples were measured, however, the females were heavier than males.

During the spring of 1951 a total of 1,968 sea lampreys from Cayuga Inlet were weighed. These data are depicted in figure 4 to illustrate the weight composition of the adult population of Cayuga Lake sea lampreys.

Growth of Parasitic-Phase Sea Lampreys

Evidence has been presented by Applegate (1950) that the sea lamprey in Lakes Huron and Michigan spend between 12 and 20 months in the parasitic phase of life in the lakes proper. Applegate's conclusion was based on measurements of specimens taken from the lakes throughout a 1½-year period. In the spring the newly transformed lampreys and the large mature individuals that were ready to enter the tributaries for spawning differed markedly in size. After the spawning

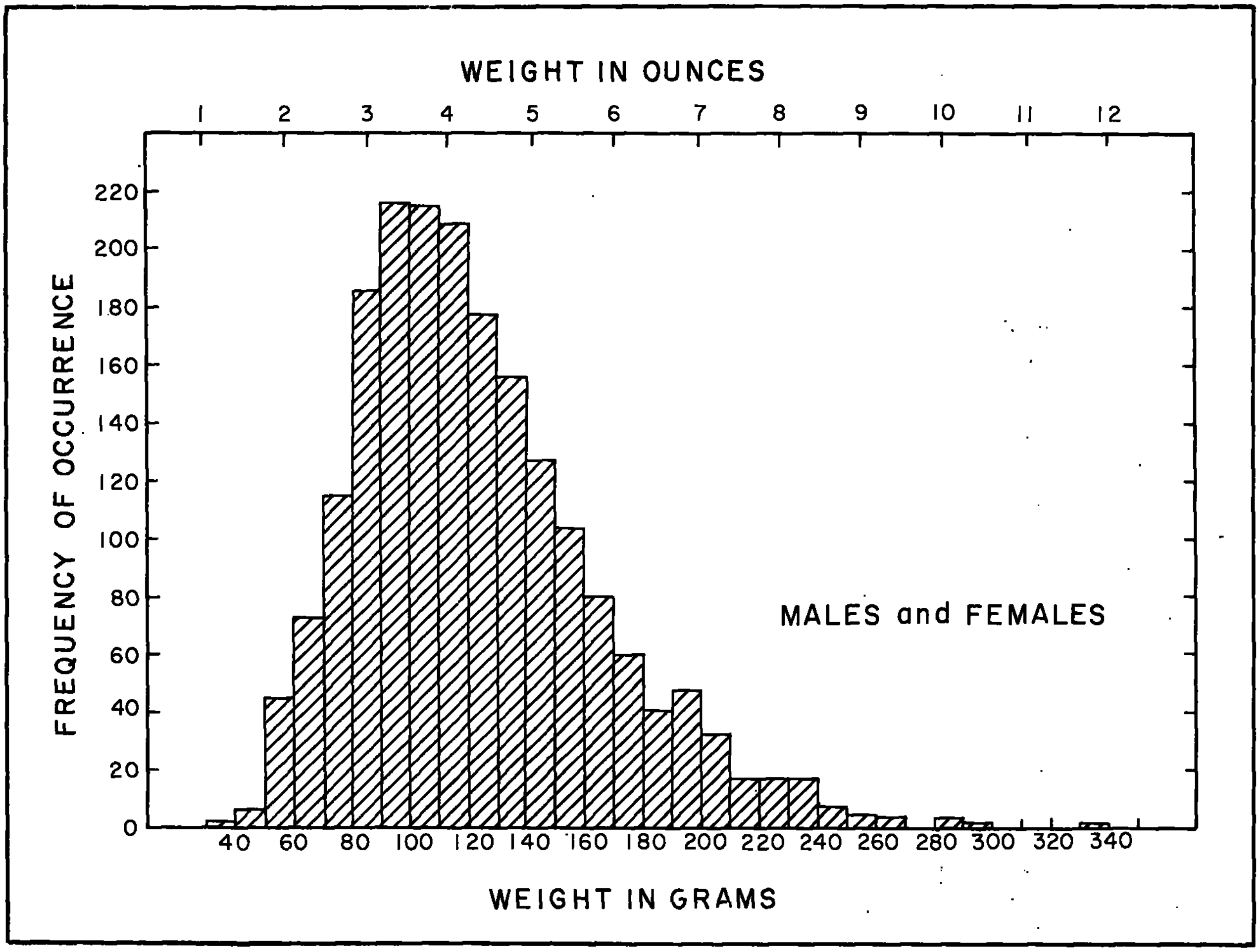

FIGURE 4.—Weight-frequency distribution of adult sea lampreys taken in 1951.

season only the small newly transformed lampreys were found in the lake.

Parasitic-phase sea lampreys taken from Cayuga Lake show the same trend of growth as Lake Huron and Lake Michigan specimens (table 3). These lampreys were captured during the gill-netting of lake trout in 1948–51. Some lampreys were entangled in the net and others adhered to the netted trout. Since both large and small lampreys are caught by this method, these specimens are considered to be representative of the population. Lampreys captured during the several years have been combined because of the small number taken in any one season.

The mean length of parasitic-phase sea lampreys in Cayuga Lake increased from 5.5 inches in March to 15.4 inches in April–May, 13 to 14 months later (table 3). Data given here include adequate

TABLE 3.—*Lengths of parasitic-phase sea lampreys from Cayuga Lake*

Month of capture	Number of specimens	Length (inches)		
		Mean	Minimum	Maximum
August–March [1]	68	5.5	4.6	6.4
April	2	6.1	6.0	6.2
May	2	9.5	8.2	10.8
June	2	11.3	10.5	12.0
July	5	10.3	8.4	12.9
August	7	13.1	11.5	14.5
September	13	12.5	8.4	18.0
October	38	13.9	9.1	19.5
November	1	19.1	19.1	19.1
January	2	15.7	14.6	16.7
April–May [2]	3,363	15.4	8.4	21.4

[1] Recently transformed lampreys captured in Cayuga Inlet.
[2] Mature lampreys captured on their spawning migration in Cayuga Inlet.

samples of newly transformed specimens and adults captured just before spawning. Mean lengths of sea lampreys captured between these two periods exhibited a distinct, if irregular, upward trend. The irregularities can be attributed to the small number of specimens representing most months.

Length-frequency distributions of parasitic-phase sea lampreys taken from Cayuga Lake and Seneca Lake during September and October combined (table 4) offer further strong evidence that only one year class is included in the samples. This finding substantiates the contention that the sea lamprey lives only 1 year (approximately) in the parasitic, feeding stage of life in the lake.

TABLE 4.—*Length-frequency distributions of sea lampreys from Cayuga and Seneca Lakes*

Total length (inches)	Frequency		Total length (inches)	Frequency	
	Cayuga Lake	Seneca Lake		Cayuga Lake	Seneca Lake
8.0– 8.9	1		16.0–16.9	6	16
9.0– 9.9	4		17.0–17.9	2	8
10.0–10.9	6		18.0–18.9	2	6
11.0–11.9	5	2	19.0–19.9	1	3
12.0–12.9	12	5	20.0–20.9		2
13.0–13.9	11	8			
14.0–14.9	9	10			
15.0–15.9	15	15	Mean length	13.7	15.5

Comparison With Size in Other Landlocked Populations

In the two preceding sections evidence was offered that size of Cayuga Lake sea lampreys was inversely related to lamprey abundance. Actually, this relation is more likely to be dependent on the ratio of the number of lampreys to the number of lake trout. This view is supported by comparisons of the sizes of sea lampreys from several areas where some measure of the lamprey-trout ratio is available.

Seneca Lake (N.Y.) is known to have few sea lampreys in relation to the number of lake trout (p. 611). A summary of lengths and weights of a series of sea lampreys from Seneca Lake and a series from Cayuga Lake, all captured during September and October (table 5), shows that the Seneca Lake sea lampreys averaged 1.8 inches (13 percent) longer and 2 ounces (59 percent) heavier than Cayuga Lake specimens.

In Lake Huron the abundance of lake trout has decreased disastrously; at the same time, the numbers of sea lampreys have increased (Hile 1949; Hile, Eschmeyer, and Lunger, 1951). Both factors operating simultaneously tend to reduce the lamprey-lake trout ratio at a rapid rate. As a result, both the length and weight of Lake Huron sea lampreys have decreased. During the 5-year period 1947–51 the average lengths of the upstream migrants in Carp Creek, a Lake Huron tributary, diminished from 17.4 to 15.8 inches (Applegate, Smith, McLain, and Patterson, 1952). The mean length of adult sea lampreys from the Ocqueoc River, another Lake Huron tributary, decreased from 17.1 inches in 1949 to 16.2 inches in 1951 (Applegate 1950; Applegate et al., 1952). Substantial reductions in weight accompanied the decreases in length. It would thus appear that Lake Huron sea lampreys are fast approaching the size of Cayuga Lake specimens, and are already smaller than those from Seneca Lake (table 6).

TABLE 5.—*Summary of lengths and weights of sea lampreys from Cayuga Lake and Seneca Lake*

Locality and years	Number of specimens	Length (inches)			Number of specimens	Weight (ounces)		
		Mean	Minimum	Maximum		Mean	Minimum	Maximum
Cayuga Lake 1948–50	74	13.7	8.4	19.5	44	3.4	1.4	9.2
Seneca Lake 1949–51	74	15.5	11.3	19.7	75	5.4	1.3	9.9

TABLE 6.—*Mean lengths and weights of sea lampreys from Cayuga Lake, Seneca Lake, and Lake Huron, 1951*

Item	Cayuga Lake Cayuga Inlet, April–May	Lake Huron [1]		Seneca Lake, lake proper, September–October [2]
		Carp Creek, April–August	Ocqueoc River, April–August	
Length (inches)	15.3	15.8	16.2	15.5
Weight (ounces)	4.3	4.1	4.6	5.4

[1] Applegate, Smith, McLain, and Patterson, 1952
[2] Seneca Lake specimens would probably attain a length greater than 17 inches and increase considerably in weight by April.

Length-Weight Relation of Adults

Length and weight of 1,906 adult migrant sea lampreys captured in Cayuga Inlet during April and May 1951 are from fresh specimens shortly after capture. This number includes both males and females and represents 20 percent of the estimated number of lampreys in the spawning migration. Lengths and weights (table 7) were derived from specimens sorted into 5-mm. length groups. The regression of weight on length is illustrated in figure 5.

The length-weight relation of Cayuga Lake sea lampreys is remarkably similar to that found by

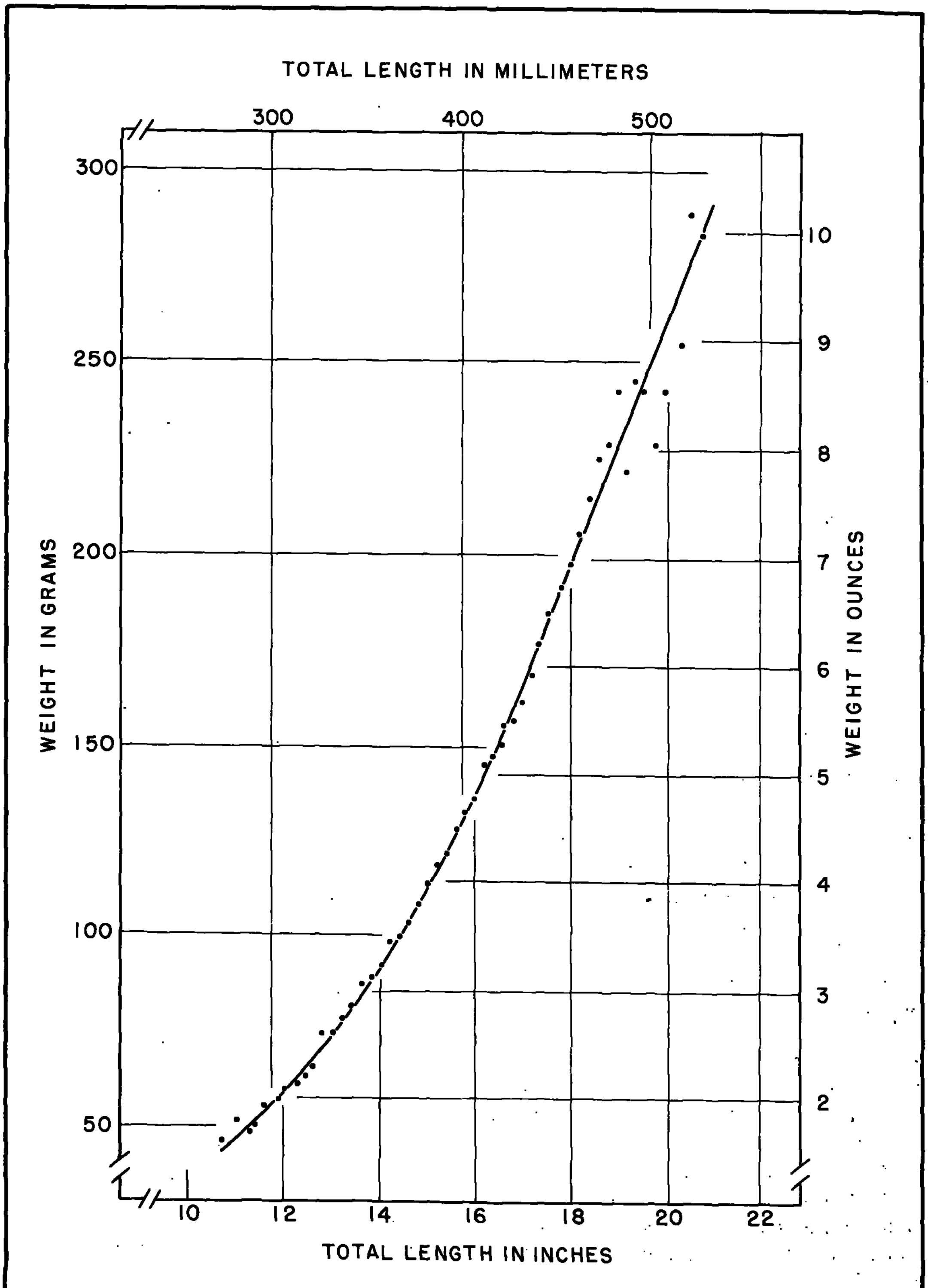

FIGURE 5.—Length-weight relation of adult sea lampreys from Cayuga Inlet, 1951.

Applegate (1950) for Lake Huron specimens. At a length of 10–12 inches their weight increased at a rate of approximately one-half ounce per inch of length. When they reached a length of 18–20 inches their weight increased at a rate of 1 ounce per inch. There was little difference in the length-weight relation between sexes.

TABLE 7.—*Length-weight relation of mature sea lampreys from Cayuga Inlet, April and May 1951*

Number of specimens	Mean length (inches)	Mean weight (ounces)	Number of specimens	Mean length (inches)	Mean weight (ounces)
1	10.7	1.62	79	16.0	4.78
1	11.1	1.80	68	16.2	5.10
2	11.3	1.71	52	16.4	5.18
6	11.5	1.76	69	16.6	5.46
6	11.7	1.94	56	16.8	5.50
10	11.9	2.00	53	17.0	5.69
5	12.0	2.09	42	17.2	5.92
13	12.3	2.16	39	17.4	6.22
17	12.5	2.22	36	17.6	6.50
22	12.7	2.29	29	17.8	6.74
18	12.9	2.62	26	18.0	6.96
44	13.1	2.61	19	18.2	7.25
38	13.3	2.76	11	18.4	7.56
53	13.5	2.80	12	18.6	7.90
63	13.7	3.06	9	18.8	7.68
72	13.9	3.12	3	19.0	8.47
75	14.0	3.24	6	19.1	7.78
88	14.2	3.44	8	19.4	8.65
92	14.4	3.49	2	19.5	8.52
96	14.6	3.62	2	19.7	8.02
78	14.8	3.82	2	20.0	8.47
118	15.0	3.99	1	20.1	11.67
89	15.2	4.15	1	20.3	8.96
94	15.4	4.27	1	20.5	10.16
77	15.6	4.50	2	20.7	9.91
100	15.8	4.66			

Detailed data, not given here, revealed a rather wide variation in weight among individuals of the same length and sex. The range was approximately an ounce for specimens 12 inches long and increased to 4 ounces for 20-inch specimens.

Morphometry

Taxonomists frequently employ body proportions as an aid in determining the taxonomic status of many animal groups, including the lampreys. Inasmuch as body proportions differ between the sexes and change with age and size, it becomes necessary first to determine the extent of these differences before valid comparisons between taxonomic categories can be undertaken. From the systematist's point of view it is just as important to know which characteristics remain constant as to know the degree of variation of the changing characteristics.

The methods of measurement and much of the terminology are those described by Hubbs and Trautman (1937).

Seasonal changes and sexual differences in body proportions

In this discussion, each of the principal sections of the sea lamprey's body has been dealt with separately to describe the relative size and sexual dimorphism during three significant periods of its life: September–October, May, and June. In September to October the sea lamprey is considered to have reached "normal" adult form. Changes accompanying sexual maturity become evident during May. By June, gross morphological modifications that are typical of spawning adults have been attained.

All measurements of body parts have been expressed as thousandths of the total length. Separate tables (nos. 8–12) have been compiled for each body section. The data in these tables are listed according to sex and collecting period, and include a frequency distribution, mean values, and measures of variation. (See figure 6.) It should be kept in mind that changes in proportional measurements of a particular body section that ostensibly appear to be increases or decreases in size, may be the result of changes in other body sections that affect the total body length.

Length over gill openings.—Length over the gill openings was the only body section that differed significantly between the sexes during the September–October period; males had the larger component (table 8). During May and June there was no difference between the sexes in this characteristic. As the season progressed, the relative length over

TABLE 8.—*Relative length over gill openings of Cayuga Lake sea lampreys in 3 collecting periods*

[Expressed as thousandths of the total length]

Relative length over gill openings	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
80–89	8	9	17						
90–99	27	12	39	12	9	21			
100–109	2	2	4	15	7	22	27	13	40
110–119				1		1	29	16	45
120–129								3	3
Mean ratio	93	88	91	101	99	100	110	111	110
Standard deviation	4.2	6.9	5.9	3.6	4.1	4.6	5.9	5.7	5.8
Standard error	0.7	1.4	0.8	0.7	1.0	0.7	0.8	1.0	0.6
Number of specimens	37	23	60	28	16	44	56	32	88
Mean total length (inches)	13.7	13.6	13.7	15.9	14.8	15.5	14.5	13.3	14.1

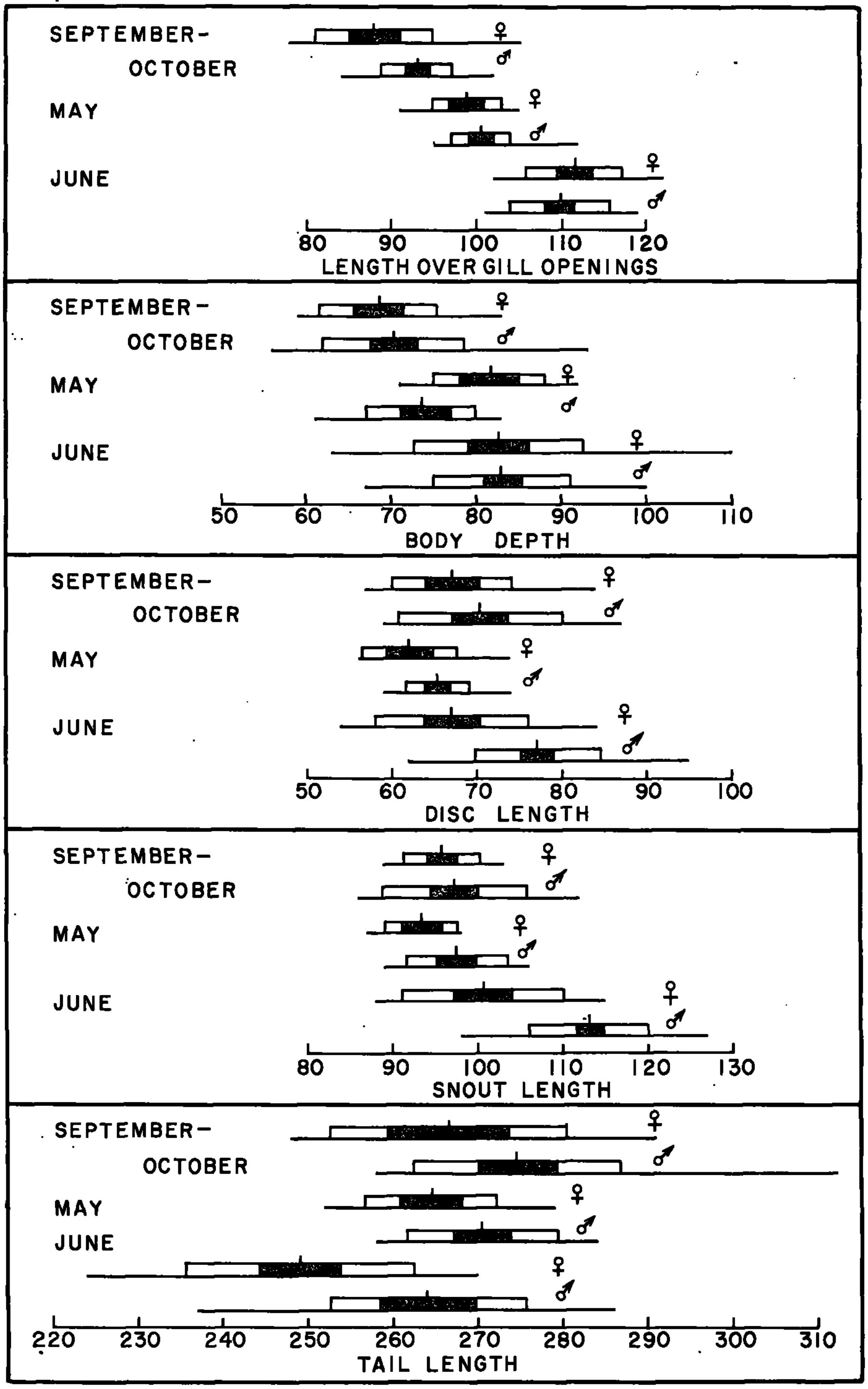

FIGURE 6.—Graphic comparison of proportional measurements of male (♂) and female (♀) sea lampreys captured in Cayuga Lake and Cayuga Inlet. Measurements are given in thousandths of the total length. (Description of symbols in caption of fig. 1.)

the gill openings increased from about ninety one-thousandths of the total body length in September–October to approximately one hundred and ten one-thousandths in June.

Body depth.—Body depth of male and female specimens was approximately equal in September–October and June, but in May, before egg deposition, the females were considerably deeper bodied than males (table 9). Males increased in body depth at a nearly constant rate from September–October through June. However, the females increased in depth very rapidly prior to spawning (May), but changed very little thereafter.

Disc length.—Males and females had discs (mouths) of about the same relative size during September–October and May (table 10). In June, the proportional disc length of male specimens was considerably larger than that for females. The disc size remained nearly constant throughout the entire year except for a slight decrease in both sexes in May and a great enlargement in male specimens in June. This difference was distinct enough to be useful in the field as an aid in determining sexes.

Snout length.—Length of the snout changed in much the same manner as the disc length (table 11). Only in June did the proportional snout length differ greatly between the sexes; in this month the males possessed the larger snouts. Only minor seasonal changes were evident except for the June specimens, at which time the size of the snout of males increased considerably.

TABLE 9.—*Relative body depth of Cayuga Lake sea lampreys in 3 collecting periods*

[Expressed as thousandths of the total length]

Relative body depth	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
50–59	1	1	2						
60–69	19	13	32	7		7	3	2	5
70–79	13	8	21	17	6	23	14	10	24
80–89	3	1	4	4	9	13	32	14	46
90–99	1		1		1	1	8	3	11
100–109							1	1	2
110–119								1	1
Mean ratio	70	68	69	73	81	76	83	83	83
Standard deviation	8.4	6.9	8.5	6.3	6.6	7.4	8.1	10.0	8.8
Standard error	1.4	1.4	1.1	1.2	1.6	1.1	1.1	1.8	0.9
Number of specimens	37	23	60	28	16	44	58	31	89
Mean total length (inches)	13.7	13.6	13.7	15.9	14.8	15.5	14.5	13.4	14.1

TABLE 10.—*Relative length of the disc of Cayuga Lake sea lampreys in 3 collecting periods*

[Expressed as thousandths of the total length]

Relative length of disc	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
50–59	2	3	5	1	4	5		8	8
60–69	18	12	30	24	12	36	7	10	17
70–79	11	7	18	3		3	32	12	44
80–89	6	1	7				16	2	18
90–99							3		3
Mean ratio	70	67	69	65	62	64	77	67	73
Standard deviation	9.7	7.2	9.0	3.8	5.6	3.0	7.5	9.0	9.4
Standard error	1.6	1.5	1.2	0.7	1.4	0.5	1.0	1.6	1.0
Number of specimens	37	23	60	28	16	44	58	32	90
Mean total length (inches)	13.7	13.6	13.7	15.9	14.8	15.5	14.5	13.3	14.1

TABLE 11.—*Relative length of the snout of Cayuga Lake sea lampreys in 3 collecting periods*

[Expressed as thousandths of the total length]

Relative length of snout	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
80–89	6	1	7	1	2	3		3	3
90–99	17	18	35	18	14	32		10	10
100–109	12	4	16	9	0	9	18	14	32
110–119	2		2				30	4	34
120–129							10		10
Mean ratio	97	96	97	97	93	96	113	101	109
Standard deviation	8.5	4.7	6.9	6.0	4.3	5.2	6.9	9.5	10.4
Standard error	1.4	1.0	0.9	1.1	1.1	0.8	0.9	1.7	1.1
Number of specimens	37	23	60	28	16	44	58	31	89
Mean total length (inches)	13.7	13.6	13.7	15.9	14.8	15.5	14.5	13.3	14.1

Tail length.—Tail length of male lampreys averaged larger than that for females during each collecting period (table 12). The differences were not large, however, until June. As the seasons progressed from fall to spring, the relative tail length consistently decreased. Tail length was the only body section in which relative size decreased. From September–October to May the change was small, but a marked decrease took place between May and June, especially in females.

Summary.—Sexual dimorphism during September–October was exhibited only by the length over the gill openings. In May, only body depth showed any appreciable differences in the sexes.

In the June collections the disc length, snout length, and tail length showed distinct differences between males and females.

Seasonal changes in the various body sections were somewhat erratic. In general, the relative size of all body sections except tail length tended to increase as the seasons progressed from September–October through June. The tail length decreased during this period.

TABLE 12.—*Relative length of the tail of Cayuga Lake sea lampreys during 3 collecting periods*

[Expressed as thousandths of the total length]

Relative length of tail	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
220–229								4	4
230–239							1	1	2
240–249		2	2				5	11	16
250–259	4	4	8	1	5	6	10	9	19
260–269	4	4	8	11	6	17	23	6	29
270–279	11	2	13	12	5	17	17	1	18
280–289	8	3	11	4		4	2		2
290–299		1	1						
300–309									
310–319	1		1						
Mean ratio	274	266	272	271	264	269	264	249	259
Standard deviation	12.2	14.1	14.0	8.8	7.9	9.2	10.8	13.3	14.9
Standard error	2.3	3.5	2.1	1.6	2.0	1.4	1.4	2.4	1.6
Number of specimens	28	16	44	28	16	44	58	32	90
Mean total length (inches)	14.3	14.3	14.3	15.9	14.8	15.5	14.5	13.3	14.1

Morphometric Comparison of Cayuga Lake and Seneca Lake Sea Lampreys

Sea lampreys from Seneca Lake superficially appeared to be longer and proportionately greater in body girth than specimens from Cayuga Lake. Even though the two lakes are connected by the Seneca River (Barge Canal), because of the location of the interconnecting river in relation to the deepwater areas of the lake, it was thought that little interchange of sea lampreys takes place between the two. In view of these conditions it was desirable to make a taxonomic comparison of specimens from the two lakes. Body proportions and the number of teeth[3] and myomeres were compared.

Body proportions.—Measurements of the following body sections were taken from collections of sea lampreys captured in both lakes during September and October: body depth, disc length,

TABLE 13.—*Relative body depth, disc length, snout length, and length over gill openings of sea lampreys from Cayuga Lake and Seneca Lake*

[Expressed as thousandths of the total length]

Length classes	Body depth		Disc length		Snout length		Length over gill openings	
	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake
50–59	2		5	17				
60–69	32	2	30	46				
70–79	21	37	18	12				
80–89	4	30	7		7	8	7	23
90–99	1	5			35	54	39	46
100–109					16	13	4	3
110–119					2			1
Mean ratio	69	80	69	63	97	95	91	92
Standard deviation	8.5	6.8	9.0	5.8	6.9	5.5	5.9	5.1
Standard error	1.1	0.8	1.2	0.7	0.9	1.3	0.8	0.6
Number of specimens	60	74	60	74	60	74	60	74
Mean total length (inches)	13.7	15.5	13.7	15.5	13.7	15.5	13.7	15.5

TABLE 14.—*Relative length of tail of sea lampreys from Cayuga Lake and Seneca Lake*

[Expressed as thousandths of the total length]

Length classes	Cayuga Lake	Seneca Lake
220–229		1
230–239		
240–249	2	1
250–259	8	11
260–269	8	25
270–279	13	25
280–289	11	8
290–299	1	3
300–309		1
310–319	1	
Mean ratio	272	270
Standard deviation	14.0	13.5
Standard error	2.1	1.6
Number of specimens	44	75
Mean total length (inches)	14.3	15.5

snout length, length over the gill openings, and tail length (tables 13 and 14; fig. 7). Comparison of these data revealed a very close agreement in the relative size of snout length, length over gill openings, and tail length in specimens from the two lakes. Distinct differences between the two samples were disclosed in the relative length of the disc and body depth.

In the previous section it was shown that disc length decreased proportionately with normal (nonbreeding) growth, and that body depth increased proportionately with normal growth. Since the Seneca Lake specimens were larger and their body proportions were consistent with changes accompanying additional growth—i.e., disc length was smaller and body depth greater—these differences were considered to be of environmental rather than genetic origin.

[3] The terms "tooth" and "teeth" are used in the broadest sense of their meaning; the sea lamprey's dental armature, consisting of cornified epithelium, does not represent true teeth.

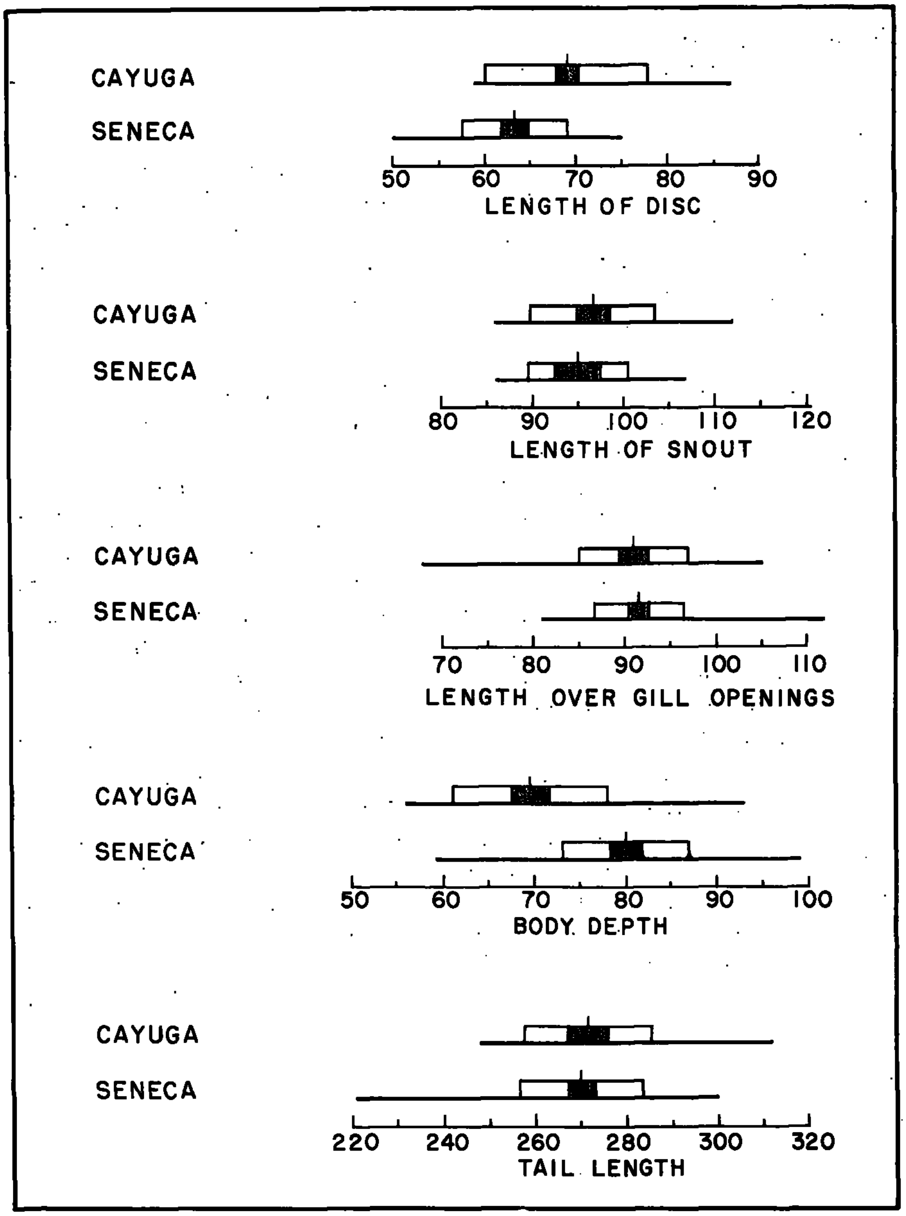

FIGURE 7.—Comparison of body sections of sea lampreys from Cayuga Lake and Seneca Lake. Measurements are given in thousandths of the total body length. (Description of symbols in caption of fig. 1.)

Teeth and myomeres.—Methods outlined by Hubbs and Trautman (1937) were followed in counting teeth and myomeres. Many of the difficulties they encountered in work on *Icthyomyzon* were present also in work on *Petromyzon*. Most troublesome was the myomere count on immature specimens, especially those that had been preserved for several years. In such specimens, the myomeres were nearly indistinguishable externally. It was necessary to slit the abdomen lengthwise, in the ventrolateral area, and count the muscle bands.

In addition to the myomeres the following series of teeth or cusps were counted: Cusps on the supraoral lamina; number of biscuspid circumorals; teeth in the anterior row; cusps on the lateral lingual lamina; cusps on the transverse lingual lamina; teeth in the lateral row; teeth in the circumoral row; and cusps on the infraoral lamina.

Variation was nil or slight in three characters: supraoral cusps; bicuspid circumorals; and the anterior row. The number of cusps on the supraoral lamina was 2 in all of the 176 specimens from Cayuga Lake and 106 from Seneca Lake. The number of bicuspid circumorals was 8 in 171 specimens of a sample of 173 from Cayuga Lake (the other 2 counts were 6 and 9) and in all 75 from Seneca Lake. The number of teeth in the anterior row was 3 in all 73 Cayuga Lake specimens. In Seneca Lake lampreys the anterior row count was 3 in 164 of 174 specimens; 9 had a count of 4, and 1 a count of 2, which gave a mean of 3.05.

Other tooth counts exhibited greater variability (table 15; fig. 8). The number of infraoral cusps ranged from 7 to 10 in Cayuga Lake lampreys (average of 8.02) and from 6 to 10 in Seneca Lake specimens (average of 7.69). In specimens whose infraoral cusps had been worn down, the outer covering was ready to be sloughed off. Invariably the distal ends of the lamina in these specimens were so constricted as to make it difficult to count the cusps. Removal of this outer sheath, however, exposed the underlying sharp, distinct cusps that could be counted accurately.

The number of teeth in the circumoral row averaged 18.3 for both Cayuga Lake and Seneca Lake samples. The number of circumoral teeth ranged from 15 to 22 in Cayuga Lake specimens and from 16 to 20 for Seneca Lake specimens. Undoubtedly the greater number of specimens examined from Cayuga Lake (174), as opposed to 75 from Seneca Lake, contributed to the greater range of this character observed in the Cayuga Lake sample.

The number of teeth in the lateral row varied little. Cayuga Lake specimens had an average of 7.3 lateral teeth (range, 5 to 8). Seneca Lake specimens had significantly fewer teeth in the lateral row, an average of 7, with extremes of 6 and 8.

Denticulations on the lingual lamina are well developed and never seemed to be so dull or worn as the circumoral teeth. For ease and accuracy in making counts of both the transverse and lateral lingual lamina, the tongue was excised.

The number of cusps on the transverse lingual lamina of Cayuga Lake specimens ranged from 12 to 19, and averaged 14.8. In Seneca Lake specimens the count varied from 12 to 18 and averaged 14.6. This small difference between the two groups was not significant.

Cusps on the lateral lingual lamina of Cayuga Lake specimens ranged from 9 to 15 and averaged 12.6. In Seneca Lake specimens the count varied from 9 to 17, with an average of 12.5. This difference between Cayuga Lake and Seneca Lake specimens was not statistically significant.

Sea lampreys from Seneca Lake had a greater number of myomeres (average, 72.7; range, 67–76) than Cayuga Lake specimens (average 71.4; range, 68–75: table 16). This difference in number of

TABLE 15.—*Counts of cusps and laminae on sea lampreys from Cayuga Lake and Seneca Lake*

Number of cusps or laminae	Lateral lingual lamina		Transverse lingual lamina		Lateral row		Circumoral row		Infraoral cusps	
	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake
5					1					
6					15	14				2
7					95	52			47	24
8					63	9			81	37
9	2	1							46	10
10	2	4							2	1
11	13	24								
12	27	46	1	3						
13	27	39	11	11						
14	17	24	10	22						
15	5	2	10	23			1			
16		1	9	9			1	1		
17		1	5	4			12	2		
18			1	2			96	43		
19			1				59	26		
20							4	3		
21										
22							1			
Mean	12.6	12.5	14.8	14.6	7.3	7.0	18.3	18.3	8.0	7.7
Standard deviation	1.4	1.3	1.5	1.3	0.7	0.6	0.8	0.8	0.8	0.8
Standard error	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1
Number of specimens	[1] 48	[1] 71	48	74	174	75	174	75	176	74

[1] Both left and right lateral lingual laminae are grouped together. The discrepancy in numbers results from broken laminae.

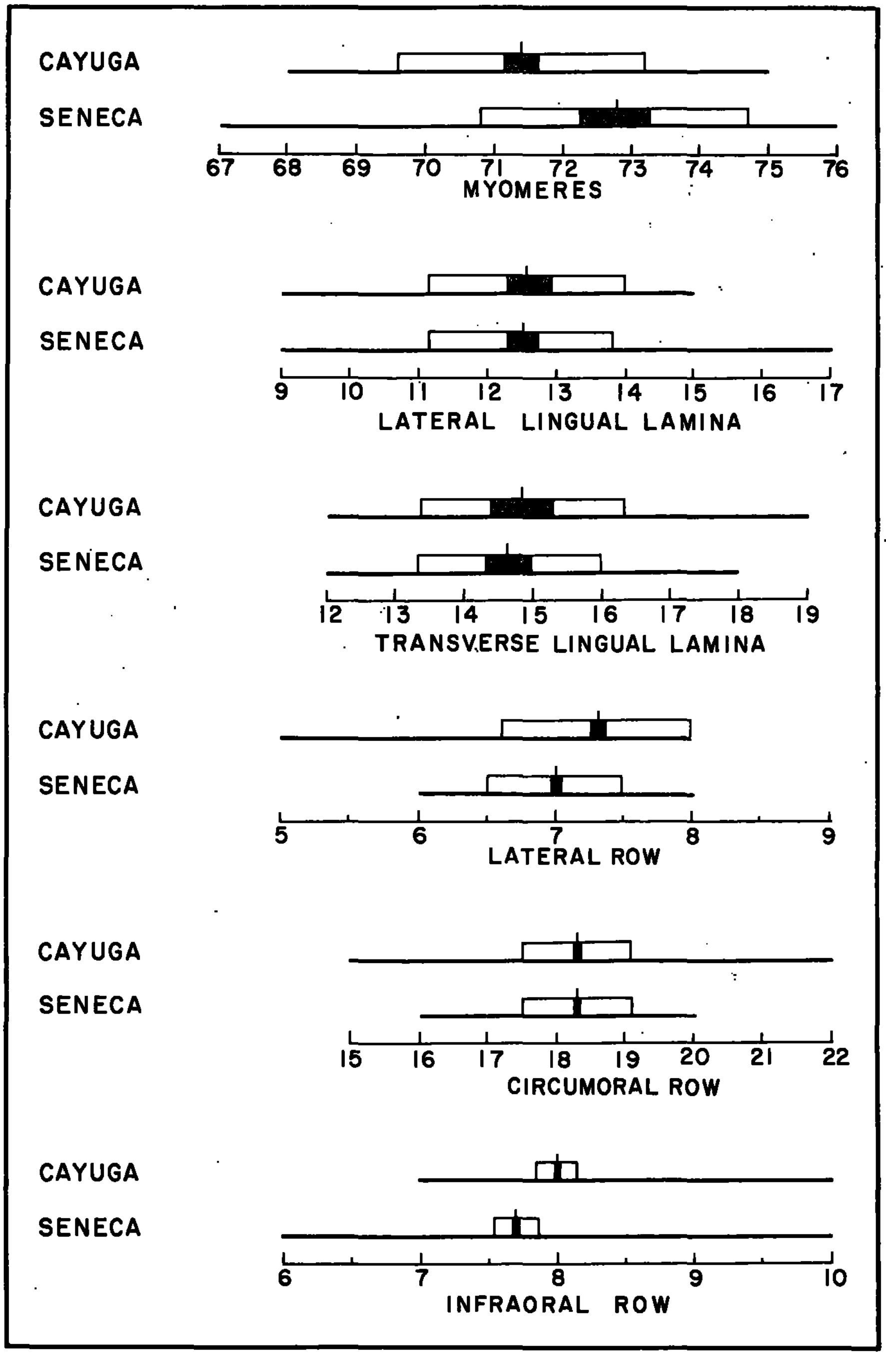

FIGURE 8.—Comparison of tooth and myomere counts of Cayuga Lake and Seneca Lake sea lampreys. (Description of symbols in caption of fig. 1.)

myomeres between the stocks is statistically significant. Even though the process of making a myomere count is slow, tedious, and subject to error, it is one of the most useful meristic characters for determining specific and infraspecific categories of lampreys.

Of all counts (teeth and myomeres) described in the preceding paragraphs, only three characters exhibited a significant difference between the Cayuga Lake and Seneca Lake stocks: number of cusps on the infraoral lamina; number of teeth in the lateral row; and the number of myomeres. A better grasp of the magnitude of differences between Cayuga Lake and Seneca Lake stocks is gained by further analysis of these three characters.

A divergence between the two populations in number of cusps on the infraoral lamina was found to be 56.2 percent. The divergence in number of teeth in the lateral row was 62.5 percent, and the divergence in the number of myomeres was 66.8 percent. Since the number of laminae cusps, teeth, and myomeres are believed to be genetic, and since the average divergence of these characters differ at the racial level, it follows that Cayuga Lake sea lampreys are to be considered a separate race from Seneca Lake sea lampreys.

TABLE 16.—*Myomere counts on sea lampreys from Cayuga Lake and Seneca Lake*

Number of myomeres	Cayuga Lake	Seneca Lake
67	------	1
68	7	------
69	20	------
70	28	7
71	34	8
72	42	9
73	25	17
74	19	8
75	4	12
76	------	1
Mean	71.4	72.7
Standard deviation	1.8	2.0
Standard error	0.1	0.2
Number of specimens	179	63

SPAWNING MIGRATION

Tributaries of Cayuga Lake

Each spring the sea lampreys pass from the depths of Cayuga Lake into the tributary streams to find suitable spawning sites. Practically all the tributaries of the lake have natural barriers near the mouth, a circumstance which substantially limits the available spawning area. The only tributaries that could possibly provide an appreciable amount of nesting territory are: Sawyer Creek, Salmon Creek, Fall Creek, Cascadilla Creek, Sixmile Creek, Cayuga Inlet, Taughannock Creek, and Canoga Creek (fig. 24).

Sea lampreys have never been reported from Sawyer Creek, Salmon Creek, or Canoga Creek, nor were they found in these creeks during this study. A few adults were seen in all the remaining streams mentioned except Sixmile Creek. However, nesting or spawning lampreys were found only in Taughannock Creek and Cayuga Inlet. Just four pairs of nesting lampreys are known to have utilized Taughannock Creek, whereas each year thousands of lampreys have been observed spawning in Cayuga Inlet. Thus, Cayuga Inlet is the only tributary of Cayuga Lake that has significant value for lamprey reproduction.

Water Conditions in Cayuga Inlet

The middle and lower portions of Cayuga Inlet exhibit water conditions typical of a marginal trout stream. At the U.S. Geological Survey dam, 5 miles upstream from the lake, the waterflow varied between 63 and 18 cubic feet per second during the period April 25 to May 23, 1951 (fig. 9). The minimum and maximum morning (7 to 8 a.m.) water temperatures during this period were 42° and 64° F. Volume of flow was greatest early in the season and decreased steadily throughout the period, with the exception of a flood which occurred on May 11. As the water volume decreased the water temperature gradually increased, reaching its highest value (64° F.) on May 22, the time of lowest waterflow (18 c.f.s.).

Migratory Behavior

Sea lampreys are believed to assemble at the mouth of Cayuga Inlet in early spring (February and March). When water from Cayuga Inlet becomes warmer than the lake water, they begin moving into the deep lower portion of the inlet. They do not move into shallow waters until the evening water temperatures reach nearly 50° F., a value usually not attained until the latter part of April. The year's first specimens were captured in Cayuga Inlet on May 4, 1950,[4] April 22, 1951, and April 19, 1952.

Water temperature and lamprey activity are closely correlated. After the lampreys arrive in the shallow portions of the stream, a drop in water temperature to the low forties drastically retards activity. Upstream migration nearly ceases, and even when handled the lampreys do not react with as much vigor as they show when temperatures are higher.

Early migrants move upstream only during darkness, hiding under rocks, logs, and debris during the daylight hours. As the season progresses their aversion to light gradually disappears and

[4] Sea lampreys are believed to have arrived in Cayuga Inlet at least 1 week prior to their capture in 1950.

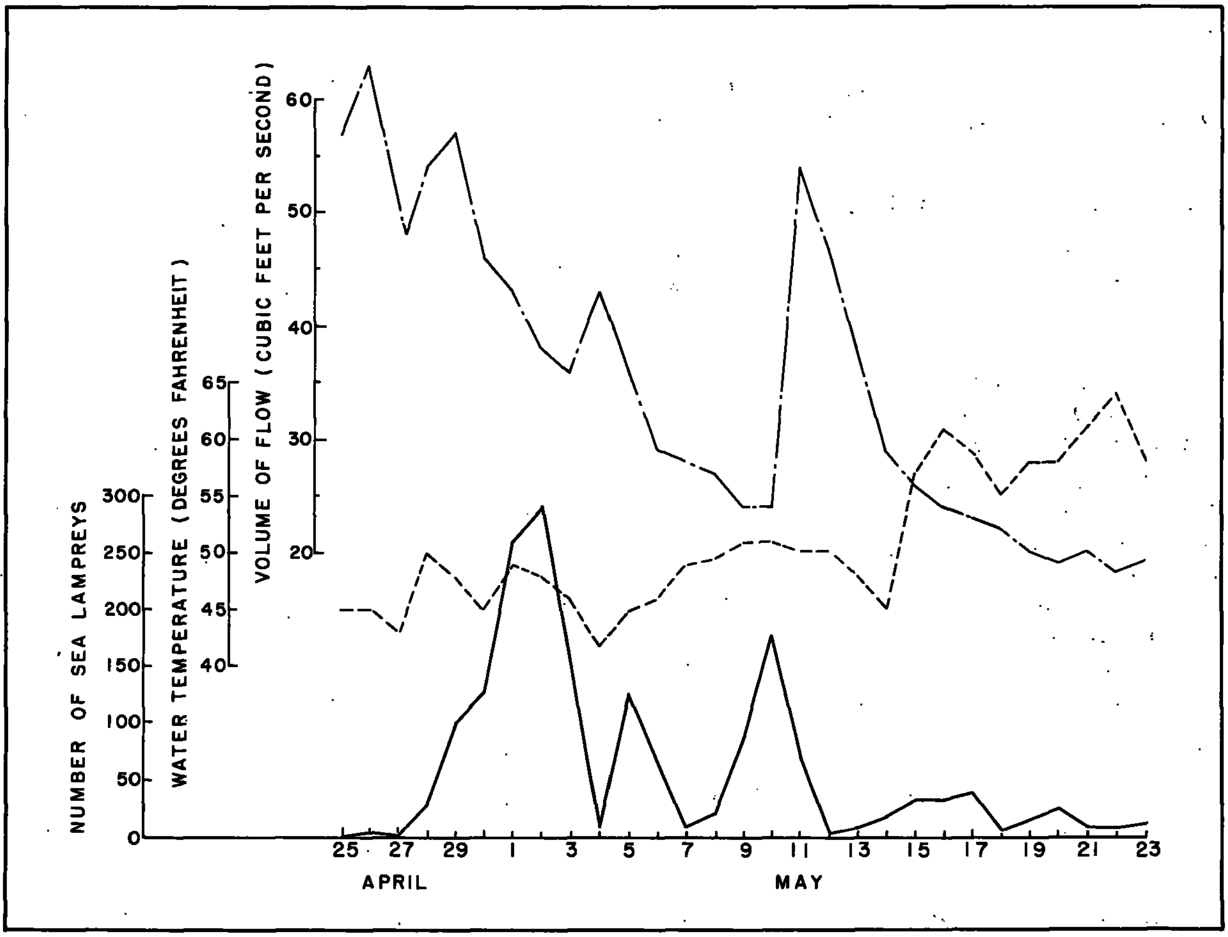

FIGURE 9.—Daily morning water temperature, average daily waterflow, and number of upstream-migrant sea lampreys captured at the U.S. Geological Survey dam, 1951.

blindness afflicts many; consequently, late arrivals move upstream during the daytime.

In favorable locations, lampreys often hide during the day in groups of several hundred. The individuals in these groups usually maintain their position by adhering with their buccal discs to solid objects below which they are hiding, or to each other. Notable exceptions were clusters of approximately 25 or 30 which were hiding during the daytime under the concrete apron (fig. 11) of the U.S. Geological Survey dam. These lampreys were packed side by side between the underside of the apron and the stream bottom, forming a mass approximately 6 inches deep and 10 inches wide. The mouths of many were plainly seen; they were open, but were not attached to any object. This behavior was observed on several occasions between May 9 and 16, 1952.

Upstream-migrant sea lampreys held in hatchery troughs invariably clung to the end of the trough where the water entered. They were so aggressive when disturbed that cover screens had to be held in place by cleats. These confined lampreys performed a search pattern of varying intensity that was closely associated with their state of nervousness. In an undisturbed group, a single lamprey left its position in the mass, backed out, slowly explored the sides of the trough, and returned to the mass. About the time one returned another backed out and explored the trough. This routine was repeated continually although not always with such precision. The number of exploring lampreys and the rapidity of their movements were in direct proportion to their state of excitement. If the group was greatly excited, all specimens frantically searched the trough for an exit.

If undisturbed for half a day or so, searches were conducted by single individuals departing at intervals of several minutes. This same type of searching activity was also performed by sea lampreys in their natural habitat in Cayuga Inlet.

Population Estimates of Spawning Adults

Each spring during the years 1950, 1951, and 1952 an estimate of the number of adult upstream-migrant sea lampreys in Cayuga Inlet was made by the mark-and-recapture method. Due to the lack of trapping devices and a suitable tag in 1950, the population estimate is questionable. Adequate facilities in 1951 and 1952 permitted the use of more accurate methods and the results were most satisfactory.

To facilitate the designation of locations in Cayuga Inlet, the stream was divided into eleven 1-mile sections assigned letters A to K from the lowermost section to the one farthest upstream. These sections conform somewhat to natural physical areas of the stream (fig. 10).

1950

It is estimated that 10,000 to 15,000 sexually mature sea lampreys entered Cayuga Inlet in the spring of 1950. This estimate is based on the results of a mark-and-recapture study in addition to three indices of abundance that are related to lamprey population density. These indices were sex ratio of lampreys in the spawning migration, size of migrant lampreys, and the incidence of lamprey attacks on lake trout. These indices of abundance were used in conjunction with accurate estimates of lamprey abundance obtained for 1951 and 1952.

A mark-and-recapture study was conducted during May 15 to May 24, 1950. Sea lampreys were captured by hand in Cayuga Inlet between Newfield station and Cayuga Lake; most were caught at the U.S. Geological Survey dam and at Newfield station. A white plastic disc 7/16-inch diameter, connected to a No. 10 Mustad-Best Kirby fishhook by a silver link, was attached to the lamprey through the median dorsal ridge just anterior to the first dorsal fin. In addition to this tag a notch was made in the dorsal fin of each specimen with a paper punch. Ninety-five marked lampreys were released in section *E*, 54 in section *A*, and 59 1½ miles downstream from section *A*. Dates and numbers of lampreys

TABLE 17.—*Estimate of the number of sea lampreys in the 1950 spawning migration in Cayuga Inlet*

Date	Number lampreys captured	Number of tagged sea lampreys at large	Product	Sum of product	Tagged sea lampreys recaptured		Estimated population
					Number per day	Sum	
	(A)	(B)	(AB)	(ΣAB)	(C)	(ΣC)	(P) [1]
May 15	186	109	20,274	20,274	1	1	20,274
May 17	50	154	7,700	27,974	1	2	13,987
May 20	96	208	19,968	47,942	----------	2	23,971
May 23	69	208	14,352	62,294	2	4	15,574
May 24	126	208	26,208	88,502	8	12	7,375
Total	527	----------	----------	88,502	----------	12	[2] 7,375

[1] $P = \frac{\Sigma AB}{\Sigma C}$.

[2] The 95-percent confidence limits are 4,210 and 12,950.

tagged and recaptured are included in table 17.

Due to a high percentage loss of tags, most of the recaptured specimens were identified from the notch made in the first dorsal fin and the wound remaining where the tag had been attached. As a result, it was impossible to determine the date they had been released. Since the date of release is a requisite for use of the Schaefer (1951) method of estimating abundance, the Schnabel method [5] was employed.

Estimates of abundance from this study varied from 7,375 to 23,971 (last column of table 17). These rather wide fluctuations in the abundance estimates are attributed to the small number of lampreys utilized in this study: total catch of 527, 208 tagged, 12 recaptured. Because of the erratic results only a very general interpretation of the data is permissible, that the 1950 migration consisted of between 7,375 and 23,971 sea lampreys.

Indices of abundance based on other characteristics of lamprey stocks that are associated with population density yielded more consistent values. The sex ratio of the 1950 spawning migration (table 26) indicates a population of 10,000–12,000 lampreys. Length composition of the 1950 spawning migration (p. 562) indicates a population of 11,000–12,000. The incidence of lamprey attacks on lake trout in 1949 (table 45) indicates a population of approximately 15,000.

The weight of evidence from both the mark-and-recapture results and the other data on density of the lamprey population support the conclusion that the 1950 spawning migration consisted of between 10,000 and 15,000 sea lampreys, and thus

[5] The formula and meaning of the letters and symbols are given in table 17.

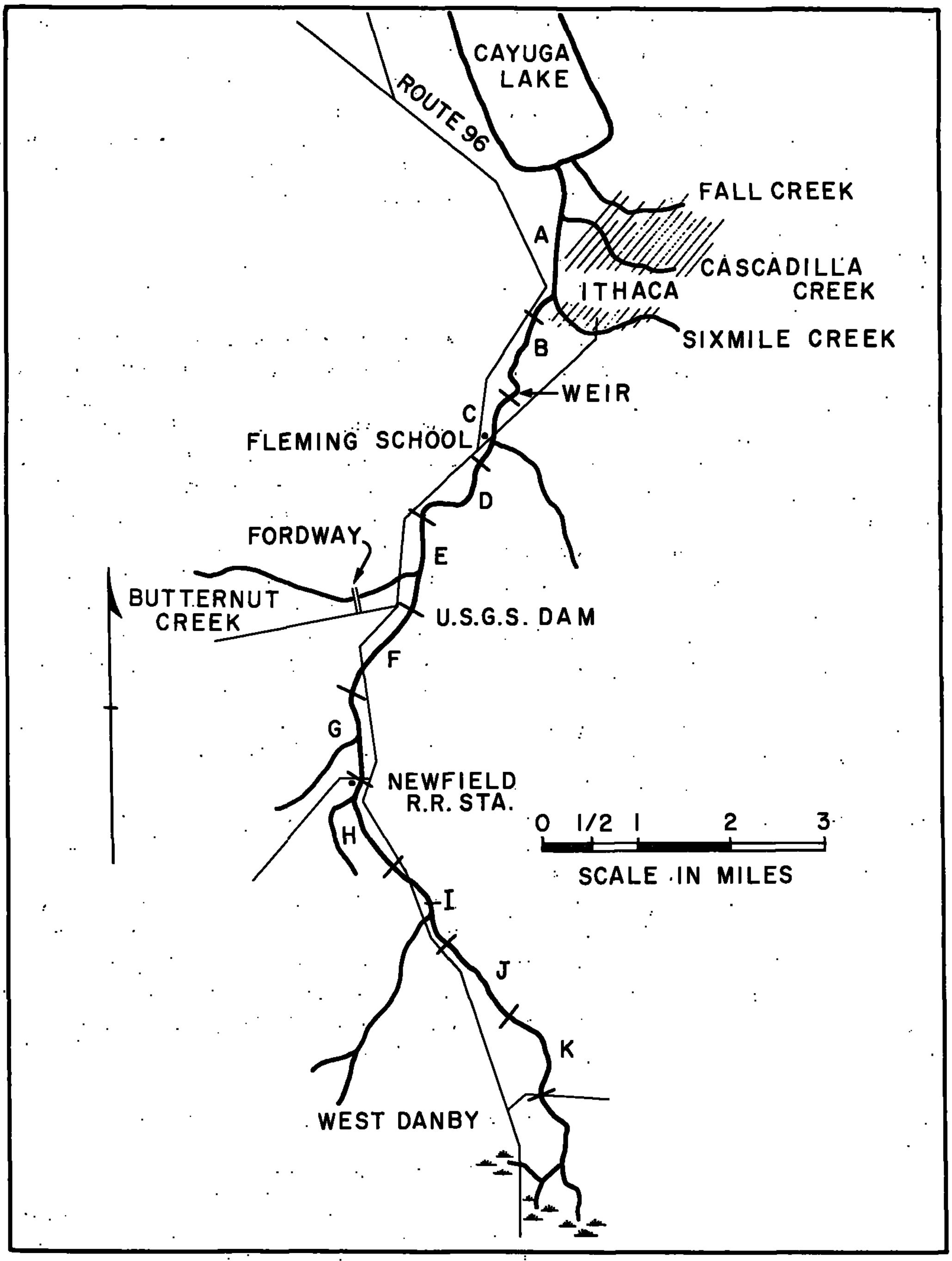

FIGURE 10.—Map of Cayuga Inlet and vicinity showing the 1-mile sections of the stream and localities mentioned in the text.

should be considered the largest migration during the 1950–52 period.

1951

The number of upstream-migrant sea lampreys that entered Cayuga Inlet in the spring of 1951 was estimated to be 9,390. This estimate is based on 960 tagged specimens and a total catch of 5,559.

During the period April 19 to June 13, migrant lampreys were captured by means of a weir, three portable lamprey traps, and by hand. The weir consisted of a barrier net placed diagonally across the stream with a boxlike trap at the upstream end. The net, 60 feet long and 3½ feet high, was made of two layers of netting for added strength. One layer of netting was ½-inch mesh, bar measure, the other was 1½ inches, bar measure. A trap box 3 feet square, constructed of ¼-inch galvanized hardware cloth on a wooden frame, had a conical entrance on the downstream face with a 1-inch opening at the apex. Rectangular portable traps (36 ×18×18 inches), were constructed of ¼-inch galvanized hardware cloth over a wooden frame. Conical entrances at each end were 16 inches deep and had 2-inch openings at the apex. A removable top was held in place with dowels and cleats.

A Petersen tag consisting of two 7/16-inch-diameter plastic discs, one red and one white, was attached to the first dorsal fin by means of a brass pin. One disc was numbered so that identification of individual specimens was possible. Tagged specimens were released as follows: 257 in section *E*; 417 in section *A*; and 286 one and one-half miles downstream from section *A*. Date and number of lampreys tagged and captured are included in table 18.

Schaefer's method for estimating the total number of specimens in a migratory population was employed. This method is well adapted for estimating the numbers of adult lampreys on their spawning run because it takes into consideration the changing abundance of lampreys in the tributary stream during the several weekly periods of tagging and recovery. Even though a variable number of tagged or marked lampreys was released in the stream during the marking periods, this number was directly proportional to the total catch of unmarked or untagged lampreys. In table 18 is a summary, by weekly periods, of the number of lampreys tagged, number of tagged lampreys recaptured, and total number of lampreys captured.

An estimate of the number of sea lampreys on the 1951 spawning run (table 19) was computed from the formula:

$$n_{ai} = m_{ai} \frac{T_a}{m_{a.}} \frac{C_i}{m_{.i}},$$

where, n_{ai}=the estimated number of lampreys based on the a^{th} tagging period and the i^{th} recovery period; m_{ai}=the number of lampreys tagged during the a^{th} period of tagging and recovered during the i^{th} period of recovery; T_a=the number of lampreys tagged during the a^{th} tagging period; m_a=the total number of tagged lampreys recovered during each a^{th} recovery period; C_i=the total number of lampreys recovered during the i^{th} recovery period; $m_{.i}$=the total number of tagged lampreys recovered during each i^{th} recovery period. The summation of n_{ai} values gave a population estimate (N) of 9,390.

Fiducial limits at the 95-percent level were calculated from the formula:

$$P = p \pm \lambda \sqrt{\frac{N-n}{N-1} \cdot \frac{pq}{n}}$$

where, P=the population estimate at the 95-percent confidence level; N=the population estimate; p=the total number of tagged lampreys divided by the population estimate N; $q=1-p$; n=the total number of lampreys captured; $\lambda=1.96$ for the 95-percent confidence limits. Upper and

TABLE 18.—*Tagging-and-recapture record of sea lampreys in the 1951 spawning migration in Cayuga Inlet*

Week of capture (i)	Number of tagged sea lampreys recaptured					Total number of sea lampreys captured (C_i)	$C_i/m_{.i}$
	Week tagged (a)				Total ($m_{.i}$)		
	Apr. 19–25	Apr. 26–May 2	May 3–9	May 10–16			
Apr. 19–25						7	
Apr. 26–May 2		46			46	1,538	33.43
May 3–9		19	9		28	626	22.36
May 10–16	1	81	26	80	188	1,718	9.14
May 17–23		59	31	130	220	1,390	6.32
May 24–30		8	1	1	10	18	1.80
May 31–June 6		25	15	20	60	212	3.53
June 7–13		3	2	2	7	50	7.14
Total tagged lampreys recaptured ($m_{a.}$)	1	241	84	233	559	5,559	
Total number of lampreys tagged (T_a)	6	384	176	394			
T_a/m_a	6	1.59	2.10	1.69			

lower population limits were determined to be 9,897 and 8,972.

1952

The number of upstream-migrant lampreys that entered Cayuga Inlet in 1952 was estimated to be 4,435. This estimate is based on 1,773 marked specimens and a total catch of 3,413. A total of 1,234 marked specimens were recaptured.

TABLE 19.—*Estimate of the number of sea lampreys in the 1951 spawning migration in Cayuga Inlet*

Week of capture (i)	Calculated number of sea lampreys [1]				
	Week tagged (a)				Total
	Apr. 19–25	Apr. 26–May 2	May 3–9	May 10–16	
Apr. 19–25					
Apr. 26–May 2		2,445			2,445
May 3–9		675	423		1,098
May 10–16	55	1,177	499	1,236	2,967
May 17–23		593	411	1,388	2,392
May 24–30		23	4	3	30
May 31–June 6		140	111	119	370
June 7–13		34	30	24	88
Total	55	5,087	1,478	2,770	9,390

[1] Values computed from data in table 18 and the formula given on p. 580.

All lampreys utilized for this population estimate were captured at the U.S. Geological Survey dam or at Newfield station during April 30 to June 3. They were caught by a portable lamprey trap and by hand. The lampreys were marked by a system of notches made in the dorsal and caudal fins, and were all released at the U.S. Geological Survey dam. They were subsequently recaptured at the dam or upstream at Newfield station. Dates and numbers of lampreys marked and captured are included in table 20.

The Schaefer method was again used to estimate the number of lampreys. Weekly summaries of tagging and recapture are listed in table 20. In table 21 are the population estimates recorded by weekly periods. The number of lampreys in the 1952 spawning run was calculated to be 4,435, with 95-percent fiducial limits of 4,108 and 4,818.

These population estimates for the 1951 and 1952 seasons are considered to be reliable. All theoretical assumptions are believed to have been adequately fulfilled.

TABLE 21.—*Estimate of the number of sea lampreys in the 1952 spawning migration in Cayuga Inlet*

Week of capture (i)	Calculated number of sea lampreys [1]					
	Week tagged (a)					Total
	Apr. 30–May 6	May 7–13	May 14–20	May 21–27	May 28–June 3	
Apr. 30–May 6	1,529					1,529
May 7–13	482	398				880
May 14–20	278	465				743
May 21–27	79	164		221		464
May 28–June 3	30	62		481	246	819
Total	2,398	1,089		702	246	4,435

[1] Values computed from data in table 20 and the formula given on p. 580.

Rate of Upstream Movement

The tagging and recapture of many lampreys at six locations along Cayuga Inlet during the spring of 1951 provided an opportunity to measure the rate at which they proceed upstream on their spawning migration (table 22).

Sea lampreys traversed the slow-moving portions of Cayuga Inlet at a rate of 1 to 2 miles per day. Farther upstream where the current is swifter, their rate of travel decreased to approximately one-third to 1 mile per day. Actual swimming velocity under average conditions approximates 1 foot per second, but frequent "rest periods" account for a large share of their time.

When the occasion demands, the lamprey is

TABLE 20.—*Tagging-and-recapture record of sea lampreys in the 1952 spawning migration in Cayuga Inlet*

Week of capture (i)	Number of tagged sea lampreys recaptured						Total number of sea lampreys captured (C_i)	$C_i/m_{.i}$
	Week tagged (a)					Total ($m_{.i}$)		
	Apr. 30–May 6	May 7–13	May 14–20	May 21–27	May 28–June 3			
Apr. 30–May 6	334					334	1,511	4.52
May 7–13	217	148				365	817	2.24
May 14–20	130	180				310	668	2.16
May 21–27	42	72		19		133	253	1.90
May 28–June 3	17	29		44	2	92	164	1.78
Total tagged lampreys recaptured ($m_{a.}$)	740	429		63	2	1,234	3,413	
Total number of lampreys tagged (T_a)	734	515		386	138			
$T_a/m_{a.}$	0.99	1.20		6.13	69.00			

capable of swimming rapidly. Sometimes, when a group of lampreys is frightened, they scatter so swiftly that a few may wriggle onto dry land to points several feet from the shore. Also, when rapids and swift currents are encountered, they ascend quickly though not without considerable effort.

TABLE 22.—*Rate of upstream movement of sea lampreys in the 1951 spawning migration in Cayuga Inlet*

Area traveled	Number of specimens	Distance (stream-miles)	Minimum number of days	Average number of days [1]	Stream gradient
Airport to weir [2]	21	2.0	1	2.3	Very low.
USGS dam to Newfield	55	2.0	2	6.0	High.
Lighthouse to weir	6	2.2	1	2.0	Very low.
Weir to USGS dam	105	2.9	1	8.2	Medium.
Cascadilla Falls to weir	5	2.9	8	12.8	Low.
Weir to Newfield	37	4.9	4	13.9	Medium and high.
Lighthouse to USGS dam	10	5.1	4	8.6	Low and medium.

[1] Not a true average rate of upstream movement because all specimens were not always captured immediately upon entering a station.
[2] Locations mentioned in this column are identified on a map of Cayuga Inlet (fig. 10, p. 579).

Late migrants ascended the stream more rapidly than did early migrants. The average time for travel from the weir upstream 2.9 miles to the U.S. Geological Survey dam was 11 days (minimum, 2 days), during the period April 22–29. Specimens that traveled the same section of stream during May 10–15 averaged 4 days (minimum of 1 day). Daily morning water temperatures at the U.S. Geological Survey dam averaged 46° F. for the April 22–29 period and 59° F. for the May 10–15 period. The stimulating effects of increased water temperatures on the lamprey's metabolic rate and spawning urge are believed the cause of the faster rate of upstream movement during the warmer period.

Barriers to Upstream Migration

Diurnal and nocturnal observations of the sea lamprey's behavior throughout the 1951 spawning migration indicated that a "partial-barrier" dam is effective in retarding upstream movement and serves as a block to some individuals.

A small dam constructed for the U.S. Geological Survey, Water Resources Division, across Cayuga Inlet 5 miles upstream from the lake offered an excellent place for observations of the lamprey's reaction to a barrier. This dam consists of a concrete wall 30 feet long and 1 foot wide (fig. 11) with an irregular concrete apron which extends 3 to 6 feet downstream. A drop of approximately 1 foot in water level is created by the dam, but the fall varies inversely with the volume of waterflow.

When early migrants first encountered this small dam they reacted by searching actively back and forth along the base for a bypass. After several days of investigation, many proceeded downstream, and were observed as much as one-half mile below the dam, slowly moving downstream, seemingly in search of a tributary.

To learn the fate of spawning-run sea lampreys which were prevented from ascending a tributary stream, Applegate and Smith (1951) captured and tagged specimens that entered the Cheboygan River in which upstream movement was blocked by a power dam. Tag returns indicated that sea lampreys will return to the lake from which they came, and then search for another tributary.

A tagging experiment on the Cayuga Lake sea lamprey indicated a reaction similar to that found by Applegate and Smith. Recovery of tagged lampreys in Cayuga Inlet proves they will return downstream at least 1 mile. In 1951, one of 59 tagged lampreys which were captured in Cayuga Inlet and released in Fall Creek (fig. 10) was recaptured in Cayuga Inlet. This lamprey had to travel 1 mile downstream to Cayuga Lake, and one-half mile in the lake to the mouth of Cayuga Inlet. Of the 92 tagged lampreys released in Cascadilla Creek, a tributary of Cayuga Inlet, 23 (25 percent) were later recaptured in Cayuga Inlet proper. They had moved 1 mile downstream.

Early arrivals in the spawning tributary attempt to reach the headwaters, whereas late arrivals occupy the lowermost reaches of the stream. Possibly the early arrivals, which are the larger, are stronger and hence more able to progress upstream farther than late arrivals. Or, the greater amount of time available to them may permit the early migrants to travel farther.

Waterflow also is a factor in upstream movement. High waters in 1952 permitted lampreys to cross the barriers and ascend to the very headwaters of Cayuga Inlet; as a result the density of nests was low throughout the stream. In 1951, moderate waterflow made the barriers more effective. That year the density of nests was high in the lower and middle section of the inlet and practically no nesting took place in the headwaters.

With the passage of time the spawning urge becomes increasingly strong. About mid-May,

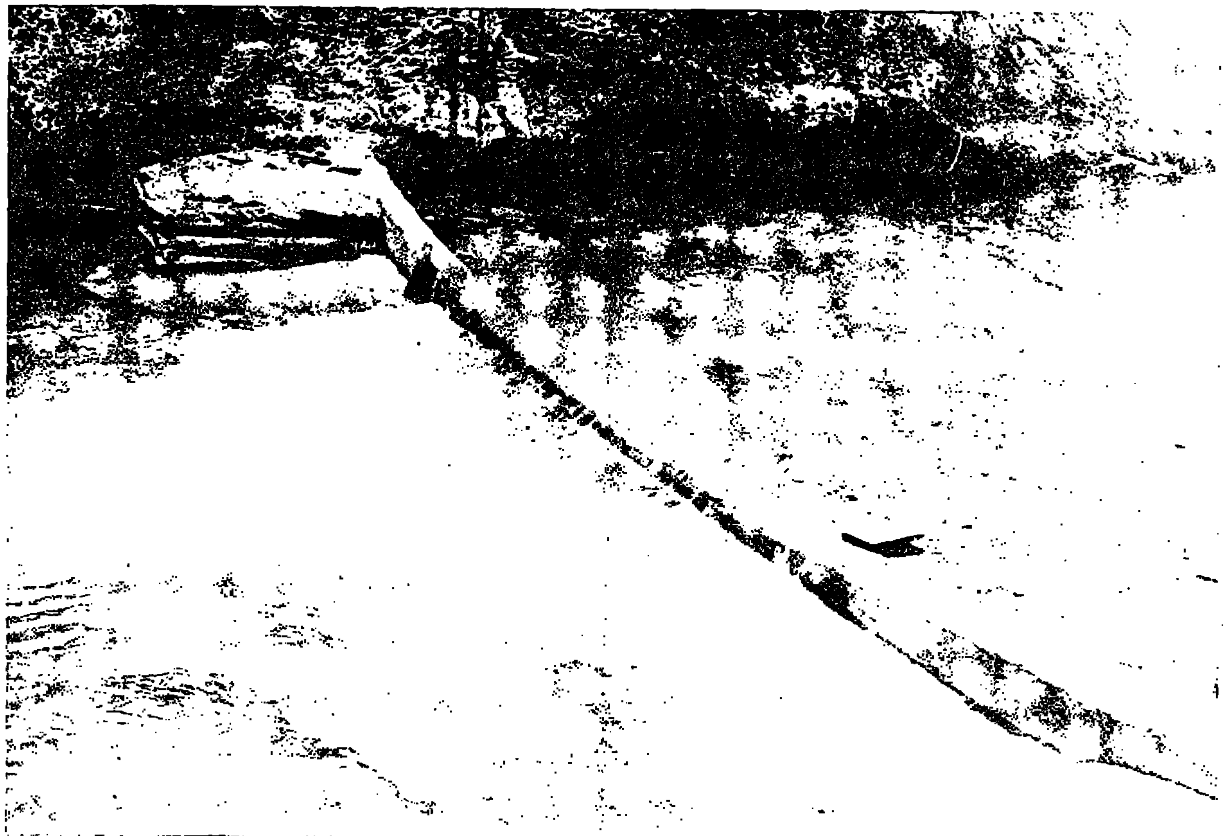

FIGURE 11.—U.S. Geological Survey Dam on Cayuga Inlet.

when the evening water temperatures approach 55°–60° F. lampreys can be found adhering to the apron below the U.S. Geological Survey dam (fig. 11). Water flowing over the dam is shallow and swift (roughly 1 to 6 inches deep, flowing at 2 feet per second), but some lampreys make their way up to the brink of the dam and rest there until capable of attempting to cross. Some individuals swim over; others slowly maneuver their body perpendicular to the current and parallel to the stream bottom, while still attached to the dam by the suctorial mouth. After sufficient rest, they quickly release their hold, swing the head upstream, and make a few very rapid swimming motions which usually carry them over the dam. Characteristically, they rest several minutes just a few feet upstream from the dam before continuing their migration.

It should be emphasized that the U.S. Geological Survey dam is by no means a complete barrier. It is surmounted by many lampreys as well as by teleost fishes. A 10-inch (estimated length) smallmouth bass, *Micropterus dolomieu*, easily swam over this dam under normal water conditions.

In 1952, between April 30 and May 6, 872 lampreys were marked and released just below the U.S. Geological Survey dam. During the 4-week period (May 7–June 3) following their release, many of these marked specimens were recaptured at the same locality where they were liberated; i.e., on the downstream side of the dam. Recorded in table 23 are the date, number, and percentage of the original number of specimens recaptured there. Since the fishing effort of the trap remained constant and the total catch decreased steadily, the decreased percentage of marked lampreys recaptured is the rate of emigration, either upstream or down. A large number of marked specimens found upstream from the dam indicates that most of the movement was upstream. Approximately 3 to 7 percent of the marked lampreys departed from below the dam each week. The most notable fact is that 10 percent of the 872 lampreys marked prior to May 6 remained below the dam for more than 4 weeks. By that time (June 3) the nesting season was well underway and upstream migration was practically nil. Thus, considering the other traits displayed by upstream-migrant sea lampreys, approximately 10 percent of the early arrivals were unable to negotiate the partial barrier created by the U.S. Geological Survey dam.

TABLE 23.—*Emigration of 872 sea lampreys marked and released below the U.S. Geological Survey dam on Cayuga Inlet, between Apr. 30 and May 6, 1952*

Recovery period	Total number of lampreys captured	Number of marked lampreys recaptured	Percentage of marked lampreys in catch
May 7–May 13	817	217	26.6
May 14–May 20	668	130	19.5
May 21–May 27	253	42	16.6
May 28–June 3	164	17	10.4

The effect of barriers on lamprey migration in Cayuga Inlet is brought out in figure 12, which shows the number of lamprey nests in each 1-mile section of Cayuga Inlet at the height of the 1951 spawning season. The numbers of nests were determined by a complete count in a section or estimated from a large sampled portion. These data are listed in Table 31.

Large concentrations of nests immediately below the obstacles readily suggest their restraining effect on the upstream migration of lampreys. The presence of few nests above the Newfield station is indicative of a nearly impassible barrier. Absence of lamprey nests in sections A and B is due to the unsuitable composition of the substrate.

Sex Ratio

The sex ratio of adult sea lampreys in the spawning run in Cayuga Inlet was first measured by

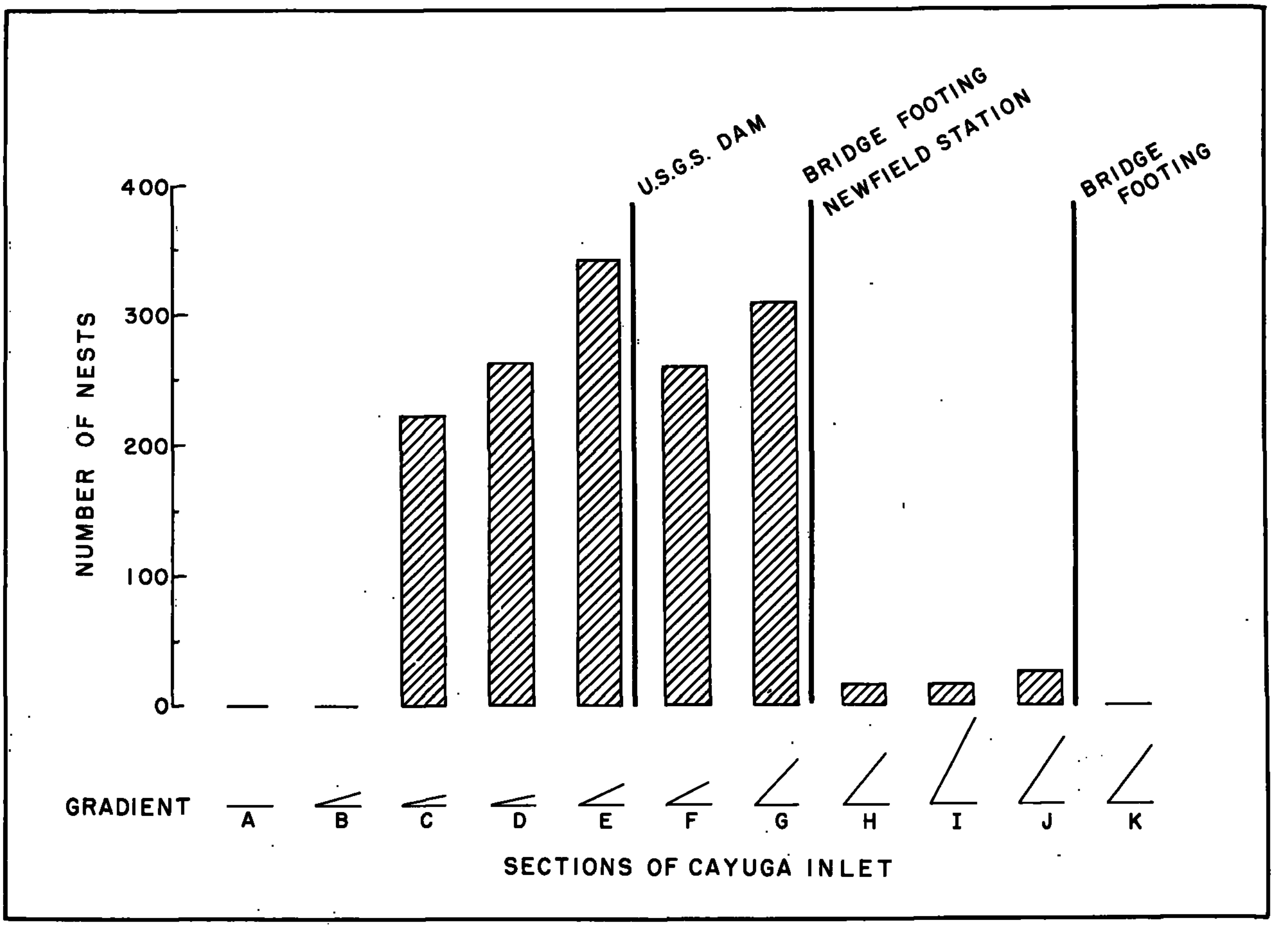

FIGURE 12.—Number of sea lamprey nests in each 1-mile section of Cayuga Inlet at the height of the 1951 spawning season. An index of stream gradient is given for each section, and obstacles to upstream movement are shown in their respective locations.

Meek (1889) in 1886. Throughout a 2-week period beginning May 21, he determined the sex of 745 lampreys, of which 480 were males and 265 were females, a ratio of 180 males per 100 females (table 24).

Surface (1899) made sex determinations for a larger sample from Cayuga Inlet during the spring of 1898. In a total of 1,686 specimens 589 were males, 551 were females, and the sex was undetermined in 546. These figures give a sex ratio of 107 males per 100 females.

Collections of 372 adult lampreys on their spawning migration in Cayuga Inlet, made in this study between May 5 and June 12, 1950, gave a sex ratio of 157 males per 100 females (table 25). Similar collections in 1951 gave a sex ratio of 155 males per 100 females (1,820 specimens, table 25). Finally, comparable collections made in 1952 had 116 males per 100 females (1,306 specimens, table 25).

TABLE 24.—*Sex ratio of 745 sea lampreys in the spawning migration in Cayuga Inlet, 1886*

[Data from Meek, 1889]

Date	Number of males	Number of females	Sex ratio (males:females)
May 21	156	69	226:100
May 25	132	110	120:100
Later (?)	106	37	286:100
Later (?)	86	49	175:100
Total	480	265	180:100

TABLE 25.—*Sex ratio of sea lampreys in the spawning migration in Cayuga Inlet during 1950, 1951, and 1952*

Date	Number of males	Number of females	Sex ratio (males:females)
1950			
May 5–7	135	88	154:100
May 15–17	34	24	142:100
May 24–30	26	14	186:100
June 8–12	32	19	169:100
Total	227	145	157:100
1951			
Apr. 22–28	120	57	210:100
Apr. 29–May 11	490	314	156:100
May 6–12	158	92	172:100
May 13–19	336	247	131:100
Total	1,107	713	155:100
1952			
May 7–10	450	348	117:100
May 20	19	18	106:100
May 26	220	166	132:100
June 3	13	36	36:100
Total	702	604	116:100

As is shown in tables 24 and 25, samples containing a small number of specimens yield apparently inconsistent estimates of the sex ratio. Some of these values are undependable because of the small sample. Others can be attributed to differential activity and availability of the sexes and to fluctuations in the actual sex ratio. Apparently, discrepant values should not be rejected arbitrarily, however, because, as suggested below, they may represent true fluctuations of the population that are not well understood.

Surface reported (1899) that males predominate among early migrants, and females among late migrants. This general trend was found in Cayuga Inlet during the present study. For instance, in 1951, the year in which the samples were largest, the ratio changed from 210 males per 100 females in late April to 131 males per 100 females in mid-May.

In addition to the general trend of a changing sex ratio, there was a secondary rise in the abundance of males that led to two "cycles" similar to the main trend. These secondary pulses occurred each year for which sex ratio data are available (last column in tables 24 and 25). Whether this secondary rise was created by segments of the population delayed in fruitless searches in or for other tributaries, is not known.

Annual differences in the sex ratio are related to the abundance of lampreys (table 26). Male specimens were relatively more abundant in years when lampreys were plentiful, approximately 3 males to 2 females. In years when lampreys were few, the sex ratio was nearly 50–50. These annual changes are large and well defined.

Other sea lamprey populations likewise exhibit a changeable sex ratio. In Lake Huron the relative abundance of male sea lampreys increased steadily from 165 to 258 males per 100 females during the years 1947–51 (Applegate, Smith, McLain, and Patterson, 1952). Over this same period the numbers of sea lampreys were increasing.

TABLE 26.—*Sex ratio and estimates of the number of sea lampreys in the spawning migrations in Cayuga Inlet*

Year	Estimated number of sea lampreys	Sex ratio (males:females)
1886 [1]		180:100
1898 [2]	1,686	107:100
1950	10,000–15,000	157:100
1951	9,390	155:100
1952	4,435	116:100

[1] Meek (1889).
[2] Surface (1899).

Size of Upstream Migrants

Early arrival of the larger sea lampreys in the spawning migration was observed by Surface (1899) in Cayuga Inlet and by Applegate (1950) for Lake Huron stocks. During 1950, 1951, and 1952 the early upstream-migrants in Cayuga Inlet were again found to be both longer and heavier than late migrants (tables 27, 28). Comparison of average lengths of early with late migrants reveals that the former averaged 0.2 to 0.7 inch longer. In weight, the early migrants averaged 0.2 and 0.6 ounce heavier in 1950 and 1952, respectively, but in 1951 their weight averaged 0.4 ounce less than that of late migrants. Although the sex ratio of upstream-migrants changed during the season, this change had no effect on the size of early and late migrants as the sexes had the same mean size.

TABLE 27.—*Mean lengths of adult sea lampreys taken early and late in the spawning migration in Cayuga Inlet*

Date	Number of specimens	Length (inches)		
		Mean	Minimum	Maximum
1950				
May 5	111	15.2	11.5	19.8
May 15	45	15.0	12.0	18.7
1951				
Apr. 28	124	15.3	12.4	19.7
May 14	162	15.0	11.4	20.3
1952				
May 7–9	516	16.2	12.0	21.3
May 21	423	15.5	11.5	20.8

TABLE 28.—*Mean weights of adult sea lampreys taken early and late in the spawning migration in Cayuga Inlet*

Date	Number of specimens	Weight (ounces)		
		Mean	Minimum	Maximum
1950				
May 5–7	203	5.1	2.2	11.3
May 15	32	4.9	2.5	7.6
1951				
Apr. 28	124	4.3	1.8	8.3
May 15	138	4.7	2.0	9.5
1952				
May 7–9	506	5.2	1.9	12.1
May 21	419	4.6	1.8	10.7

Body Color

Recently transformed sea lampreys are bluish-black [6] dorsally and laterally and silvery-white ventrally. With increasing age the epidermis becomes dark olive. The body is mottled by black pigment in the dermal layer, especially on the dorsal surface; the ventral surface is nonpigmented. At the height of the spawning season the dark-olive epidermal layer changes to a medal-bronze on the majority of individuals, although there is much variation. A few lampreys, often the largest and most mature, develop a xanthine-orange coloration. Others, often the smallest and least mature, remain bluish-black or dark-olive.

Pigmentation on the dorsal fin is sparse and rather indistinct in comparison with that on the trunk. A band of skin along the base of both dorsal fins is pigmented much the same as the trunk. An indistinct band, approximately one-fourth the fin height, on the margin of the dorsal fins is nonpigmented. The caudal fin bears dark pigmentation on its posterior portion which diminishes anteriorly. A ridgelike continuation of the ventral portion of the caudal fin forward to the urogenital opening is nonpigmented.

In 1951 a study was made of the correlations between color and size, sex, and time during the spawning period. To facilitate the recording and calculation, five color categories were established and given index numbers as follows: (1) xanthine orange; (2) raw sienna; (3) medal bronze; (4) dark olive; and (5) bluish-black. This series is listed here in reverse order of color changes that occur as sexual maturity is approached. Numbers of specimens were: 183 males and 110 females captured on the spawning run in Cayuga Inlet during the period April 26–30, 1951; 152 males and 144 females taken during the period May 13–16, 1951.

The linear regressions of color on length (fig. 13) illustrates the tendency for large lampreys to be lighter and more colorful than small ones. Males were lighter and a more golden color than females of similar size. Early migrants were approximately one color category lighter than late migrants. A measure of closeness of the relation between color and total length is provided by the correlation coefficient. Correlation coefficients for the April collections, as shown in the tabulation, indicate considerable variation. Correlation coefficients for the May collections are rather high, indicating relatively little variation; however, only the females in the May collections have a significantly high value (indicated by asterisk).

Individual records of 20 specimens whose color was recorded when they were captured on their upstream migration and tagged, and again recorded after spawning was completed, were used as an

[6] Color standards employed in this description are those given by Ridgway (1912).

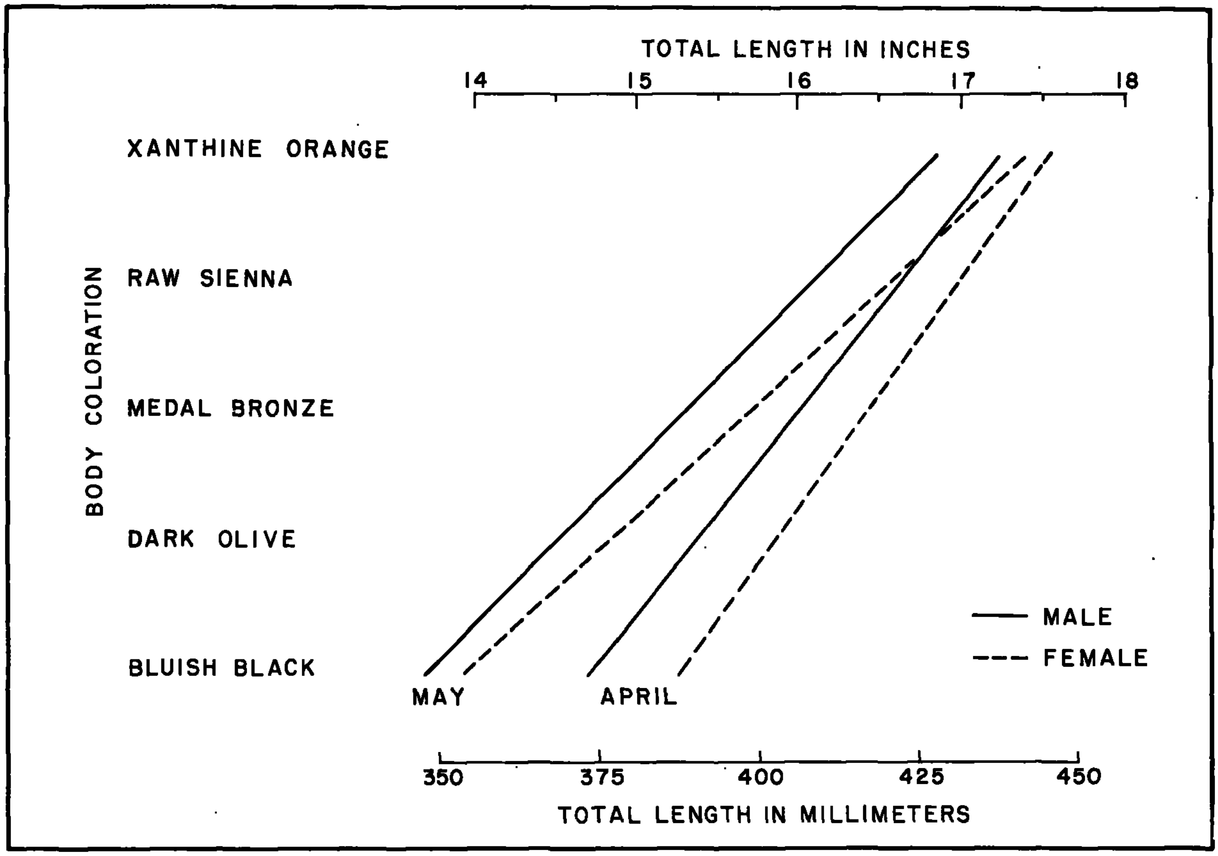

FIGURE 13.—Regression of body coloration on total length of mature sea lampreys during April and May April collections represent early migrants; May collections represent late migrants.

Date collected and sex	Correlation coefficient	Probability level
April		
Male	0.6568	0.21
Female	.5722	.28
May		
Male	.8428	.08
Female	.8901	*.04

indication of color transition that occurs during the spawning period. All migrants acquired a lighter color of from one-half to two color categories. The late migrants which were generally darker made the greatest change.

SPAWNING HABITS

The spawning habits of the Cayuga Lake sea lamprey have been reported by Gage (1893) and Surface (1899). Coventry (1922) and Applegate (1950) have reported on the spawning habits of sea lamprey populations in the Great Lakes. In view of the considerable available data on this subject, only a brief summary will be presented here of observations made in Cayuga Inlet during the present investigation.

Sea lampreys that arrive in the spawning tributary in mid-April spend 4 to 5 weeks in the stream before they begin nest construction. Those that do not arrive until mid-May spend less than a day in the spawning tributary before nesting. Practically all of the prespawning period is occupied in moving upstream to suitable nesting sites. Late arrivals utilize the low reaches of the stream, and therefore spend little time in upstream travel (p. 582).

Nest Building

Water temperature seems to have a strong influence on the time of spawning. In Cayuga Inlet, nest building usually starts toward the latter part of May, when the evening water temperatures approach 65° F. During the first few evenings of nest building, the lampreys' movements are slow and, if the water cools enough during the evening, nest excavation may last for only a few hours. These abortive attempts at nest construction usually result in small pockets that are later abandoned, though they may be enlarged by other lampreys at a later date.

Sea lampreys utilize only certain portions of the stream for spawning. The principal physical characters that affect the suitability of an area as a nesting site are the type of substrate and water velocity. For successful spawning the lamprey requires a substrate of stones small enough to be moved and some fine sand to help sink and cover the eggs. Also, a rather swift flow of water seems to be required. The nests are commonly located at the downstream end of a pool, where the rate of flow is at least 2 feet per second. In Cayuga Inlet, the center of the stream presents more attractive nesting sites than do areas along the bank.

The lamprey nest is a shallow, irregular, bowl-shaped pocket excavated in the streambed. For nest construction the lamprey attaches its suctorial mouth to a stone to be moved; if necessary the stone is loosened from the bottom by a few violent jerks. It is then carried to the edge of the nest and dropped. Most stones are placed in a crescent-shaped pile at the downstream edge, but a few are carried to the upstream edge. Gravel usually less than 1 inch in diameter remains to make the nest floor. Most of the silt particles are stirred up by the writhing bodies and carried out of the nest by the current during the excavation. Rocks comprising the streambed of Cayuga Inlet are predominantly shales. In table 29 are listed a number of nest measurements and the size of stones lining the nest floor. The stone diameters of the rubble represent only the larger flat surfaces.

The nests are usually oval with the long axis parallel with the water current. Nest size varies greatly but most are approximately 1 to 1½ feet in diameter, and 3 to 5 inches deep. Nearly all nests are located in water one-half to 2 feet deep.

Customarily, males begin the nest construction and are later joined by a female who assists with the work. Males habitually start several nests which they abandon. Usually they proceed upstream as the nests are constructed and deserted.

Occasionally several males or several females are together in one nest. These communal nests are large, often 2 to 3 feet in diameter. Lack of suitable nesting area does not appear to be the cause of communal nesting. The fact that they are more commonly found toward the latter part of the nesting season suggests that the arrangement may be a timesaving device of late spawners.

TABLE 29.—*Measurements (inches) and materials in the floor of sea lamprey nests as observed in section E of Cayuga Inlet on May 30, 1951*

Depth in center	Dimensions of nest		Depth to downstream summit	Bottom type in floor of nest [1]
	Length	Width		
11.5	18	11	8.5	P, M.
11	10	8	8.5	P, M.
11.5	10	7	7.0	M, P, E.
13.5	13	14	9.0	M, P, E, R.
12.5	10	10	7.5	M, P, E.
12	19	15	7.0	M, P, E.
10	12	8	8.0	M, P.
9.5	13	9	7.5	M, P, E.
10.5	13	10	7.5	E, M, P.
12	14	17	8.0	M, E, P, R.
11	16	15	6.0	E, M, P, R.
9.5	12	9	5.5	M, P, R.
8.5	11	5	4.0	M, S, P.
8.5	11	9	4.0	P, M, E.
16	21	12	11.0	M, P.
16.5	22	11	11.0	M, R, P.
13	13	12	8.5	E, R, P.
12	19	13	5.5	R, M, E.
13	10	9	9.0	E, M, R.
15	18	16	8.5	M, P. R.
15.5	13	9	10.0	R, M, P.
17	29	19	10.0	R, E, M.

[1] Size of material in the floor of each nest was recorded in order of dominance: P pea gravel, 3/16 to 3/8 inch in diameter; M marble gravel, ½ to 1 inch in diameter; E egg gravel, 1¼ to 2½ inches in diameter; R rubble; S sand.

Time of Construction and Location of Nests

The first nesting activity of the 1951 season was observed on the night of May 21 in section *E* of Cayuga Inlet. Four male sea lampreys were seen on nests in the earliest stage of construction. Large-scale nest building started on May 25. By May 30 a majority of the nests had been constructed, and spawning reached a peak May 30–June 1. After June 1, nest building dropped off rapidly and consisted mostly of enlarging previously existing nests. No spawning or nest building was observed after June 10.

During the 1951 spawning period, May 21 to June 7, counts were made of the number of nests in each of eleven 1-mile sections (fig. 10) of Cayuga Inlet. All sections were examined at least twice, and the most heavily populated areas as many as six times. Some nest counts include an examination of the entire section; most counts however, were based on samples of one-quarter to three-quarters of a section. To provide a measure of nest-building and spawning activity, nests were classified as occupied or unoccupied (table 30). Any nest in which one or more lampreys were found was considered occupied. On May 21, all nests were occupied. The percentage of occupied nests decreased irregularly to about 50 percent on May 24–25 and approximately 20 percent by the end of the month. On June 6 and 7 the percentage of occupied nests had decreased to 12.

In sections *C* through *G* where the spawning population was high, superimposition of one nest on another and the indefinite boundaries between adjoining nests prevented accurate determination of the total number of nests. In areas where spawners were less numerous, nest building and spawning were orderly. In such areas no superimposition or consolidation of nests was observed and usually but one pair of lampreys was seen in one nest.

TABLE 30.—*Occupancy of sea lamprey nests in Cayuga Inlet, between May 21 and June 7, 1951*

[No observations on May 28 or June 2–5]

Date	Number of nests		Percentage of nests	
	Occupied	Unoccupied	Occupied	Unoccupied
May 21	4	0	100	0
May 22	3	2	60	40
May 23	4	10	29	71
May 24	6	6	50	50
May 25	110	129	46	54
May 26	88	170	34	66
May 27	34	48	41	59
May 29	33	131	20	80
May 30	91	160	36	64
May 31	49	339	13	87
June 1	52	187	22	78
June 6	28	225	11	89
June 7	31	213	13	87

The number of nests per section of stream as of May 30–June 1 is considered a reliable index to the total number (table 31 and fig. 12). This period was chosen because it was the last date when accurate nest counts could be made. The figures given are believed to be only slightly lower than the actual total numbers.

The greatest density of nests, one per 15 feet of stream, was found in section *E*, the area immediately downstream from the U.S. Geological Survey dam. The first nest-building activities were in this section. Section *G*, the area just below Newfield station, ranked second in nesting density with one nest per 17 feet of stream. Sections *D*, *F*, and *C* followed in decreasing order. Densities were extremely low in sections *H*, *I*, *J*, and *K*, all located upstream from the Newfield station. These sections may be considered as of little importance for lamprey spawning when low or moderate water levels, similar to those of 1951, prevail (see fig. 9 for water volumes).

Some nests were not used for spawning, whereas others were utilized by several pairs. An investigation into the number of nests actually utilized

TABLE 31.—*Number and density of sea lamprey nests in each 1-mile section of Cayuga Inlet, May 30–June 1, 1951*

[See fig. 10 for locations of sections]

Section	Number of nests	Feet of stream per nest	Section	Number of nests	Feet of stream per nest
A	0		G	311	17
B	0		H	19	278
C	223	24	I	19	278
D	264	20	J	27	189
E	343	15	K	1	5,280
F	261	20			

was made June 9 and 12, 1951, when 137 nests were examined for eggs. A shallow rectangular funnel, its mouth 18 inches square, made of brass screen, 60 meshes per inch, was placed downstream from each nest. A few large stones were placed alongside and slightly behind each nest to guide the water current into the funnel. When the funnel was in position the sand and gravel in the nest pocket was scooped up with a shovel, lifted to the water's surface, then slowly poured back into the nest to free the lamprey eggs. This process was repeated until some eggs were obtained or until all material in and around the nest had been thoroughly sifted. Lamprey eggs and occasionally sucker eggs from the nest site drifted downstream into the screen. The results revealed 59 (43 percent) nests with sea lamprey eggs, and 78 (57 percent) nests without. Five nests contained an estimated 10,000 eggs or more. Only a few hundred were recovered from most nests which contained eggs.

Spawning

Gage (1893 and 1928) and Surface (1899) have previously reported on the spawning of the Cayuga Lake sea lamprey. A recent and more detailed description was given by Applegate (1950) of spawning in the Ocqueoc River, a tributary of Lake Huron. Since Applegate's description agrees well with observations made in Cayuga Inlet, comments are limited here to an explanation of figure 14. (*A*) The female, on the left, is securely anchored by her oral disc to a stone at the upstream edge of the nest; the male is brushing his oral disc along the dorsolateral portion of the female from the region of the first dorsal fin forward to the head; (*B*) the male, above and to the right, has just adhered to the top of the female's head and has bent the posterior portion of his body to the left in preparation to hold the female; (*C*) the

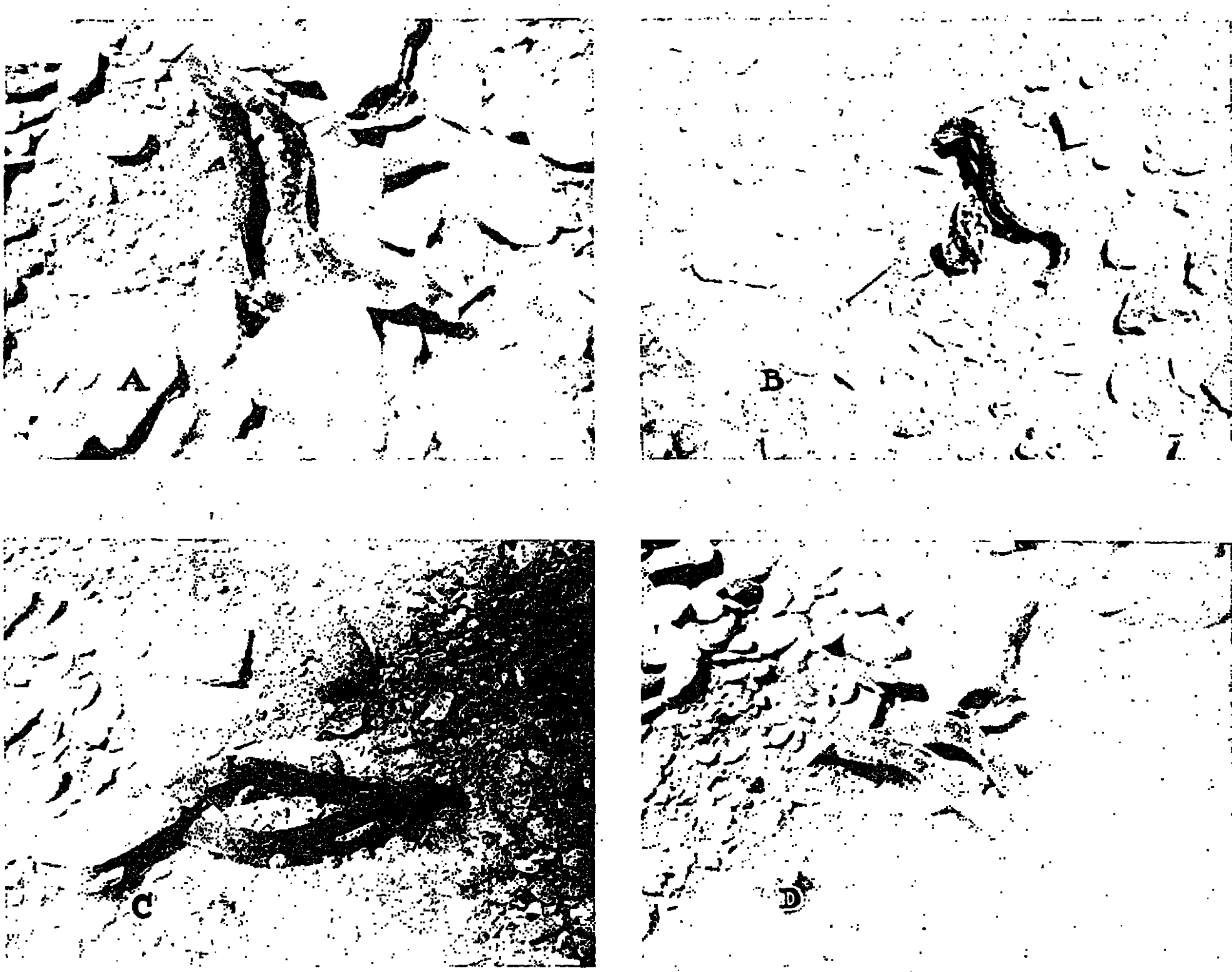

FIGURE 14.—A pair of spawning sea lampreys in Cayuga Inlet, May 1951.

male, above, has completely encircled the female by spiraling the posterior portion of his trunk about her (note the thin opaque covering of the male's eye; he is blind); (*D*) in the final stage, the male, above and to the right, and the female rapidly vibrate their bodies as both eggs and sperm are emitted from their closely approximated vents (fine particles of sand stirred from the floor of the nest by the vibrating lampreys adhere to the sticky surface of the eggs and aid considerably in retaining them in the nest).

Actual copulation lasts only a few seconds, but is repeated at intervals of one minute to one-half hour depending on water temperature, time within the spawning season, and other factors. Spawning by a pair of sea lampreys commonly lasts about 1½ to 2 days.

Fecundity

Surface (1899) placed the production of eggs by Cayuga Lake sea lampreys at an average of 27,500 (range of 25,000 to 30,000), and Gage (1928) gave the fecundity of three specimens as 63,000, 65,000, and 108,270 eggs. Applegate (1950) determined a mean of 61,500 eggs (corresponding mean length of 17.4 inches) and a range of 24,021 to 107,138 in sea lampreys from Lake Huron tributaries. Vladykov's (1951) estimates of 72,870 eggs for sea lampreys from Lake Michigan and 55,913 for Lake Huron specimens agree well with Applegate's findings.

The gravimetric method has been found to be the most desirable means for calculating the number of eggs in a sea lamprey ovary. Detailed studies by Applegate (1950) on the ovary of the sea lamprey from Lake Huron tributaries, revealed no appreciable size differences of ova from the anterior, middle, and posterior portions. In accordance with the results of Applegate's studies, the method used in calculating the number of eggs contained in Cayuga Lake specimens was as follows: total body length and weight of the specimen were measured; the ovary was dissected from the body, weighed, and preserved in 5-percent formalin; at a later date, the ovary was removed from the preservative, drained, and blotted dry as possible; the entire ovary was weighed to the nearest 0.01 gram; a small portion (1.00–1.55 grams) from the midsection of the ovary was removed and weighed to the nearest 0.01 gram; the total number of eggs in the sample was counted and the number of eggs in the entire ovary was computed.

Determinations of fecundity were made for 29 sea lampreys collected in Cayuga Inlet on April 30, 1951. The size of each specimen and the number of eggs each contained are listed in table 32. These lampreys averaged 15.6 inches in length; minimum and maximum lengths, 11.7 and 20.1 inches; total body weight averaged 5.1 ounces; and weight extremes were 1.8 and 11.7 ounces. None of the lampreys had deposited any eggs prior to capture, since spawning did not take place until 1 month after they were collected. The regression of number of eggs on the total length of lamprey is presented in figure 15. The regression line was fitted mathematically. Extreme egg counts among the specimens were 14,000 and 85,000.

Average length of female lampreys in the 1951 spawning migration in Cayuga Inlet was 15.2 inches. A female of this size produces approximately 43,000 eggs.

It is obvious from figure 15 that great variation in egg number occurred even among lampreys of the same length. The major source of this variation was diversity in ovary size. Large females tended to have a proportionately larger ovary and fewer eggs per unit weight of ovary.

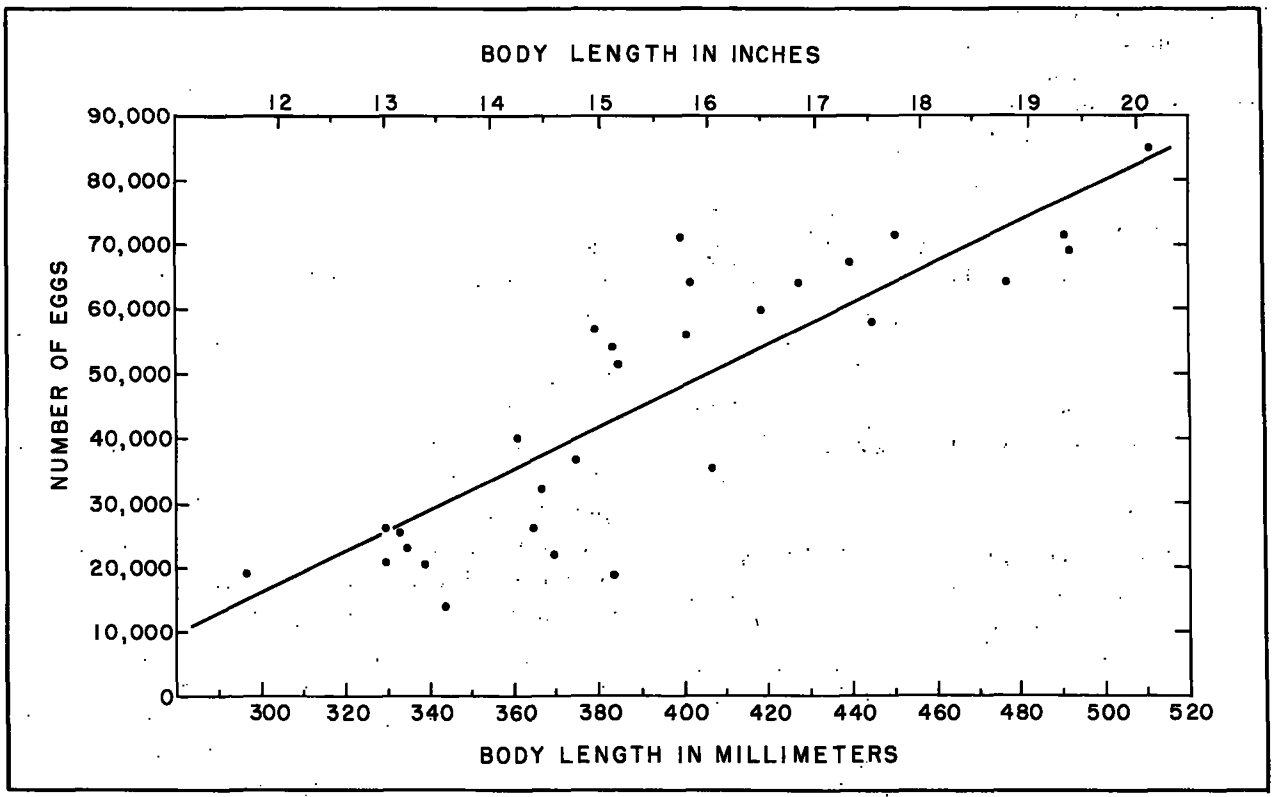

FIGURE 15.—Regression of the number of eggs per female sea lamprey on total length.

TABLE 32.—*Number of eggs in relation to body size and ovary weight of sea lampreys collected in Cayuga Inlet on Apr. 30, 1951*

Length (inches)	Weight (ounces)	Weight of ovary (ounces)	Number of eggs		
			Total	Per ounce of body weight	Per ounce of ovary weight
11.7	1.8	0.21	19,107	10,615	90,985
13.0	2.3	.29	20,821	9,053	71,796
13.0	2.6	.28	26,214	10,082	93,621
13.1	2.4	.30	25,636	10,681	85,453
13.2	2.4	.30	23,089	9,619	76,963
13.3	3.3	.29	20,606	6,244	71,055
13.5	2.6	.17	13,974	5,373	82,200
14.2	3.6	.67	40,139	11,149	59,909
14.4	3.7	.34	26,140	7,064	76,882
14.5	4.2	.49	32,195	7,664	65,704
14.6	4.1	.37	21,692	5,290	58,627
14.8	3.5	.47	36,689	10,482	78,061
15.0	5.0	.92	57,234	11,445	62,211
15.1	3.8	.31	18,747	4,932	60,474
15.1	6.2	.92	54,128	8,730	58,833
15.2	4.4	.67	48,797	11,090	72,830
15.7	5.6	.87	71,324	12,735	81,982
15.8	4.9	.61	55,851	11,398	91,559
15.8	5.4	.74	64,608	11,963	87,308
16.0	4.7	.52	35,429	7,538	68,132
16.5	5.2	.60	59,844	11,507	99,740
16.8	6.2	1.12	63,905	10,307	57,058
17.5	7.9	1.28	58,279	7,377	45,530
17.7	8.3	1.24	71,597	8,626	57,739
18.0	7.6	.97	66,850	8,796	68,946
18.8	8.5	1.07	63,974	7,526	59,788
19.3	8.5	1.13	71,427	8,403	63,210
19.3	10.0	1.41	68,861	6,886	48,838
20.1	11.7	1.56	85,162	7,405	54,591

Ovary development and growth takes place at a rapid rate during the 2 weeks immediately prior to spawning. A comparison was made of the ovary weights from a series of 22 lampreys collected in Cayuga Inlet on May 15, 1951, with 29 collected on April 30, 1951.

Date of capture	Mean total length	Mean body weight	Mean ovary weight	Ovary as percentage of body weight
	Inches	*Ounces*	*Ounces*	
Apr. 30	15.6	5.1	0.69	13.5
May 15	15.5	4.9	.86	17.6

In the April 30 collection the ovary comprised 13.5 percent of total body weight, whereas in the May 15 collection the ovary made up 17.6 percent of total body weight.

Postspawning Habits and Morphological Changes

Evidence gathered by Surface (1899), Gage (1928), Shetter (1949), and Applegate (1950) indicates that sea lampreys die soon after spawning. This evidence is based on anatomical degeneration of digestive and excretory organs, absence of immature ova in the ovary, sloughing of the epidermis, frequent blindness, field observations of dead and dying specimens, and field experiments in which spent lampreys were held in cages in their natural habitat. However, doubts concerning the fate of spent sea lampreys still existed.

Additional evidence which substantiates the contention that sea lampreys die after spawning was obtained during the spring and summer of 1951. The lamprey weir installed in Cayuga Inlet caught all postspawning, downstream-migrant lampreys. The total catch amounted to only 238 specimens, 2.5 percent of the estimated 9,390 that entered the stream for spawning. Eighty to ninety percent of the 238 specimens were dead, and the remaining 10 to 20 percent that were still alive were in such a debilitated physical state that none of them were likely to survive more than a few days.

After spawning has been completed, the lamprey is in such an exhausted and emaciated condition that it is unable to hold its position in the spawning grounds. Attempts to swim upstream or across the stream result in their being carried downstream by the water current. Excursions along many miles of spawning area of Cayuga Inlet revealed surprisingly few dead lampreys. Thousands of lampreys were known to be present in the stream and hundreds were observed building nests and spawning, but fewer than 100 dead lampreys were found lodged against branches, rocks, and other natural obstacles. Nighttime as well as daytime inspection trips indicated that very few sea lampreys were removed by scavengers and predators. The great discrepancy in numbers was explained when digging in the silt-laden bottoms of deep pools revealed large numbers of dead lampreys.

Most of the spent lampreys taken in the weir had spawned in the 1-mile area immediately adjacent to and upstream from the weir, section *C*. Of the 20 tagged specimens observed spawning and subsequently caught in the weir, 15 had spawned in section *C*, 3 in section *D*, and 2 in section *E* (fig. 10). None of the hundreds of tagged specimens observed spawning farther upstream were among those later captured at the weir. It thus appears that spent lampreys are rarely carried downstream more than 3 miles, and usually not more than 1 mile, before becoming entangled in debris or buried in the stream bottom.

Measurements of intestinal diameters provide an index of the progressive atrophy. Six specimens captured in August had a mean intestinal diameter of 0.67 inch. In 55 spent lampreys captured in June the mean intestinal diameter was 0.06 inch. Since the intestine had no noticeable taper, this measurement was taken at approximately the midregion. These values indicate a shrinkage of nearly 94 percent in the diameter of the sea lamprey's intestine prior to and during the spawning period.

Loss of Body Weight and Length

Length measurements and weights of 27 male and 37 female sea lampreys that were tagged on their upstream migration and recaptured after spawning, provided information on the absolute and percentage loss in weight and length (table 33).

Loss in weight during the spawning season amounted to 8.5 percent for males and 34.1 percent for females. There is little evidence of correlation between prespawning weight and subsequent percentage loss of weight.

Greater weight of sex products discharged by females at spawning accounts for part, but by no means all, of the sex difference in total loss of weight (table 34). In prespawning samples the testis made up 2.9 percent of the total weight of males and the ovary 17.5 percent of the total weight of females. The gonads did not disappear entirely, however, at spawning. An estimated 26 percent of the testis and 1 percent of the ovaries were present in the postspawning lampreys; consequently, the maximum estimated losses through discharge of sex products were 2.1 (2.9×0.74) percent for males and 17.3 (17.5×0.99) percent for females. Additional weight losses are accordingly 6.4 ($8.5-2.1$) percent for males and 16.8 ($34.1-17.3$) percent for females. The loss of weight in females, in addition to that attributable to discharge of sex products, is between 2 and 3 times that of males.

TABLE 33.—*Losses in length and weight of mature sea lampreys during the spawning season*

Item and sex	Prespawning value			Decrease			Percentage of decrease		
	Average	Minimum	Maximum	Average	Minimum	Maximum	Average	Minimum	Maximum
Length (inches):									
Males	14.9	12.6	18.0	1.7	0.8	2.6	10.9	5.9	16.8
Females	15.6	13.1	18.6	2.8	1.8	3.9	17.9	12.5	23.6
Weight (ounces):									
Males	3.30	2.26	6.35	.33	.04	1.06	8.5	.9	19.3
Females	4.52	2.29	7.80	1.54	.49	2.72	34.1	16.7	48.5

TABLE 34.—*Mean percentage composition of total weight made up by gonads and percentage losses in weight due to deposition of reproductive products and from other causes*

[Figures in parentheses are the number of specimens upon which the mean values are based]

Sex	Percentage				
	Body weight made-up by gonad		Loss in weight during spawning	Gonad remaining after spawning	Unaccountable loss in weight
	Apr. 19	May 15	May 30–June 8	May 30–June 8	May 15–June 8
Male	1.5 (10)	2.9 (10)	8.5 (27)	26 (10)	6.4
Female	12.8 (26)	17.5 (41)	34.1 (37)	1 (16)	16.8

Loss in length was 11 percent in males and 17.9 percent in females. In absolute measures this shrinkage amounted to a loss of several inches in total length. The sex difference in percentage loss of length was smaller than in percentage loss in weight. The percentage loss in length tended to be greater among the longer than among the shorter males, but in females no correlation between length and relative decrease in length was detectable.

EGG DEVELOPMENT AND HABITS OF AMMOCOETES

Egg Development

Freshly deposited sea lamprey eggs are light tan or cream color, nearly spherical, and have an average diameter of approximately 1 millimeter. This small size permits them to fall into the interstices of the gravel in the nest bottom where they are covered and protected during incubation.

An experiment in artificial propagation was conducted at the Cornell Experimental Fish Hatchery. One large partially spent female and several ripe male sea lampreys were used. Milt from one male lamprey was expelled into a basin which contained approximately one teaspoonful of water. Then the eggs, an estimated 15,000, were discharged into the basin, and milt from another male was added. The eggs were stirred with a feather for 1 minute. Next 1 cupful of water was added and the contents stirred for 10 minutes. The liquid was then decanted and replaced by 1 quart of water. After the eggs were stirred rather slowly for one-half hour they were placed in a Downing hatching jar. The water volume passing through the jar was adjusted to keep the eggs in motion without danger of flushing them from the jar.

One-third of the eggs hatched on June 17 (13 days), and the remainder the following day (14 days). Daily morning water temperatures during this period averaged 60.7° F. (extremes of 57° and 65° F.). The source of water used in hatching these eggs was Cascadilla Creek, in which water temperatures are similar to those of Cayuga Inlet.

At hatching, the anterior portion of the trunk emerges from the chorion. The posterior portion may remain within the egg case for as long as 1 day after the anterior end emerges. The yolk sac, which is located ventrally on the posterior half or two-thirds of the body, is expanded only slightly at its anterior portion, but ends in a globular mass posteriorly. This enlargement of the yolk sac tends to hold the posterior end of the ammocoete's body within the shell.

Habits of Ammocoetes

The first 2 days after hatching, the ammocoetes remained rather inactive. At this time they were 4 mm. long, still opaque, and of cream or light tan color. The caudal portion of the trunk, which was made up largely of yolk sac at this stage, was curved ventrally and anteriorly to give them a hooked appearance. This hook shape disappeared the third day after hatching, when the ammocoetes had absorbed most of the yolk. They very soon became somewhat translucent with a light suffusion of brown pigment dorsally and dorsolaterally.

After the yolk had been absorbed the ammocoetes became active and burrowed rapidly into the soft bottom. Partially buried specimens exhibited a negative phototropism. Newly hatched ammocoetes remain in the nest for several days, but later emerge in search of other niches. In Michigan, Applegate (1950) found that newly hatched ammocoetes left the nest between 18 and 22 days after fertilization. In Cayuga Inlet, the newly hatched ammocoetes were located along the stream margins, buried in the fine sand-silt sediment. Possibly they were present in the deeper waters also, but they may have been overlooked because of the difficulty in seeing such small creatures in deep water.

Larger ammocoetes occupy various habitats, but most commonly are found in sand and silt deposits into which they can easily burrow. Portions of the stream with medium to strong water currents and suitable sediments appear to be most satisfactory. Ammocoetes and transforming lampreys do not emerge from their burrows unless disturbed or unless radical changes occur in water conditions.

Observations on ammocoetes held in aquariums revealed their method of burrowing. They penetrate the bottom sediments by thrusting the head downward perpendicular to the bottom and making very rapid undulatory motions. As soon as the snout and head enter the bottom they draw the body downward by constant undulation of the head and snout in an S-shaped pattern. After the trunk is approximately two-thirds buried, the swimming motions of the posterior end cease, but the undulations of the anterior end continue to pull the body into the sediment. The ammocoetes begin to turn in a horizontal direction after approximately half the body is buried. They then gradually move toward the surface of the sediment until a second opening to the water has been made. This maneuver forms a U- or crescent-shaped burrow. The sediment fills in the burrow behind the posterior end of the ammocoete. All the water which provides food and oxygen passes through the remaining entrance.

Mucus secreted by the ammocoete lines the burrow and holds the particles of the bottom material in place. This lining prevents the entrance to the burrow from collapsing when the ammocoete retracts within it. The burrow is believed to be a stable excavation within which the ammocoete lives until driven from it, or until it is destroyed by floods or other forces. Once the ammocoete leaves the burrow it constructs a new one immediately. The length of the burrow is usually less than twice the occupant's length and commonly only 1½ times its length. When mildly disturbed, the ammocoete moves backward, away from the mouth of the burrow. When severely disturbed it leaves the burrow and swims rapidly away to enter the bottom sediment at another location.

Details of the respiration and feeding processes are not thoroughly known. Expansion and contraction of the branchial chamber, together with action of the velum, pump a continuous stream of water into the ammocoete's oral chamber and out the gill openings. The oral papillae spread branchlike across the entrance to the oral hood. These papillae constitute an excellent strainer to prevent large undesirable matter from entering, and a coating of mucus adds to its effectiveness. Water passes through the branchlike sieve into the gill chambers, and after leaving the gill pouches continues to move backward along the ammocoete's body and gradually filters upward through the sediment.

Food and Feeding

Creaser and Hann (1928) reported micro-organisms, primarily algae, in the digestive tracts of ammocoetes. The most common kinds of algae were diatoms and desmids. Sand grains were found in all ammocoetes examined. Although the number of protozoans was small, the authors believed that they probably furnished a generous portion of the diet, but were more quickly digested than the hard diatoms and desmids. Analysis of the water and bottom deposits from the habitat in which the larvae were living indicated that lamprey larvae obtained their food from the water and not from the sediments in which they burrowed.

Results of analyses for a few ammocoetes from Cayuga Inlet correspond closely with the observations made by Creaser and Hann. The only important difference was that Cayuga Inlet specimens contained a relatively large amount of periphyton. Crystals of sand were common, although as a rule the particles were very fine (0.125–0.062 mm.), only a fraction the size of sand grains predominant in the area.

Of importance in feeding is the endosytle, a mucus-secreting gland, located in the floor of the pharynx. According to Newth (1930), dorsoventral ridges lead out of the endostyle to form a hollow cone of mucus threads to which the food particles adhere as the water passes through. The mucus thread, with its adherent particles, is slowly drawn caudally into the alimentary tract. The accumulated mat of foreign particles is periodically thrown off the oral papillae by a reversal of the water current. Thus it appears that the only selection of "food" by ammocoetes is on the basis of particle size.

Duration of Larval Life

Past estimates of the duration of larval life of the sea lamprey have been based on different sizes of ammocoetes taken at any one time and, in more critical studies, on the identification of age groups determined from modes in length-frequency distributions. Use of the Petersen method is so well established that detailed comments on it need not be given here. Ordinarily the youngest age groups can be identified easily and accurately. Interpretations become less dependable in older groups in which extensive overlap of the distribution of adjacent age groups tends more and more to obscure the modes.

Schultz (1930) explored three statistical methods for evaluating the significance of modes as indicators of age groups in the length-frequency distribution of several thousand ammocoetes of *Lampetra planeri*. Results of this work are summarized by his statement: "A statistical analysis of the data shows the minor modes are not significant and do not represent year classes. They are rather accidental modes owing to sampling." Other workers, however, among them Okkelberg (1921 and 1922) and Hardisty (1951), have employed this method with apparently satisfactory results. The lack of a better method compelled its use in the present inquiry.

Earlier investigators of the sea lamprey in Cayuga Lake gave no quantitative data upon which their estimates of length of larval life were based. Surface (1899) stated that the ammocoete stage lasted at least 3 or possibly 4 years. Gage (1928), who based his opinion on observations of ammocoetes captured throughout the year, believed that the duration of larval life "could not be less than 4 years."

The most detailed study of the duration of larval life of the sea lamprey was that carried out by Applegate (1950) in Michigan. Length-frequency distributions of extensive collections made during August, October, and May led him to conclude that the length of larval life, including the period when transformation is occurring, was 4 years. He also stated that a rest period of 1 year, the last year of larval life, was possible.

The present study of the duration of larval life of Cayuga Lake sea lampreys was based on ammocoetes taken from a 1-mile stretch, section *C*, of Cayuga Inlet (fig. 10) located approximately 2 miles upstream from Cayuga Lake. Water depth in this section approached a maximum of 5 feet in the deepest pools; however, most of the area was considerably shallower, so that ammocoete collections were made with reasonable efficiency. Collections were made during July 1950 and 1951 by digging, seining, and with the aid of an electric shocker. Collections in August 1951 were made entirely by use of the electric shocker. Small ammocoetes (young of the year and yearlings) were not readily collected by this method. However, since young and yearlings form distinct groups in the length-frequency distribution, relatively few specimens were necessary to establish their modal lengths.

Total length, from the anterior tip of the oral hood to the posterior margin of the caudal fin, was measured to the nearest mm. Weight was recorded to the nearest 0.01 gram. All measurements were made on fresh specimens anesthetized in a 1- to 3-percent solution of urethane.

Characteristics described by Vladykov (1950) made it possible to distinguish sea lamprey ammocoetes from larvae of the American brook lamprey, *Lampetra lamottei*, the only species of lamprey other than the sea lamprey that occurs in Cayuga Inlet. If any misidentifications of species took place, they were among the young of the year and yearlings.

In the discussion of the data on the length-frequency distribution of Cayuga Lake ammocoetes (table 35), attention is given first to measurements made on specimens collected in July (cols. 3, 4, 5, table 35; fig. 16) since in these collections only members of age groups 0 and I were taken in sufficient numbers to establish their modal lengths. Distinct modes at lengths of 0.47 and 1.46 inches represent age group 0 (approximately 1 month old) and age group I, respectively. Less definite modes at lengths of 2.64, 3.54 (estimated from minor peaks at lengths of 3.23 and 3.82 inches), 4.21, 5, 5.59, and 6.10 inches are presumed to represent the average lengths of age groups II through VII. It is recognized that some of these modes are based on a few specimens and could be due to chance variation alone. Specimens in the stage of transformation were not present in the July collections since metamorphosis does not begin until August, or at least it is not externally detectable until then.

Comparison of length frequencies of sea lamprey ammocoetes collected in July and in August 1951 indicates definitely that young-of-the-year (age group 0) ammocoetes were not represented in the August collection; furthermore, few if any 1-year-olds (age group I) were taken in August. This judgment, based primarily on comparisons with

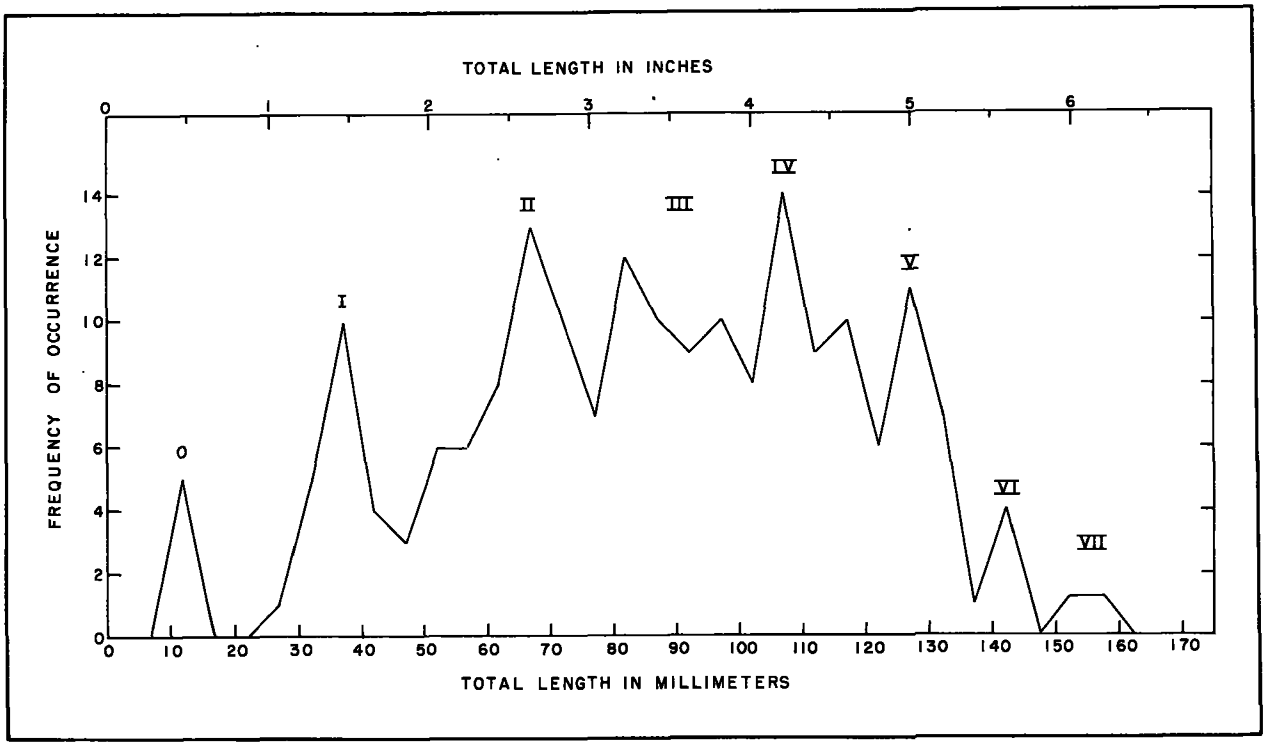

FIGURE 16.—Length-frequency distribution of sea lamprey ammocoetes taken from Cayuga Inlet during July.

TABLE 35.—*Length-frequency distribution of ammocoetes and transforming sea lampreys collected in Cayuga Inlet during July and August*

[The lengths are grouped by 5-mm. intervals]

Length class (millimeters)	Midpoint of length class (inches)	Length-frequency distribution of ammocoetes					Transforming specimens, August 1951
		July			August 1951	Total July and August	
		1950	1951	Total			
<5	0.08						
5-9	.27						
10-14	.47	5		5		5	
15-19	.67						
20-24	.87						
25-29	1.06	1		1		1	
30-34	1.26	5		5		5	
35-39	1.46	10		10		10	
40-44	1.65	4		4	2	6	
45-49	1.85	3		3	2	5	
50-54	2.05	3	3	6	6	12	
55-59	2.24	5	1	6	5	11	
60-64	2.44	8		8	5	13	
65-69	2.64	12	1	13	4	17	
70-74	2.83	10		10		10	
75-79	3.03	6	1	7	3	10	
80-84	3.23	11	1	12	10	22	
85-89	3.43	7	3	10	1	11	
90-94	3.62	9		9	6	15	
95-99	3.82	7	3	10	8	18	
100-104	4.02	6	2	8	10	18	
105-109	4.21	10	4	14	13	27	
110-114	4.41	2	7	9	15	24	
115-119	4.61	5	5	10	10	20	1
120-124	4.80	3	3	6	23	29	1
125-129	5.00	3	8	11	21	32	3
130-134	5.20	1	6	7	14	21	5
135-139	5.39		1	1	7	8	12
140-144	5.59	1	3	4	7	11	11
145-149	5.79				6	6	7
150-154	5.98		1	1	2	3	5
155-159	6.18		1	1	1	2	2
160-164	6.38						3

July collections from Cayuga Inlet, is also supported by data presented by Applegate (1950), who demonstrated that in Michigan the 0 group had a mean length of 0.63 inch and age group I had a length of 1.77 inches. It seems reasonable to assume, therefore, that the mode at 2.24 inches in figure 17 represents age-group II. It follows then, that modes at lengths of 3.23, 4.21 (corrected from the asymmetrical mode at 4.41) 4.80, and 5.51 inches represent age groups III through VI. Transforming ammocoetes (VII group) form a mode at approximately 5.51 inches.

Grouping of the July and August catches of ammocoetes and transforming sea lampreys resulted in a somewhat smoother length-frequency distribution (cols. 7, 8, table 35; fig. 18). Distinct modes at 0.47, 1.46, 2.36 (corrected from minor modes at 2.05 and 2.64), 3.23, 4.21, 5, and 5.59 inches represent age groups 0 through VI. The transforming lampreys form a nearly normal distribution with a modal length of 5.39 inches (age group VII).

Weights as well as lengths are available for ammocoetes and transforming sea lampreys collected from Cayuga Inlet during August 1951 (table 36; fig. 19). Six definite modes are present

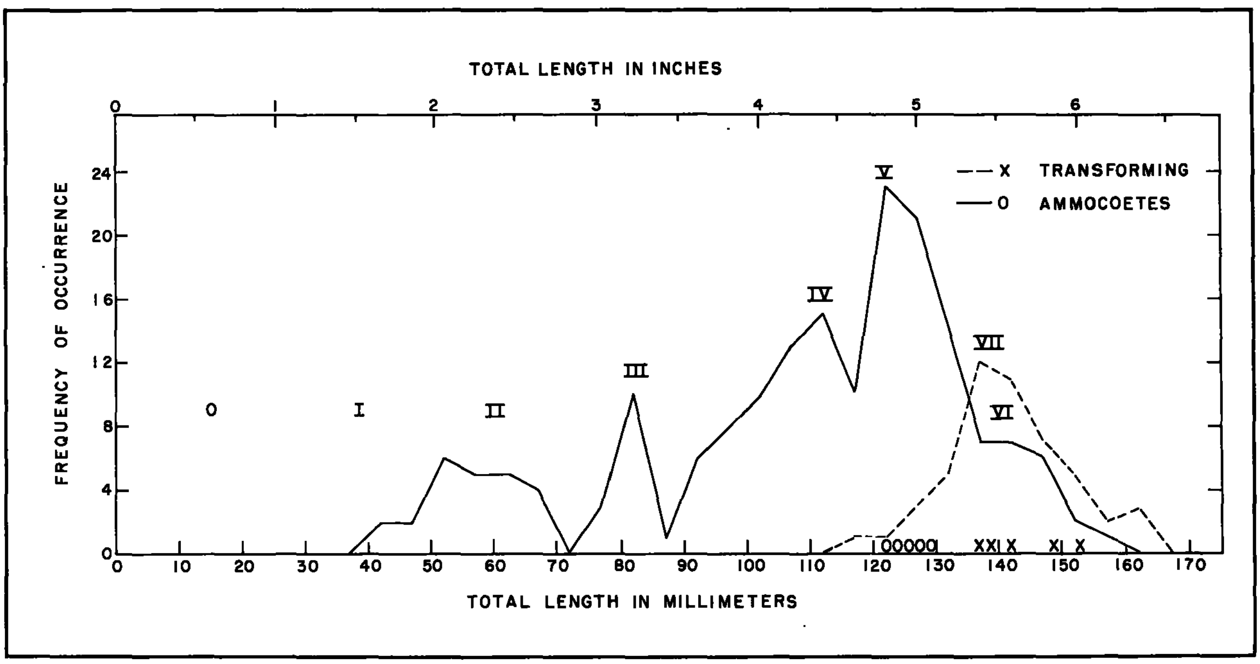

FIGURE 17.—Length-frequency distribution of sea lamprey ammocoetes and transforming specimens taken from Cayuga Inlet during August.

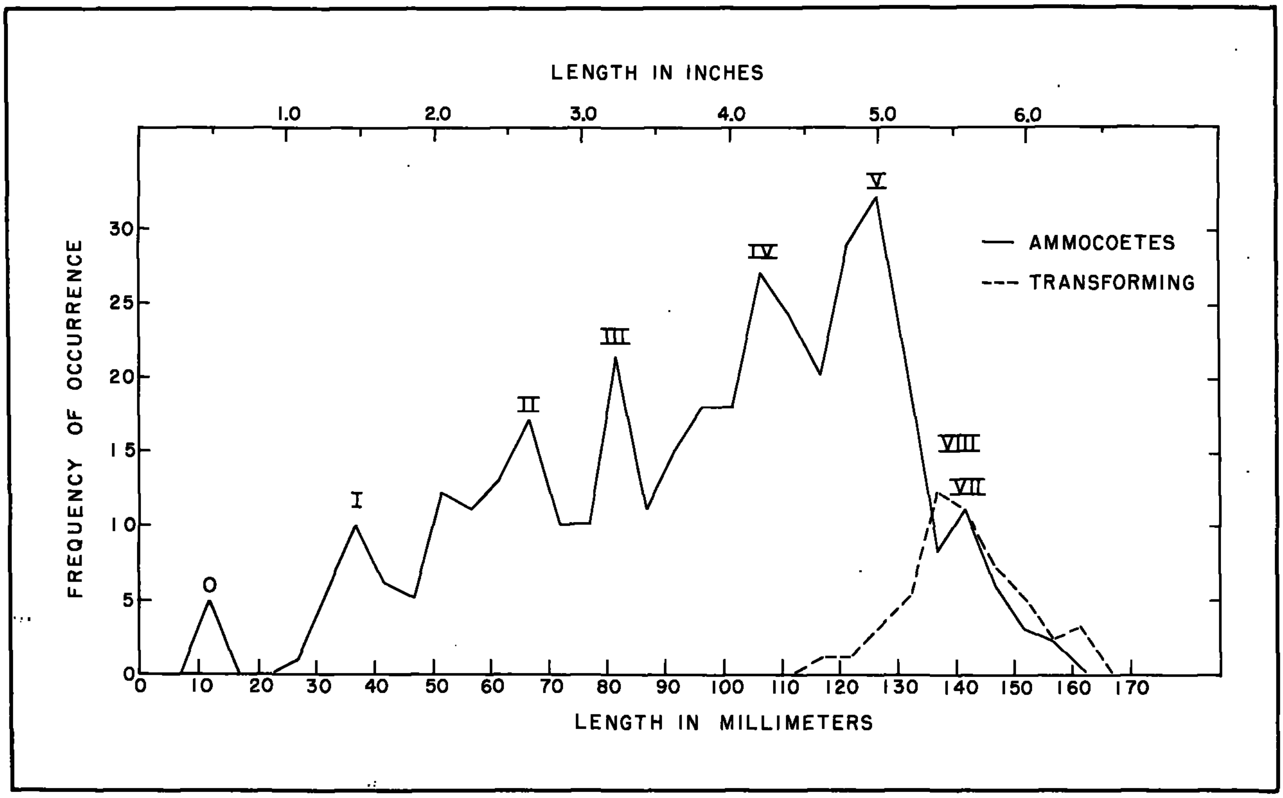

FIGURE 18.—Length-frequency distribution of sea lamprey ammocoetes (solid line) and transforming specimens (broken line) taken from Cayuga Inlet during July and August.

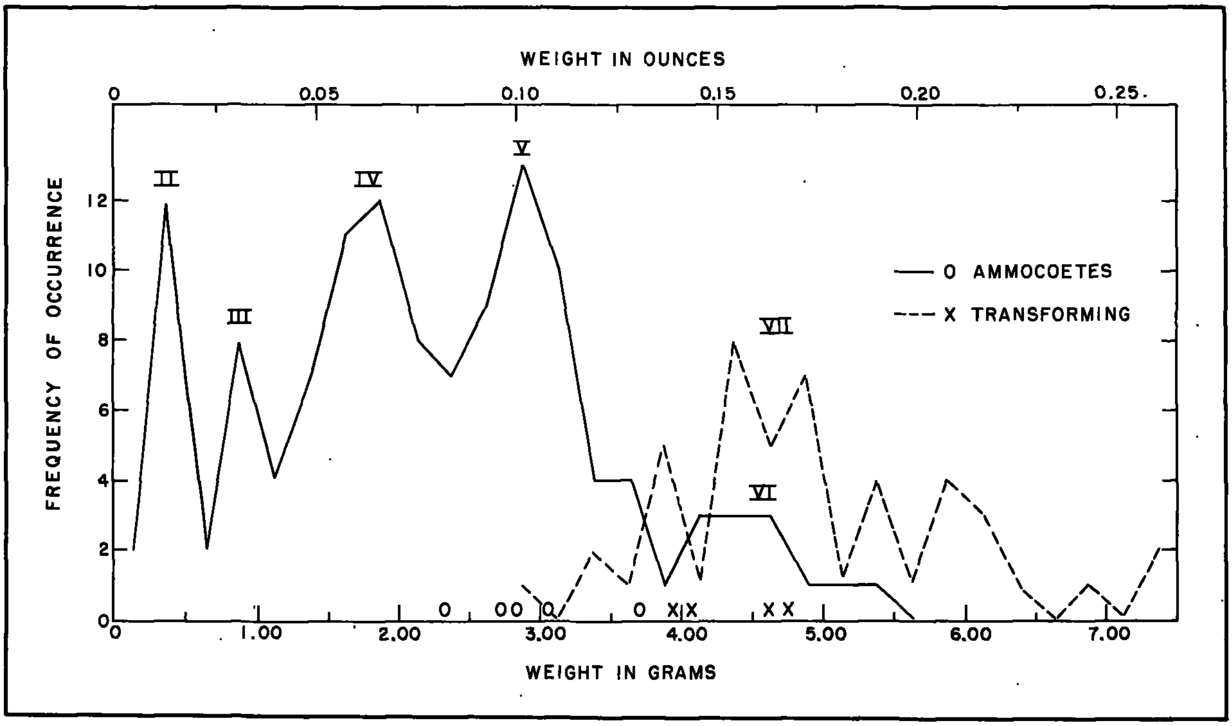

FIGURE 19.—Weight-frequency distribution of sea lamprey ammocoetes and transforming specimens taken from Cayuga Inlet, August 1951.

in the weight-frequency graph, the largest of which is composed of the transforming ammocoetes (believed to be only one age group). Since age groups 0 and I were established to be lacking in the August collections, a justified assignment of ages to the modes on the weight-frequency graph is as follows: 0.013 ounce, age group II; 0.031 ounce, age group III; 0.066 ounce, age group IV; 0.101 ounce, age group V; 0.154 ounce, age group VI; 0.172 ounce, age group VII (the transforming ammocoetes).

TABLE 36.—*Weight-frequency distribution of ammocoetes and transforming sea lampreys collected in Cayuga Inlet during August*

[Weights are grouped by 0.25-gram intervals]

Weight class (grams)	Midpoint of weight class (tenths of ounces)	Frequency	
		Ammocoetes	Transforming sea lampreys
<0.25	0.04	2	
0.25–0.49	.13	12	
0.50–0.74	.22	2	----------
0.75–0.99	.31	8	----------
1.00–1.24	.40	4	----------
1.25–1.49	.48	7	----------
1.50–1.74	.57	11	----------
1.75–1.99	.66	12	----------
2.00–2.24	.75	8	----------
2.25–2.49	.84	7	----------
2.50–1.74	.92	9	----------
2.75–2.99	1.01	13	1
3.00–3.24	1.10	10	----------
3.25–3.49	1.19	4	2
3.50–3.74	1.28	4	1
3.75–3.99	1.36	2	5
4.00–4.24	1.45	3	1
4.25–4.49	1.54	3	8
4.50–4.74	1.63	3	5
4.75–4.99	1.72	1	7
5.00–5.24	1.81	1	1
5.25–5.49	1.89	1	4
5.50–5.74	1.98	----------	1
5.75–5.99	2.07	----------	4
6.00–6.24	2.16	----------	3
6.25–6.49	2.25	----------	1
6.50–6.74	2.33	----------	----------
6.75–6.99	2.42	----------	1
7.00–7.24	2.51	----------	----------
7.25–7.49	2.60	----------	2

The distinctiveness of the modes in the weight-frequency distribution (fig. 19) is striking. Even more significant is the agreement between estimates of age made independently from length and weight distributions. From the data on the length-weight relation of ammocoetes (table 37; fig. 20) it is seen that modal lengths and modal weights agree; it may be concluded that the same general groups of ammocoetes were identified by the two methods. Although analyses of the length and weight frequencies led to the same results, the weight-frequency method seems to be the better because of greater precision in defining age groups.

TABLE 37.—*Length-weight relationship of ammocoetes and transforming sea lampreys from Cayuga Inlet*

AMMOCOETES

Length (inches)	Weight (ounces)	Length (inches)	Weight (ounces)	Length (inches)	Weight (ounces)
1.65	0.006	4.13	0.063	4.96	0.102
1.97	.009	4.13	.065	4.96	.106
2.05	.009	4.17	.056	5.00	.092
2.09	.012	4.17	.063	5.00	.098
2.13	.010	4.17	.067	5.00	.099
2.20	.011	4.17	.069	5.04	.103
2.20	.013	4.21	.060	5.04	.108
2.24	.012	4.21	.066	5.04	.127
2.32	.016	4.25	.069	5.08	.098
2.40	.015	4.29	.040	5.08	.099
2.40	.015	4.33	.067	5.08	.103
2.40	.016	4.33	.073	5.08	.106
2.40	.017	4.33	.074	5.12	.110
2.68	.018	4.37	.062	5.12	.115
2.68	.019	4.41	.060	5.16	.106
2.72	.021	4.41	.079	5.16	.107
2.95	.023	4.45	.069	5.16	.110
3.07	.028	4.45	.070	5.20	.110
3.11	.030	4.45	.078	5.20	.111
3.23	.029	4.49	.066	5.20	.115
3.23	.032	4.49	.077	5.24	.104
3.27	.032	4.49	.079	5.24	.108
3.31	.032	4.57	.078	5.27	.112
3.31	.036	4.57	.080	5.27	.117
3.31	.038	4.57	.080	5.27	.124
3.39	.031	4.57	.088	5.31	.109
3.62	.045	4.65	.079	5.43	.142
3.66	.038	4.65	.082	5.47	.132
3.66	.045	4.65	.095	5.51	.136
3.74	.045	4.72	.082	5.51	.150
3.74	.059	4.76	.082	5.55	.143
3.78	.057	4.80	.086	5.55	.147
3.86	.050	4.80	.091	5.59	.152
3.86	.057	4.84	.089	5.63	.131
3.90	.055	4.84	.090	5.71	.163
3.98	.048	4.88	.095	5.83	.158
3.98	.048	4.92	.089	5.87	.168
4.02	.050	4.92	.096	5.87	.168
4.06	.056	4.92	.099	5.94	.193
4.09	.057	4.92	.106	6.02	.162
4.09	.060	4.96	.097	6.14	.185
4.13	.063	4.96	.100		

TRANSFORMING SEA LAMPREYS

Length (inches)	Weight (ounces)	Length (inches)	Weight (ounces)	Length (inches)	Weight (ounces)
4.69	0.117	5.43	0.159	5.79	0.167
4.88	.102	5.47	.151	5.79	.173
5.00	.123	5.47	.160	5.79	.198
5.12	.133	5.51	.166	5.79	.207
5.12	.134	5.51	.173	5.83	.183
5.20	.127	5.55	.148	5.90	.207
5.20	.133	5.59	.169	5.98	.221
5.20	.155	5.59	.188	6.02	.204
5.24	.139	5.63	.173	6.06	.215
5.27	.155	5.67	.156	6.06	.243
5.35	.139	5.67	.167	6.22	.209
5.35	.151	5.67	.171	6.26	.213
5.39	.152	5.67	.172	6.34	.258
5.39	.165	5.67	.188	6.42	.258
5.39	.172	5.71	.168	6.46	.228
5.43	.154	5.75	.192		

The most questionable aspect in the interpretation of the length-frequency data on Cayuga Lake ammocoetes concerns the validity of age group VI, a group for which the mode was little apparent in the August frequencies and whose size was slightly, if at all, greater than that of transforming lampreys. Evidence that the VI group is valid was obtained from experiments with marked specimens. In this experiment a series of sea lamprey

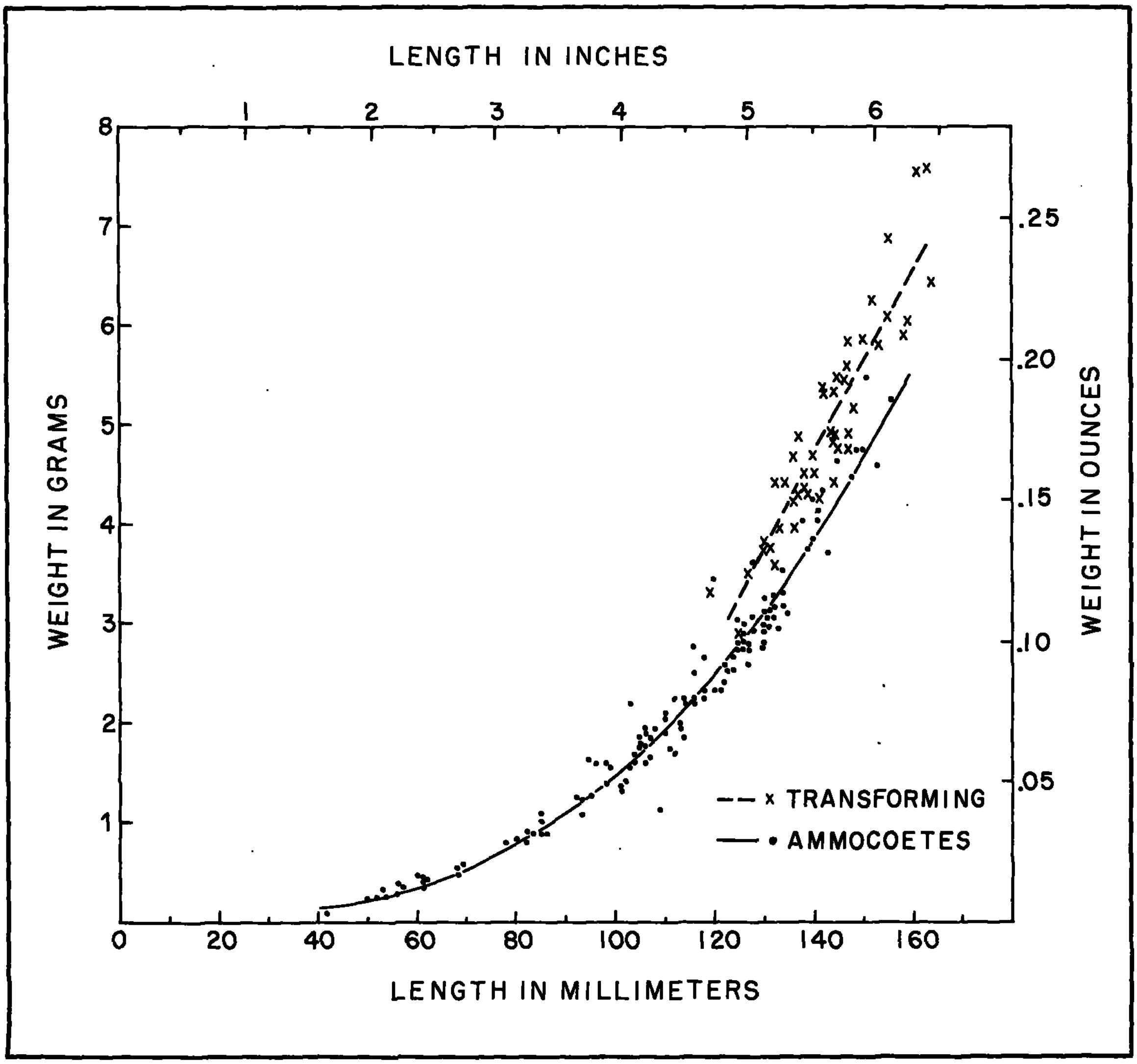

FIGURE 20.—Length-weight relationship of sea lamprey ammocoetes and transforming specimens taken from Cayuga Inlet during August. Regression formulas: for ammocoetes, $Y=1.63-0.0354\ X+0.0004\ X^2$; for transforming lampreys, $Y=5.02+0.1667\ X-0.0003\ X^2$.

ammocoetes captured in Cayuga Inlet were marked with cadmium sulfide or mercuric sulfide, as described by Wigley (1952), and installed in an outdoor hatchery raceway. The raceway bottom was covered with several inches of sand and silt, and water was supplied from Cascadilla Creek. Marked specimens with body lengths of 5.43, 5.43, 5.59, 5.91, and 6.02 inches (approximately the length of age group VI) on August 24, 1951, began transforming in August 1952. Furthermore, marked specimens 4.80, 4.80, 4.92, 4.92, and 5.12 inches long (about the length of age group V) on August 6, 1951, kept in the same raceway with the previous group, did not transform in 1952. These specimens are plotted in the length- and weight-frequencies of figures 17 and 19. This information and the modes indicated in all length- and weight-frequency distributions not only give convincing evidence that the recognition of age group VI is valid, but lends support to the validation of recognizing other modes in the length- and weight-frequency distributions.

Although the present study has yielded the strongest evidence for a larval life of 7 years, as compared with 3 to 5 years propounded by previous investigators, these findings should be accepted with reservation. It should be emphasized, however, that most of the estimates of the duration of larval life which have been made were nothing more than subjective estimates based on relatively small samples. Moreover, prior to 1950 zoologists were unable to identify ammocoetes of the several species of lampreys. In view of the methods employed in the present investigation, and the consistency of the results, the findings presented herein are believed to be reliable.

Growth of sea lamprey ammocoetes was such that the annual increment in body length decreased with age, whereas the annual increment in body weight increased with age (table 38). The yearly increase in body length during the first 2 years of life was approximately 1 inch. Then, from the second year until time of transformation at the age of 7 years, the annual increase in length declined steadily. During the seventh year of life (age group VI) the length increment was approximately one-half inch. A loss in length of nearly one-half inch took place during the initial stages of transformation.

TABLE 38.—*Growth of ammocoetes in Cayuga Inlet as estimated from length-frequencies of specimens collected during July and August*

Age group	July		August		July and August	
	Length (inches)	Increment of length	Length (inches)	Increment of length	Length (inches)	Increment of length
0	0.47				0.47	
I	1.46	0.99			1.46	0.99
II	2.64	1.18	2.24		2.36	.90
III	3.54	.90	3.23	0.99	3.23	.87
IV	4.21	.67	4.21	.98	4.21	.98
V	5.00	.79	4.80	.59	5.00	.79
VI	5.59	.59	5.51	.71	5.59	.59
VII	6.10	.51	[1] 5.51	0	[1] 5.39	(—.20)

[1] Transforming sea lampreys.

Body weight of ammocoetes increased slowly during their early years but increased progressively with age. The annual increments in weight during the third through seventh years of life were: 0.018, 0.035, 0.035, 0.053, and 0.018 ounce. Ammocoetes in age group VII weighed 0.183 ounce just prior to transformation.

Transformation and Downstream Movement

The anatomical changes that take place during the transformation from the larval to the parasitic stage have been described by Gage (1928). According to Gage, transformation starts between mid-July and early September. This statement agrees with my observations. Few sea lampreys were found in the transforming stage in early August. In late August numerous specimens were in an advanced stage of transformation but few were in the early stage. These observations suggest that gross, externally visible morphological changes are completed within a period of 1 or 2 weeks after transformation begins. In contrast, it appears that internal changes are not completed before January and probably not until March.

Progress of transformation was followed in a group of sea lampreys kept in a hatchery trough, the bottom of which was provided with sediment from a streambed. From time to time during October, November, and December five specimens were dug from the sediment and put in company with a 7-inch rainbow trout, *Salmo gairdneri*, for a 10-day period. None of the lampreys fed upon or attempted to feed upon the trout. By March 13 all transforming or transformed sea lampreys kept in the trough had emerged from the bottom sediment and were clinging to the head end of the trough. A 7.8-inch brook trout, *Salvelinus fontinalis*, placed in the trough on that day, was immediately attacked by two of the lampreys. Later examination proved they had been feeding.

Measurements and weights of marked transforming sea lampreys kept in hatchery troughs under conditions corresponding to those described in the preceding paragraph provided information on changes in length and weight during transformation. Of 14 transforming specimens installed on August 24, 1951, and reweighed and remeasured on March 13, 1952, all lost weight (table 39). The individual losses ranged from 0.011 to 0.026 ounce, an average 0.019 ounce. Length, however, increased in 13 (the length of one specimen did not change). Increases in length ranged from 0.09 to 0.51 inch and averaged (for all 14) 0.28 inch.

Transforming sea lampreys in Cayuga Inlet were commonly found in bottom sediments composed of gravel one-fourth to three-fourth inch in diameter. Smaller ammocoetes, as has been shown, usually inhabit sediments of sand and silt where the particle size is much smaller.

The capture of transforming and large-sized ammocoetes in the very headwaters of Cayuga Inlet, in the vicinity of West Danby (fig. 10, section *K*), indicates that no important downstream movement takes place during the larval period in that portion of the stream. Since the stream is small in that area, roughly 2 to 6 feet wide and with a flow of 1 to 5 cubic feet per second, it is doubtful whether floods are severe enough to wash out the ammocoetes and force them downstream. In the middle and lower reaches of Cayuga Inlet, severe floods surely must be capable of such action, but data on actual effects of flooding are not available.

TABLE 39.—*Length and weight of transforming sea lampreys measured Aug. 24, 1951, and Mar. 13, 1952*

[The lampreys were marked individually]

Length (inches)			Weight (ounces)		
Aug. 24, 1951	Mar. 13, 1952	Difference	Aug. 24, 1951	Mar. 13, 1952	Difference
5.00	5.51	+0.51	0.123	0.112	−0.011
5.20	5.28	+.09	0.127	.105	−.022
5.28	5.51	+.24	0.155	.135	−.019
5.35	5.79	+.43	0.151	.136	−.014
5.39	5.67	+.28	0.152	.128	−.024
5.43	5.43	0	0.142	.124	−.018
5.47	5.67	+.20	0.151	.133	−.018
5.67	5.75	+.09	0.172	.146	−.026
5.79	6.02	+.24	0.167	.153	−.014
5.79	6.14	+.35	0.172	.152	−.020
5.79	6.22	+.43	0.207	.186	−.022
6.02	6.26	+.24	0.204	.183	−.020
6.10	6.42	+.31	0.215	.195	−.020
6.22	6.69	+.47	0.209	.187	−.022
Mean		+.28	Mean		−.019

Six transforming sea lampreys captured in Cayuga Inlet during August 1951 were examined for food content. None of the digestive tracts contained food; in fact, they were almost without a lumen. That newly transformed sea lampreys can endure long periods without food was indicated by the survival of two specimens in a hatchery raceway from August until the following May, a 9-month period.

PARASITIC HABITS

Sea Lamprey Parasitism on Lake Trout in Cayuga and Seneca Lakes

The direct estimation of possible harmful effects of the sea lamprey upon populations of lake trout is made difficult by the deepwater habitat of both lampreys and trout. Biologists have long recognized the sea lamprey as a dangerous predator on food and game fishes. Half a century ago Surface (1898) made the statement, "* * * we have no doubt that in this region [Finger Lakes] the lampreys destroy more fish than do all the other enemies of fish or all of the fishermen combined."

He based this statement on the frequency of lamprey scars and wounds on fish from Cayuga Lake. According to Surface, more than 90 percent of the brown bullheads, *Ictalurus* [*Ameiurus*] *nebulosus*, nearly 80 percent of the white suckers, *Catostomus commersoni*, and nearly all the lake trout, *Salvelinus* [*Cristivomer*] *namaycush*, had suffered attacks by the sea lamprey.

Three decades later, Gage (1928) calculated that approximately 3 pounds of fish blood were necessary to feed one lamprey from youth to maturity. In his aquarium studies, Gage also found that most fish of relatively large size survived the lamprey's attack; small ones succumbed.

In 1949, Webster [7] placed rainbow trout, smallmouth bass, and white suckers, all 18 inches or less in length, in aquariums with nearly full-grown sea lampreys. One attack by a large (9 to 17 inches) lamprey was usually sufficient to cause death to fish of all three species.

More ominous evidence of the sea lamprey's devastating capabilities comes from the Great Lakes. Commercial lake trout catches declined disastrously in both Lake Huron and Lake Michigan during the years of tremendous increase in the sea lamprey population (Hile, 1949; Hile, Eschmeyer, and Lunger, 1951).

Royce (1950) compared the body weights of lake trout from Seneca Lake in which the species had suffered varying degrees of lamprey parasitism. He found no statistical differences in weight related to lamprey parasitism. The lake trout studied by Royce were relatively large, 22 to 33 inches long.

Information for the present study on the lamprey's effect on the lake trout in Cayuga Lake was gathered during 1949–51 activities of the New York State Conservation Department, Finger Lakes investigations,[8] which included the capture of lake trout from Cayuga Lake each summer and fall. The trout were taken by means of experimental gill nets with mesh sizes that ranged from 1 to 6 inches, extension measure. Lake trout 5 to 31 inches in fork length were caught. Nets were set during the afternoon and lifted the following morning. Possibly the congregation of lake trout caught in the nets attracted the sea lamprey to them in unnatural numbers, and, of course, the lake trout were helpless to escape attack. Be-

[7] Mortality caused by lamprey eels in aquarium experiments. Unpublished research memorandum, Department of Conservation, Cornell University, January 17, 1949. 4 pages.

[8] Data from the Finger Lakes investigations are published with permission from Dr. D. A. Webster.

cause of the relatively short time the nets were fishing, it is believed that the data are not unduly biased by attacks on trout in the nets.

A total of 1,372 lake trout were examined for lamprey scars and wounds. All were measured, but to minimize injury from handling during warm weather, only about 700 were weighed. Fork length [9] was measured to the nearest 0.1 inch and weight was measured on a Chatillon spring balance to the nearest ounce.

In this discussion, a wound is any place of lamprey attachment where the skin has been perforated and has not healed. Hemorrhaged blood vessels and inflamed tissues produce a red appearance. A scar is a wound that has healed. The lacerated tissues have coalesced and the red coloration has disappeared. The condition of marks was rarely such as to make the classification (scar or wound) questionable. That initial healing may take place within a few days was indicated by observations on brook trout held in hatchery troughs.

Loss of body weight resulting from sea lamprey attacks

Before analysis to detect and measure possible effects of sea lamprey attacks on the weight of lake trout could be undertaken, it was necessary to determine whether or not the length-weight relation differed between the sexes or from year to year. For this purpose 19 unscarred males and 19 unscarred females were selected at random from each of the collections made in 1949, 1950, and 1951. The analysis of covariance (after transformation of lengths and weights to logarithms to assure approximately linear regression) disclosed no significant differences among the several groups. Data for the sexes and the different years of capture could accordingly be combined in all further analyses.

Relation between body weight and number of scars and wounds.—Death is not inevitable to all lake trout that are attacked by a sea lamprey. The numerous trout that possess scars or wounds resulting from sea lamprey attacks offer proof. However, trout which have survived an attack may or may not have suffered a setback in growth. From the loss of blood alone it seemed likely that losses in body weight would result. Furthermore, it was reasoned that any immediate weight loss would be directly correlated with the number of lamprey wounds, and a permanent weight loss would be directly correlated with the number of lamprey scars.

Royce (1950) demonstrated that thinness was not correlated with the number of lamprey attacks on relatively large lake trout. The possibility remained, however, that small lake trout might suffer adverse effects from lamprey attacks; consequently the present study was restricted to lake trout ranging from 9 to 22 inches in length.

Lake trout whose lengths were within the size range just mentioned were divided into three major classes based on the number of scars borne by each trout. Each class was subdivided into three classes based on the number of wounds borne by each trout (table 40). The major classes were as follows: Trout without lamprey scars; trout with one lamprey scar; and trout with two or more lamprey scars. Subclasses were: trout without lamprey wounds; trout with one lamprey wound; and trout with two or more lamprey wounds. Fifteen lake trout were taken at random from each category to provide a total of 135 specimens for the analysis.

TABLE 40.—*Mean adjusted weights and rank order of weight classes of 9 groups of lake trout*

Class		Adjusted weight (ounces)	Total rank order	Wound rank order	Scar class adjusted weight (ounces)	Scar class rank order
Number of scars	Number of wounds					
0	0	27.1	1	1		
	1	25.6	4	2		
	2+	23.7	8	3	25.4	1 or 2
1	0	26.0	3	1		
	1	25.2	5	2		
	2+	25.1	6	3	25.4	1 or 2
2+	0	26.8	2	1		
	1	25.1	7	2		
	2+	23.7	9	3	25.1	3

The hypothesis that there was no difference in weight among the scar classes or among the wound subclasses was tested by an analysis of covariance. The analysis for scars produced an F value that was not significant, thus indicating that the null hypothesis should be accepted (table 40). The adjusted weights of the scar classes indicate that lake trout with the highest incidence of lamprey scars are the thinnest, but, as is shown by the scar-class rank order, the trend is not consistent.

[9] The conversion formula for transforming fork length to total length is: $T=1.082\ F+0.045$, where T equals total length and F equals fork length. Initial study on the recovery and relative survival of fingerling and yearling lake trout stocked in Cayuga Lake, by William G. Bentley, M.S. thesis, Cornell University, June 1950.

According to these data, sea lamprey attacks, indicated by scars, do not produce a significant permanent change of weight.

The analysis for wounds produced an F value that is highly significant ($F=6.74$ where $F_{.01}=4.78$). Reference to the wound rank column in table 40 reveals exactly the order that would be expected on an a priori basis; i.e., the lake trout with the greatest number of wounds weigh the least. It is concluded from these data that lake trout which survive a sea lamprey attack suffer a significant temporary loss in weight.

Relation between the size of lake trout and the effect of sea lamprey attacks.—To learn the effect of sea lamprey attacks on trout of different sizes, and at the same time to verify the previous conclusion that lake trout with more lamprey wounds are thinner than those with fewer wounds, another analysis of covariance was carried out. Trout in three length classes and three wound-incidence classes were tested for thinness. To obtain sufficient range in size, lake trout between 10 and 25.9 inches in length were utilized. The lake trout were divided into the major classes according to their length, and each class was subdivided according to the number of lamprey wounds on each trout (table 41). The length classes were: 10 to 15.9 inches; 16 to 20.9 inches; and, 21 to 25.9 inches. The subclasses were: trout without lamprey wounds, trout with one lamprey wound, and trout with two or more lamprey wounds. Twenty-three trout were taken at random from each of the nine categories, giving a total of 207 lake trout in this analysis.

Results of the covariance analysis reveal a highly significant difference in weight among the wound classes ($F=19.62$ where $F_{.01}=4.71$). Reference to the adjusted-body-weight column and the wound-rank column in table 41 discloses that lake trout with the greatest number of sea lamprey wounds are the thinnest. This finding supports the conclusion reached in the previous analysis.

That small lake trout suffer more severe weight losses than do large trout is indicated by the highly significant F value ($F=51.27$ where $F_{0.01}=3.41$) in the test for interaction of lamprey wounds on lake trout body length. Furthermore, when the nonwounded subclass in each length class is omitted from the calculation of mean adjusted weights, the smallest trout (10 to 15.9 inches) are much lighter than the larger trout. The two larger length classes (16 to 20.9 inches, and 21 to 25.9 inches) have the same mean weight.

TABLE 41.—*Mean adjusted weights and rank order of length classes and wound classes of lake trout*

Class: Length (inches)	Class: Number of wounds	Adjusted weight (ounces)	Total rank order	Wound rank order	Length class adjusted weight (ounces)	Length class rank order [1]
10.0–15.9	0	37.5	3	1		
	1	35.2	6	2		
	2+	31.4	9	3	33.3	3
16.0–20.9	0	39.1	1	1		
	1	36.6	5	2		
	2+	35.2	7	3	35.9	1 or 2
21.0–25.9	0	36.7	4	2		
	1	37.8	2	1		
	2+	34.0	8	3	35.9	1 or 2

[1] The nonwounded groups in each length class omitted.

The length-weight relation of three categories of lake trout, grouped according to the incidence of sea lamprey wounds sustained by each trout, is shown in figure 21. Regression formula for each group is given in the caption.

Length of trout and incidence of sea lamprey attacks

The number of sea lamprey attacks sustained by lake trout was directly correlated with the size of the trout. On the average, the largest trout possessed the greatest number of both lamprey scars and lamprey wounds. Since the perforation of the trout's body by the lamprey leaves a permanent mark, it was to be expected that the largest trout, which are the oldest and consequently have been subjected to predation by lampreys for the longest period, would bear the greatest number of lamprey scars. The incidence of lamprey wounds would be expected to be the same for trout of all sizes unless a differential mortality removed certain size groups or unless the lampreys selected certain size groups as hosts.

Unfortunately, it is nearly impossible to ascertain the actual relation between size of hosts and incidence of sea lamprey parasitism, due to the fact that some hosts succumb as a result of lamprey attacks. With the information available it has been possible to present only the incidence of lamprey attacks upon those lake trout which survived and were subsequently captured. Thus the mortality of lake trout resulting from lamprey attacks has an important bearing upon the data presented here. It must be kept in mind also that the size of lamprey in comparison to the host's size is of fundamental significance.

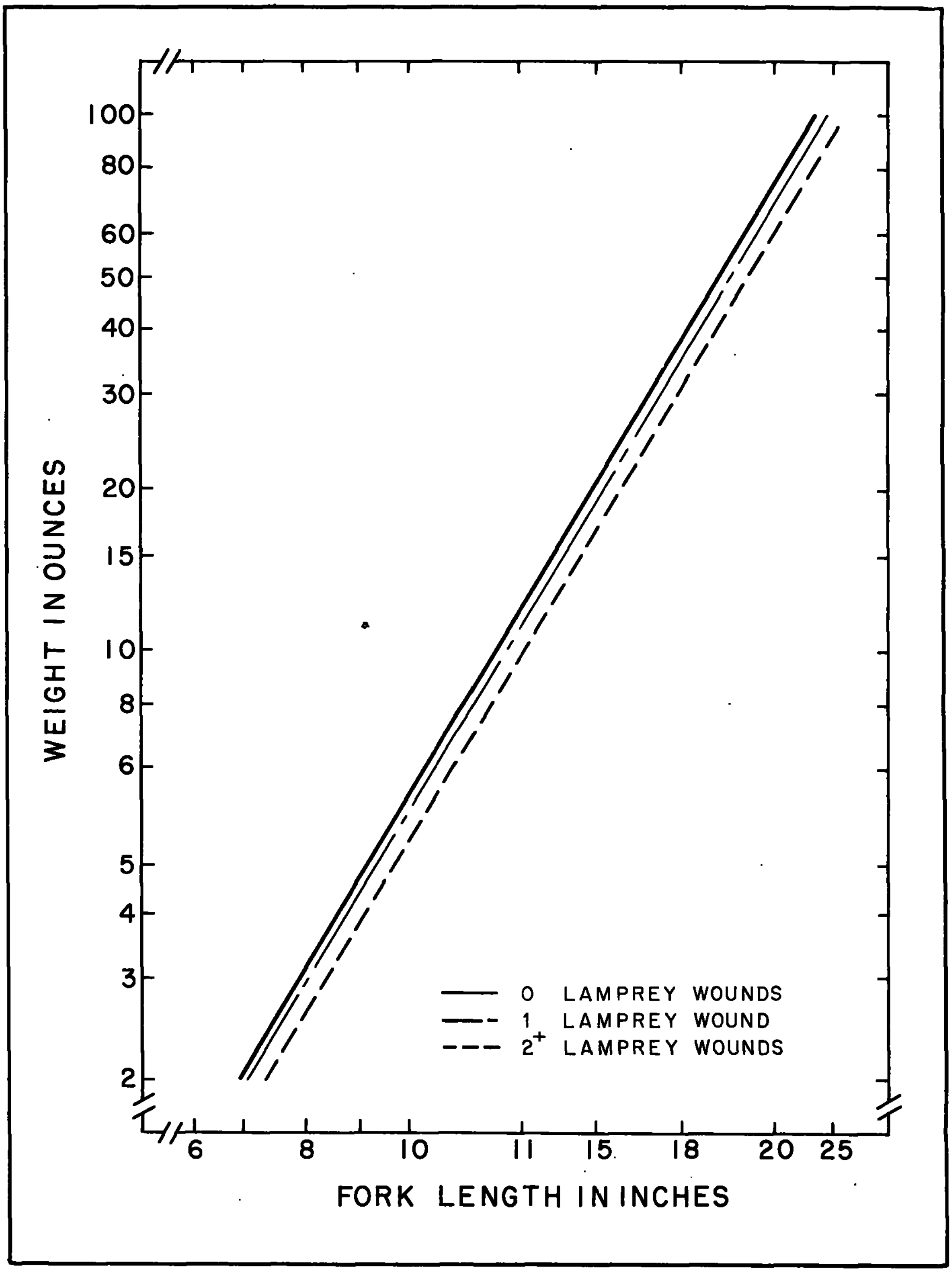

FIGURE 21.—Length-weight relation of 132 lake trout from Cayuga Lake, separated into 3 groups according to the number of sea lamprey wounds sustained by each trout. Regression formulas: unwounded trout (solid line), log $W=1.5557+3.169 \log L$; trout with one lamprey wound (broken line), log $W=1.5765+3.1057 \log L$; trout with two or more lamprey wounds (dashed line), log $W=1.5325+3.1432 \log L$.

The number of sea lamprey marks (both scars and wounds) increased progressively with body length (tables 42, 43, and 44). Trout between 5 and 9 inches long rarely had suffered lamprey attacks. Trout from 9 to 16 inches in length showed a gradually increasing rate of attack. At a length of approximately 16 inches the apparent rate of attack increased rapidly and reached its peak of roughly 11 marks per trout for the largest specimens, which were approximately 30 inches long.

It may be asked whether sea lampreys prefer large lake trout as their host, or whether they feed

TABLE 42.—*Incidence of sea lamprey attacks on lake trout from Cayuga Lake, 1949*

Length class (inches)	Average length	Number of lake trout	Wounds		Scars		Marks [1]	
			Percentage of trout with wounds	Average number per trout	Percentage of trout with scars	Average number per trout	Percentage of trout with marks	Average number per trout
5.0–5.9	5.9	1	0	0	0	0	0	0
6.0–6.9	6.5	4	0	0	0	0	0	0
7.0–7.9		0						
8.0–8.9	8.4	7	14.3	0.14	14.3	0.14	28.6	0.29
9.0–9.9	9.4	8	25.0	.33	12.5	.11	25.0	.50
10.0–10.9	10.5	17	35.3	.82	17.6	.35	35.3	1.18
11.0–11.9	11.5	10	50.0	.60	20.0	.20	60.0	.80
12.0–12.9	12.5	12	58.3	1.17	33.3	.50	66.7	1.67
13.0–13.9	13.4	11	27.3	.36	9.1	.09	27.3	.45
14.0–14.9	14.5	8	37.5	.50	37.5	.37	50.0	.88
15.0–15.9	15.5	5	60.0	.80	20.0	.40	60.0	1.20
16.0–16.9	16.5	5	60.0	1.00	60.0	1.00	80.0	2.20
17.0–17.9	17.3	10	50.0	1.00	50.0	1.10	60.0	2.10
18.0–18.9	18.4	7	71.5	1.43	71.5	2.29	71.4	3.71
19.0–19.9	19.5	13	46.2	.46	92.3	2.00	92.0	2.46
20.0–20.9	20.4	23	65.3	1.43	95.7	1.91	100.0	3.35
21.0–21.9	21.4	27	59.2	1.52	96.4	2.89	96.3	4.41
22.0–22.9	22.5	46	63.1	1.09	95.7	3.22	100.0	4.30
23.0–23.9	23.4	67	59.7	1.27	100.0	3.73	100.0	5.00
24.0–24.9	24.5	43	72.1	2.21	95.3	5.02	97.7	7.23
25.0–25.9	25.4	50	66.0	1.51	100.0	5.12	100.0	6.50
26.0–26.9	26.4	44	75.0	2.00	100.0	3.76	100.0	5.89
27.0–27.9	27.3	34	70.7	2.44	100.0	3.59	100.0	6.03
28.0–28.9	28.4	11	54.5	1.55	100.0	6.45	100.0	8.00
29.0–29.9	29.3	3	100.0	3.00	100.0	7.33	100.0	10.33
30.0–30.9		0						
31.0–31.9	31.1	1	100.0	3.00	100.0	7.00	100.0	10.00

[1] Scars and wounds combined.

TABLE 43.—*Incidence of sea lamprey attacks on lake trout from Cayuga Lake, 1950*

Length class (inches)	Average length	Number of lake trout	Wounds		Scars		Marks [1]	
			Percentage of trout with wounds	Average number per trout	Percentage of trout with scars	Average number per trout	Percentage of trout with marks	Average number per trout
5.0–5.9	5.6	3	0	0	0	0	0	0
6.0–6.9	6.3	8	0	0	0	0	0	0
7.0–7.9	7.5	5	0	0	0	0	0	0
8.0–8.9	8.6	19	5.3	0.05	0	0	5.0	0.05
9.0–9.9	9.5	12	0	0	0	0	0	0
10.0–10.9	10.6	20	0	0	5.0	0.05	5.0	.05
11.0–11.9	11.4	27	11.1	.15	14.8	.22	14.8	.37
12.0–12.9	12.4	26	15.4	.20	3.8	.04	15.4	.23
13.0–13.9	13.4	27	25.9	.48	7.4	.07	33.3	.56
14.0–14.9	14.4	25	24.0	.32	12.0	.12	24.0	.44
15.0–15.9	15.5	19	57.9	.84	21.0	.37	68.4	1.21
16.0–16.9	16.4	18	33.3	.44	27.8	.72	50.0	1.17
17.0–17.9	17.4	13	38.5	.54	23.1	.23	61.5	.77
18.0–18.9	18.4	7	71.5	1.14	71.5	1.00	85.7	2.14
19.0–19.9	19.4	17	82.3	1.30	70.7	1.94	88.2	3.24
20.0–20.9	20.5	16	56.2	.56	87.4	2.32	93.8	2.88
21.0–21.9	21.5	20	55.0	.70	95.0	2.45	100.0	3.15
22.0–22.9	22.5	45	75.0	1.15	97.8	3.29	97.8	4.44
23.0–23.9	23.5	57	68.4	1.21	100.0	3.86	100.0	5.07
24.0–24.9	24.3	45	55.5	1.07	100.0	4.18	100.0	5.24
25.0–25.9	25.4	41	67.5	1.32	100.0	3.87	100.0	6.41
26.0–26.9	26.3	37	64.9	1.49	97.3	5.57	100.0	7.05
27.0–27.9	27.3	12	75.0	1.58	100.0	6.92	100.0	8.50
28.0–28.9	28.4	7	42.8	.71	100.0	7.58	100.0	8.29
29.0–29.9	29.0	2	100.0	2.50	100.0	8.50	100.0	11.00
30.0–30.9	30.1	1	100.0	1.00	100.0	14.00	100.0	15.00

[1] Scars and wounds combined.

TABLE 44.—*Incidence of sea lamprey attacks on lake trout from Cayuga Lake, 1951*

Length class (inches)	Average length	Number of lake trout	Wounds		Scars		Marks [1]	
			Percentage of trout with wounds	Average number per trout	Percentage of trout with scars	Average number per trout	Percentage of trout with marks	Average number per trout
5.0–5.9	5.5	2	0	0	0	0	0	0
6.0–6.9	6.5	2	0	0	0	0	0	0
7.0–7.9								
8.0–8.9	8.5	6	0	0	0	0	0	0
9.0–9.9	9.4	4	0	0	0	0	0	0
10.0–10.9	10.6	7	0	0	0	0	0	0
11.0–11.9	11.3	16	6.3	0.06	0	0	6.3	0.06
12.0–12.9	12.5	15	13.3	.20	6.7	0.07	20.0	.27
13.0–13.9	13.4	10	10.0	.10	30.0	.50	40.0	.60
14.0–14.9	14.5	22	13.6	.18	4.5	.05	18.2	.23
15.0–15.9	15.5	9	22.2	.22	11.1	.11	33.3	.33
16.0–16.9	16.4	12	58.3	.58	16.6	.25	58.3	.83
17.0–17.9	17.4	4	0	0	50.0	.75	50.0	.75
18.0–18.9	18.4	7	28.5	.29	57.2	.86	57.1	1.14
19.0–19.9	19.5	14	71.4	1.00	57.2	1.00	92.9	2.00
20.0–20.9	20.6	14	42.8	.50	78.5	.71	78.6	2.21
21.0–21.9	21.4	24	50.0	.67	79.3	2.00	91.7	2.67
22.0–22.9	22.5	30	30.0	.40	86.7	3.33	90.0	3.73
23.0–23.9	23.4	41	39.0	.63	100.0	3.51	100.0	4.15
24.0–24.9	24.5	52	57.7	.86	98.0	4.49	98.1	5.25
25.0–25.9	25.4	25	52.0	.72	96.0	5.20	100.0	5.92
26.0–26.9	26.2	20	50.0	1.05	100.0	5.95	100.0	7.00
27.0–27.9	27.3	8	62.5	1.63	100.0	6.38	100.0	8.00
28.0–28.9	28.3	2	50.0	1.00	100.0	10.50	100.0	11.50
29.0–29.9	29.3	1	0	0	100.0	6.00	100.0	6.00

[1] Scars and wounds combined.

at random on any trout they encounter. Since the largest trout possessed the highest incidence of lamprey attacks, the data presented in the preceding sections suggest preference for large trout. However, if lampreys do prefer large hosts, the percentage of trout bearing lamprey wounds (scars not considered) would be expected to increase progressively from the smallest trout to the largest.

The percentage of lake trout that possessed lamprey wounds was calculated separately for each of the three years 1949–51 (tables 42–44, fig. 22). The few specimens between 14 and 20 inches long cause rather wide fluctuations in the percentages of wounded trout within that range. Because small trout are known to have a considerably higher mortality than large ones, the relation between the size of trout and incidence of attacks is probably most unreliable for the small specimens. Since the inflections of the line fitted to the data in figure 22 were a critical part of this relation, especially that portion pertaining to the large trout, it was necessary to employ statistical methods rigorous enough to show the less obvious trends in this regression. A test of the orthogonal polynomial series (F test) revealed that the third degree polynomial regression was required (regression formulas are given in the caption of fig. 22).

The percentage of wounded lake trout leveled off at the greater lengths in 2 of the 3 years, 1950 and 1951; in 1949 the percentage continued to increase. If only the larger lake trout (20 inches or greater) are considered, it is apparent that very little increase in the percentage of wounded trout accompanies the increased body length. The lack of a continued increase in the incidence of lamprey wounds on the largest trout suggests that there is no selection for size of host specimens in this size range. The evidence is not conclusive, but it is definitely known that lampreys prey upon trout 8.2 inches up to the very largest. There is some indication that they do not necessarily prefer the large trout, at least not over the size range where they may reasonably be expected to survive an attack.

Annual variations in incidence of sea lamprey attacks

Incidence of sea lamprey attacks upon lake trout differed noticeably from year to year, and was directly correlated with the abundance of lampreys. Yearly differences in the incidence of lamprey wounds were especially noticeably because wounds are inflicted by only one year class of lampreys. During any one year the rate of wounding can be expected to reveal annual fluctuations more clearly than scars, which are accumulated over a period of years. For this reason

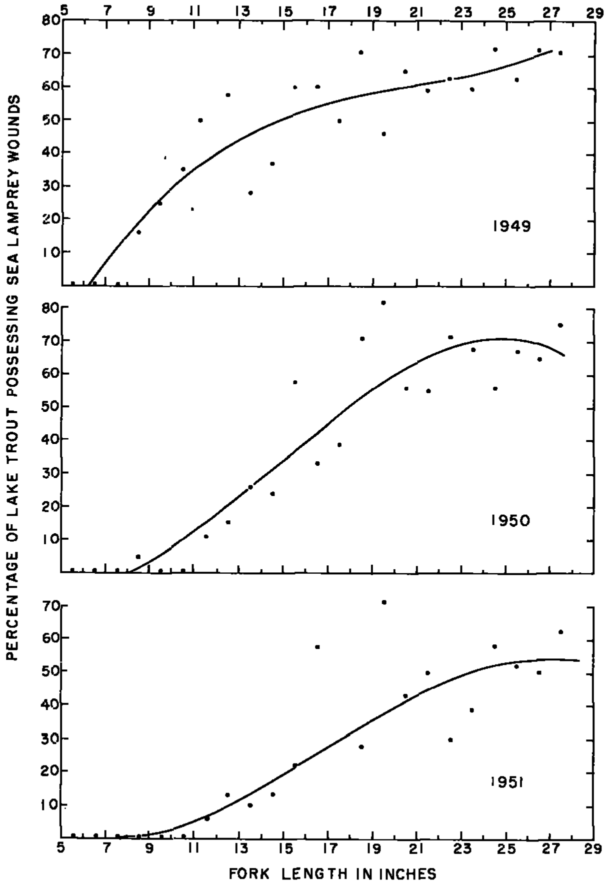

FIGURE 22.—Regressions of the percentage of lake trout possessing sea lamprey wounds on body length of lake trout for 1949, 1950, and 1951. Regression formulas: 1949, $Y=88.7628+18.8330\ X-0.8337\ X^2+0.0132\ X^3$; 1950, $Y=28.7041-11.1589\ X+1.1443\ X^2-0.0252\ X^3$; 1951, $Y=16.2757-6.3353\ X+0.6322\ X^2-0.0128\ X^3$.

further discussion is based entirely on the wounds, except to mention that annual variations in attacks on trout are evident also in the incidence of scarring.

Annual differences in the rate of lamprey parasitism show most clearly in the average number of lamprey wounds borne by lake trout. The values listed in column 5 of tables 42, 43, and 44 have been smoothed by a moving average of 3 and plotted in figure 23. It is readily apparent that the average number of wounds per trout decreased steadily during the period 1949–51. Trout of almost all sizes showed this trend.

Another measure of the intensity of lamprey parasitism is the percentage of lake trout possessing lamprey wounds (column 4 in tables 42, 43, and 44; fig. 22). The percentages of trout bearing lamprey wounds are 60, 46, and 38 for the years 1949–51. Each year the percentage of wounded trout exhibited a marked decrease; however, the yearly differences in this relation are less pronounced than are those of the number of wounds because of the high incidence of parasitism among the large trout in all years.

The most plausible explanation of the decline in sea lamprey parasitism upon lake trout from the high incidence in 1949 to the low in 1951 is that it resulted primarily from the decline in abundance of lampreys. This view is supported by the data in table 45 in which are listed the estimated numbers of sea lampreys, mean numbers of lamprey wounds per lake trout, and minimum lengths of lake trout bearing lamprey wounds for each year from 1949 through 1951.

Since the number of lampreys varied widely from one year to another, it is reasonable to assume that the ratio of lampreys to lake trout was principally dependent on the fluctuation in lamprey abundance. An estimate of the number of sea lampreys in the lake during a particular year can be determined from the number of spawning migrants. Except for a brief period in early spring, only one year class of parasitic-phase sea lampreys is present in the lake. Their abundance can be closely estimated by determining the number of migrants that enter Cayuga Inlet for spawning the following spring. Thus, the number of sea lampreys in Cayuga Lake during 1950 and 1951 was determined from the number of sea lampreys in the spawning migration in 1951 and 1952, respectively.

All three measures of lamprey parasitism indicate more intensive feeding in years when lampreys were most abundant, and less feeding when lampreys were fewer. As shown in table 45, the average number of lamprey wounds per trout decreased as the number of lampreys decreased. Also, the percentage of lake trout bearing sea lamprey wounds decreased as the number of lampreys decreased. The small size of the shortest trout bearing lamprey wounds when lampreys were most numerous further indicates more intensive feeding when lampreys are abundant.

Incidence of Sea Lamprey Parasitism in Various Parts of Cayuga Lake

Lake trout taken in July and August 1949–51 from five sections of Cayuga Lake differed consid-

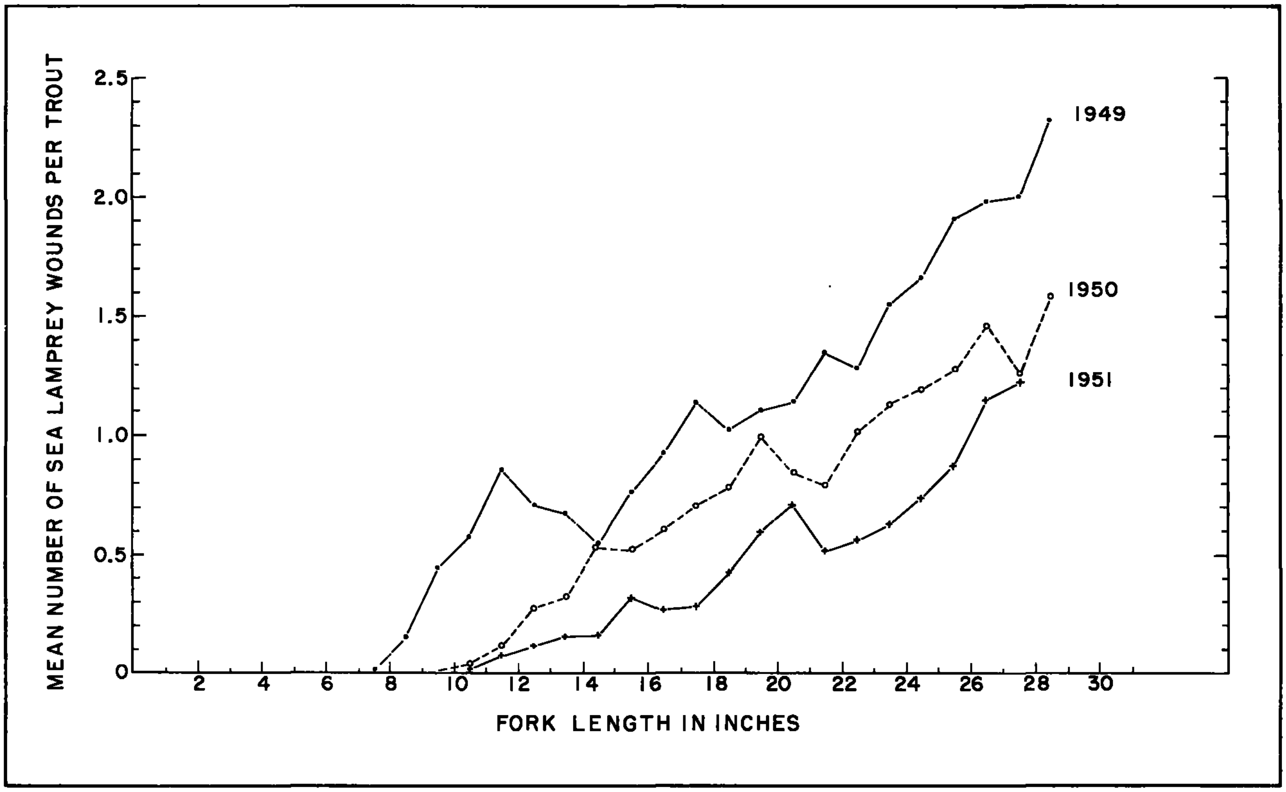

FIGURE 23.—Mean number of sea lamprey wounds on lake trout 8 to 30 inches in length during 1949, 1950, and 1951.

TABLE 45.—*Incidence of sea lamprey attacks on lake trout and sea lamprey abundance in Cayuga Lake, 1949–51*

Item	Year		
	1949	1950	1951
Number of sea lampreys	10,000–15,000	9,390	4,435
Average number of sea lamprey wounds per lake trout	1.21	0.81	0.46
Percentage of lake trout bearing sea lamprey wounds	60	46	38
Smallest lake trout bearing sea lamprey wounds (inches)	8.2	8.9	11.3

erably in both the percentage of trout wounded and in the mean number of wounds per fish. Cayuga Inlet, the only significant source of lampreys, enters the southern end of the lake, Section I (fig. 24 shows boundaries of the five sampling sections). This section extends northward 7 miles. Section II, a relatively small area off Flat Rock and Taughannock and Frontenac Points, is the major spawning ground for lake trout in Cayuga Lake. Across the lake and somewhat northward another small area, section IV, extending from Kings Ferry north to Willets, is a summer concentration area. Section III is the deep, middle portion of the lake. Section V is the northern, relatively shallow end of the lake.

Trout from section II and IV exhibited a high incidence of lamprey wounds, whereas those from sections I, III, and V showed a lower degree of parasitism (table 46). The unweighted mean numbers of lamprey wounds per trout in sections II and IV were 0.83 and 0.85, respectively. In Sections I, III, and V the mean values were 0.38, 0.44, and 0.44. The percentage of trout bearing wounds produced a similar picture. In sections II and IV the unweighted mean percentages of wounded trout were 44 and 54, respectively. Sections I, III, and V had mean percentages ranging between 26 and 38. Chi-square tests of independence indicated that differences in the incidence of parasitism among the 5 sections are significant. Section IV, the principal summer habitat of lake trout, ranked highest both in percentage of wounded fish and in number of wounds.

Seasonal trends in feeding activity of sea lampreys

Changes in feeding activity with time of year may be judged from monthly records of incidence

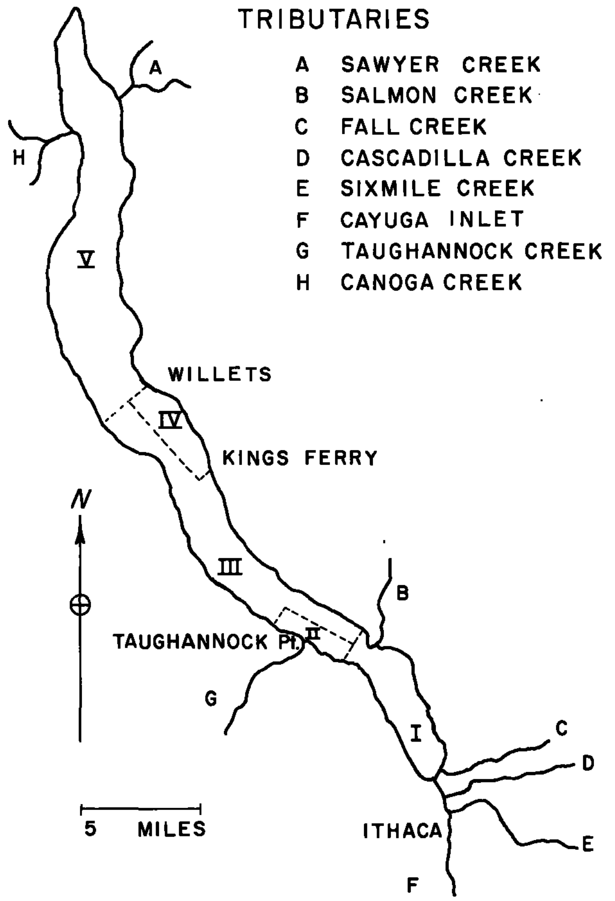

FIGURE 24.—Cayuga Lake and its major tributaries showing the five sampling sections of the lake. (Modified from Galligan, 1950; footnote 10.)

of lamprey wounds (table 47). To reduce bias arising from size differences, only large trout (between 20 and 31 inches long) were employed in the preparation of the table. As a further precaution the data are given only for lake trout from sections II and IV of Cayuga Lake to avoid bias from locality differences. Lake trout in these two areas are believed to form a single population. According to Galligan,[10] large trout gather in section IV during the summer and migrate to section II in the fall for spawning.

Feeding activity appeared to have reached a peak during August and September. A decline in feeding started in September and continued through October and November. In July the feeding activity was considerably less than maximum and was on a level with that for November.

[10] The distribution of lake trout and associated species in Cayuga Lake, by James P. Galligan, M.S. thesis, Cornell University, September 1951.

TABLE 46.—*Incidence of sea lamprey wounds on lake trout from 5 sections of Cayuga Lake*

[Boundaries of sections are shown in fig. 24]

Section of lake	Length (inches)	Number of trout	Number of trout with wounds	Percentage of trout with wounds	Mean number of wounds per trout
I	7.0–12.9	16	3	19	0.19
	13.0–19.9	7	5	71	.71
	20.0–30.9	12	3	25	.25
Total or mean		35	11	38	.38
II	7.0–12.9	17	4	24	.59
	13.0–19.9	22	12	55	.96
	20.0–30.9	19	10	53	.95
Total or mean		58	26	44	.83
III	7.0–12.9	45	6	11	.16
	13.0–19.9	54	18	33	.41
	20.0–30.9	12	8	67	.75
Total or mean		111	32	37	.44
IV	7.0–12.9	30	12	40	.67
	13.0–19.9	56	33	59	.80
	20.0–30.9	142	90	63	1.90
Total or mean		228	135	54	.85
V	7.0–12.9	11	1	9	.09
	13.0–19.9	22	4	18	.23
	20.0–30.9	2	1	50	1.00
Total or mean		35	6	26	.44

A chi-square test of independence for the 5 months gave a value corresponding to $p=0.03$. It is to be concluded that monthly variations in the percentage of wounded lake trout in the 20- to 31-inch size group are significant.

TABLE 47.—*Incidence of sea lamprey wounds on lake trout during July–November*

[All trout were 20.0 to 30.9 inches long. See fig. 24 for location of sections II and IV]

Month of capture	Section of Cayuga Lake	Number of trout	Number of wounded trout	Average number of wounds	Percentage of trout with wounds
July	IV	76	43	1.07	57
August	IV	66	47	1.12	70
September	II	177	117	1.72	66
October	II	366	218	1.25	60
November	II	55	29	1.05	53

Lake trout in the 13- to 19-inch length group resembled those of the 20- to 31-inch group in showing highest incidence of lamprey attacks during August and September.

The percentages of wounded lake trout in the 7- to 12-inch length group during July and August were 22 and 23 percent, respectively. None, however, of the small number of specimens in this size group captured during September, October, and November possessed a lamprey wound. Since the lampreys have more than doubled in length and increased in weight more than tenfold by October, perhaps the lower incidence of predation on small trout reflects a shift in the size of host they prefer, or, an attack after September may have been fatal because of the lamprey's greater size.

Comparison of sea lamprey parasitism in Seneca and Cayuga Lakes

Lake trout in Cayuga Lake suffer a much higher incidence of sea lamprey parasitism than do lake trout in Seneca Lake. Evidence on this subject was gathered from both lakes in September and October 1950. Gill-net fishing by New York State personnel in Seneca Lake for spawning lake trout provided a total of 181 lake trout for examination. All trout were between 21.0 and 31.9 inches long. From Cayuga Lake 131 lake trout ranging in length from 21.0 to 30.9 inches were gill-netted.

The records of lamprey parasitism on these two groups of fish (table 48) reveal that the percentage of lake trout bearing sea lamprey wounds was only 18.2 for Seneca Lake specimens but was 65.7 for Cayuga Lake fish. The average number of wounds per trout was 0.28 in Seneca Lake and 1.34 in Cayuga Lake. Incidence of sea lamprey scars on lake trout was also much higher in Cayuga Lake (4.68 per fish) than in Seneca Lake (2.45 per fish). Since sea lamprey scars persist for many years, the difference in scarring rate indicates that lamprey depredations on lake trout were the higher in Cayuga Lake not only in 1950, but also during several preceding years. It may be inferred that the number of lampreys in proportion to the number of lake trout is three to five times higher in Cayuga Lake than in Seneca Lake.

TABLE 48.—*Incidence of sea lamprey parasitism on lake trout from Seneca Lake and Cayuga Lake*

[Based on trout caught in gill nets in September and October 1950. Samples include only trout between 21.0 and 31.9 inches long]

Lake	Trout with lamprey wounds		Average number of wounds	Trout with lamprey scars		Average number of scars
	Number	Percentage		Number	Percentage	
Cayuga	86	65.7	1.34	130	99.3	4.68
Seneca	33	18.2	.28	152	84.0	2.45

Location of attachment on the fish's body

Sea lampreys attach themselves most frequently to certain particular areas on their hosts' bodies. By recording the location of each lamprey scar and wound, according to the plan indicated in figure 25, the concentration of attachment in various body areas was determined. Fish for this analysis were 103 lake trout taken by gill nets in Seneca Lake on October 12 and 17, 1950. The percentage of scars was by far the highest (45 percent) in the pectoral region, section B (table 49). Next in order of scarring incidence were: prepelvic region (26 percent), section C; pelvic region (23 percent), section D; head region (5 percent), section A; and, caudal region (1 percent), section E. Only 10 scars and 2 wounds of the total number of attacks (310) were above the lateral line. Lennon (1954) reported a similar distribution of lamprey attachments on brook, brown, and rainbow trout from Lake Huron.

Wounds were distributed over the body much the same as scars. The principal difference lay in the greater incidence of wounds in the head and pectoral regions (chi-square test of independence

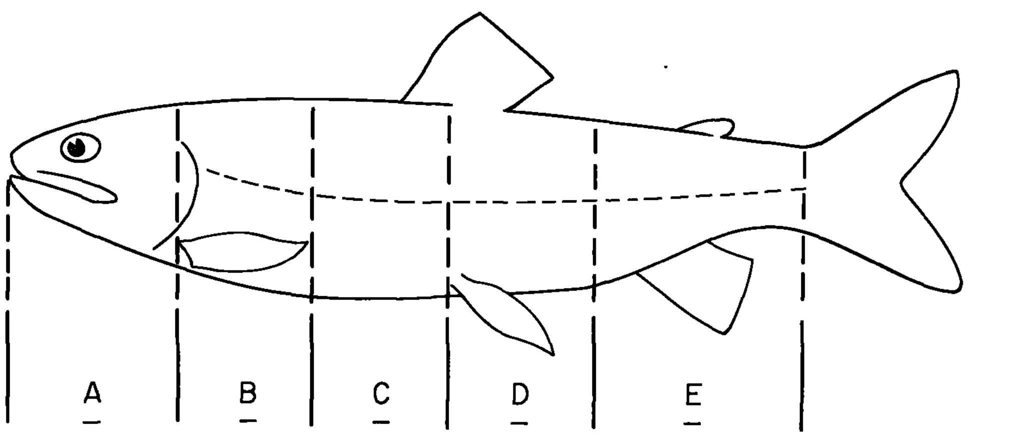

FIGURE 25.—Outline of a lake trout showing the 5 body regions for designating the location of sea lamprey attachment.

TABLE 49.—*Location of sea lamprey attachments on lake trout*

[The areas of attachment are indicated in fig. 25]

Item	Area of attachment					Total
	A	B	C	D	E	
SCARS:						
Number	13	127	71	65	2	278
Percentage	5	45	26	23	1	100
WOUNDS:						
Number	7	17	3	4	1	32
Percentage	22	53	9	13	3	100

yielded a value corresponding to $p=0.008$). Two explanations may be offered for this disparity. First, the superimposition of lamprey attachment over a previously existing scar would obliterate the original scar. Secondly, the mortality may be higher from wounds in the head and pectoral region than from wounds in other sections of the body.

Sea Lamprey Parasitism on the White Sucker

Information on the incidence of sea lamprey attacks on white suckers was obtained by the examination of spawning-run fish collected by means of an electric shocker from Butternut Creek, a tributary of Cayuga Inlet, on May 3, 1951, and May 6, 1952. Most of these suckers are believed to have been lake-dwelling fish that had ascended the stream to spawn. Possibly some stream-resident suckers were included.

The data on attacks on white suckers give no indication of difference between 1951 and 1952. White suckers less than 11 inches long bore no scars or wounds in either 1951 (15 fish) or 1952 (22 fish). At the greater lengths the percentage of scarred or wounded fish tended to increase with increase in size, as is brought out clearly by the following comparison of incidence of attacks in suckers 11.0–13.9 inches long and in fish 14 inches long or longer.

Fork length (inches)	1951			1952		
	Number of fish	Number with scars or wounds	Percentage	Number of fish	Number with scars or wounds	Percentage
11.0–13.9	109	21	19	76	17	22
>13.9	49	20	41	47	18	38

This trend toward a greater incidence of sea lamprey attacks among the larger white suckers is the same as that observed by Hall and Elliott (1954) in Lake Huron.

The cause for the increase in the incidence of sea lamprey attacks with increase in the size of white suckers is not known. Possibly the smaller fish are less able than larger ones to survive attack. Again, mechanical difficulties of attachment may give the smaller suckers a degree of immunity from lamprey predation.

PARASITES AND PREDATORS OF THE LAMPREY

Parasites

In the one previously published report on parasites of the sea lamprey in the Finger Lakes area, Van Cleave and Mueller (1934), who examined 12 sea lampreys from Oneida Lake, found trematode larvae. In more extensive studies, on mature sea lampreys from the Ocqueoc River and Carp Creek, tributaries of Lake Huron, Applegate (1950) and McLain (1952) reported parasitization to be rather low, generally less than 20 percent. Most common internal parasites were acanthocephalans of the genus *Echinorhynchus*, cestodes (*Triaenophorus*), and nematodes (*Cammallanus*). Externally, the leech *Pisicola milneri* was occasionally present.

The examination of 25 sexually mature sea lampreys from Cayuga Inlet during 1951 and of 53 in 1952 disclosed only one internal parasite, a small (1.5 mm.) acanthocephalan of the family Neoechinorhynchidae in the intestinal tract of a medium-sized female from the 1952 collection.

No external parasites were evident at any time during the 1950 spawning migration, but an epidemic of leeches occurred during the 1951 and 1952 migrations. The leech, *Pisicola zebra* Moore,[11] is approximately ¼-inch long and ⅙-inch wide. These leeches usually adhered in clusters to the dorsal and posterior edges of the first and second dorsal fins and the tip of the caudal fin. The leeches reached a peak of abundance on May 14, 1951, when they were present on 93 percent of the lampreys. At this time it was estimated that most of the infested lampreys carried approximately 50 to 300 leeches. The only visible damage to the lamprey was a slight erosion of the fin margins where the leeches had been attached.

[11] Identified by Dr. Marvin C. Meyer, University of Maine.

Predators

Numerous mammals and birds, a few reptiles, amphibians, and fishes were cited as predators on the sea lamprey by Surface (1899). He gave definite evidence of predation on the sea lamprey for the little green heron, the common water snake, and minnows of the genera *Rhinichthys* and *Notropis*. In Michigan, Applegate (1950) reported that walleye, northern pike, brown trout, raccoon, dogs, great blue heron, and sea gulls preyed on sea lampreys. The sea gull was the only predator of importance.

Daily excursions along Cayuga Inlet throughout the sea lamprey migratory and spawning season of 1951 and numerous visits during the 1950 and 1952 seasons, revealed amazingly little evidence of predation on spawning lampreys. Lampreys are especially vulnerable to predation while in the shallows of the tributary streams. It would be easy for almost any of the common predaceous animals to capture them. Nevertheless, the only animal actually witnessed devouring a sea lamprey was the common water snake, *Natrix sipedon*. In addition, six partially eaten lamprey carcasses were found along Cayuga Inlet during the three seasons of study. They appeared to have been killed by carnivores.

The only evidence of predation on sea lampreys in Cayuga Lake by fish was an unconfirmed report by a fisherman that he had found a sea lamprey in the stomach of a lake trout. Stomach analysis of hundreds of fish from Cayuga Lake, especially lake trout, have not produced a single instance of predation on the sea lamprey.

The only important predators on the sea lamprey in Cayuga Inlet are the small minnows that feed on the eggs. At the time of egg deposition, groups of these small fish gather just below the downstream rims of the nests. When the eggs are emitted, they quickly dart into the nest and seize as many eggs as possible before being frightened away by the spawners. Spawning lampreys never make an effort to drive these intruders from the nest, but the spawning actions seem to frighten the minnows. On June 4, 1951, the stomachs of six blacknose dace, *Rhinichthys atratulus*, contained numerous lamprey eggs.

CONTROL METHODS

Interrelationships between the sea lamprey and their host species in Cayuga Lake are only partially understood. In Lake Michigan and Lake Huron this parasite is very destructive to food and game fishes, and the sea lamprey is undoubtedly the cause of the destruction of many lake trout in Cayuga Lake. Their depredation on this fish in Cayuga Lake is compensated in part by their usefulness as an extraordinary, primitive creature for study by students in neighboring educational institutions. It is the writer's view that a program for reduction of numbers of sea lampreys in Cayuga Lake may be desirable, but that a supply should be maintained for scientific use.

Trapping operations in Cayuga Inlet have indicated the feasibility of reducing and possibly eradicating the Cayuga Lake population of sea lampreys by capturing spawning-run migrants. Also, the importance of extensive breeding and nursery areas as a factor in the abundance of the sea lamprey suggests the possibility of lowering the population level by reducing the spawning area available to them. Three methods of control appear to be practical:

1. Construction of a small barrier dam across Cayuga Inlet, 3 miles upstream from Cayuga Lake, would cut off extensive spawning areas. The initial expenditure would amount to several thousand dollars, but in the long run the dam would be more economical than traps or weirs since a barrier dam requires little or no maintenance. It blocks the migration of sea lampreys, but permits migration of game fishes. A head of 1½ to 2 feet should be effective under normal water conditions. A dam similar in design to the U.S. Geological Survey dam (fig. 11) would be suitable. A better but more expensive structure was described by Applegate and Smith (1950). An overhanging lip on the downstream side of the dam is essential.

2. An electromechanical weir and trap, similar to the one operated on the Kewaunee River, Wis. (Applegate, Smith, and Nielson 1952), should be the most efficient. The major disadvantage of this method is the expense. The device would cost several thousand dollars to purchase and install, and operational expenses would amount to several hundred dollars each spring.

3. Construction of a lamprey trap on the downstream side of the U.S. Geological Survey dam would provide an inexpensive control. This method would limit the lamprey to about 3 miles of spawning territory and bar it from 7 miles of

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spawning stream above the dam. It is estimated that about 75 percent of the entire spawning run could be captured. A trap suitable for this purpose would cost less than $50 and would require less than 50 man-hours annually for maintenance and operation.

SUMMARY

The recent invasion of the upper Great Lakes by the sea lamprey, and its depredation on the food and game fish have necessitated an investigation to discover methods of controlling this parasite. One aspect of the program was the present study of a long-established population of the landlocked sea lamprey.

Geological formation of the Great Lakes and the Finger Lakes of New York State, and the present distribution of the sea lamprey, lead to the conclusion that the lamprey entered Cayuga Lake by way of the "Champlain Sea" or the Hudson-Champlain estuary and Mohawk outlet during the latter part of the Pleistocene period.

Fieldwork was conducted from May 1950 to August 1952. Mature lampreys were captured in Cayuga Inlet by a weir, portable traps, and by hand. In all, 9,480 adult lampreys were captured. Of this number, 1,168 were tagged and 1,773 were fin-clipped and released in Cayuga Lake tributaries. Lake trout were taken by gill nets from Cayuga and Seneca Lakes. Immature, parasitic-phase lampreys were collected by removal of those adhering to lake trout taken in gill nets. Digging, seining, and electric shocking were employed for collecting larval lampreys in Cayuga Inlet.

In 1950, 1951, and 1952 the mean total lengths of adult, upstream-migrant lampreys were 15.0, 15.3, and 15.9 inches, respectively. The annual differences in length were significant, but the differences in length between males and females were not. Mean weights of upstream-migrant sea lampreys for 1950, 1951, and 1952 were 4.97, 4.34, and 4.94 ounces, respectively. In 1951, Cayuga Lake sea lampreys were approximately the same size as those taken in Carp Creek, a tributary of Lake Huron. This same year the largest landlocked sea lampreys were taken in Seneca Lake, N.Y. Mean length and weight of parasitic-phase sea lampreys captured in Cayuga Lake in September and October were 13.7 inches and 3.8 ounces. Mean length and weight of Seneca Lake sea lampreys captured during the same months were 15.5 inches and 5.3 ounces.

Transformation from the ammocoete to the adult stage began in August and terminated in March. Parasitic feeding began in March and continued approximately 14 months. During the early transformation stage the sea lamprey decreased approximately one-half inch in length. For the following 6 or 7 months, while buried in the stream bottom and in a nonfeeding phase of life, they increased approximately one-fourth inch in length and at the same time lost about 0.02 ounce in weight. After emerging from the bottom and starting their parasitic phase of life in the lake, they increased in length from 5.5 inches in March to 15.4 inches in April-May of the following year. Length-frequency distributions of specimens from both Cayuga and Seneca Lakes prove that lampreys spend only 1 full year in the lake. Essentially only one age group is present in the lake at any one time.

The length-weight relation was determined from 1,906 adult lampreys captured in Cayuga Inlet during April and May 1951.

Body proportions changed with the attainment of maturity. These proportions differed significantly between sexes at one time or another between September–October and the following June, and a majority of these proportions differed most at spawning time. Teeth, tooth-cusp, and myomere counts of Cayuga Lake specimens and Seneca Lake specimens reveal a divergence of the two populations at a racial level.

Of eight tributaries available to the lamprey for spawning, Cayuga Inlet was the only one used to any appreciable extent. The sea lampreys usually enter Cayuga Inlet during the last 2 weeks of April. Sea lampreys that arrived in the tributaries for spawning in mid-April spent 4–5 weeks in the stream before initiating nest construction. Activity of lampreys on the spawning migration was closely associated with water temperature.

Estimates of the number of lampreys in the spawning migration were: 1950, 10,000–15,000; 1951, 9,390; 1952, 4,435. Estimates were based on marking and recapture.

The rate of upstream travel was about 1 to 2 miles per day in the slow-moving portions of Cayuga Inlet. In the swifter, upstream area the rate of travel decreased to approximately one-

third to 1 mile per day. Upstream movement was slower during the early part of the migratory period than later. Low dams effectively retarded and sometimes blocked upstream migration of adult lampreys.

The numbers of males per 100 females in the spawning migrations were: 1950, 157; 1951, 155; 1952, 116. The relative abundance of males varied directly with the estimated total number of lampreys in the spawning run. Males were predominant among early migrants and females among late arrivals.

Coloration of mature lampreys during the spawning season varied with size, sex, and the time within the season.

Selection of nesting sites was affected by barriers to upstream migration, current velocities, substrate composition, and nesting densities. Some well-situated and apparently completed nests were not used for spawning, whereas others were utilized by several pairs. In a sample of 137 nests, only 43 percent contained lamprey eggs.

A female of average size produces approximately 43,000 eggs. Maximum and minimum numbers were: 85,162 for a 20.1-inch, 11.7-ounce lamprey, and 13,974 for a 13.5-inch, 2.6-ounce specimen.

The incubation period was 14 days at an average water temperature of 60.7° F.

A pronounced decrease in both length (11 percent for males; 18 percent for females) and weight (9 percent for males; 34 percent for females) took place during the spawning period.

Cayuga Lake sea lampreys die within a few days after spawning. Only 2.5 percent (238) of the estimated number of lampreys in the 1951 spawning run returned downstream to the weir during and after the spawning season. All were spent and approximately 80 or 90 percent were dead; the remainder were so debilitated that all were believed incapable of recuperating. Tagged or marked lampreys were not observed in the spawning runs in subsequent years. Although thousands of spent lampreys die in Cayuga Inlet each spring, few are seen without a thorough search of the deep pools.

A larval life of 7 years, including the period of metamorphosis, was ascertained from length- and weight-frequency distributions of ammocoetes. Mean lengths and weights in August for age groups II–VII were: II, 2.24 inches and 0.013 ounce; III, 3.23 inches and 0.031 ounce; IV, 4.21 inches and 0.066 ounce; V, 4.80 inches and 0.101 ounce; VI, 5.51 inches and 0.154 ounce; VII, 5.51 inches and 0.172 ounce. Weight-frequency distributions produced more definite modes for recognizing age groups than the more commonly employed length-frequency method.

Intensity of lamprey parasitism upon lake trout differed substantially from year to year, and was directly correlated with the abundance of lampreys. In Cayuga Lake the percentage of trout bearing lamprey wounds was 60 percent in 1949, 46 in 1950, and 38 percent in 1951. Lamprey scars, which are accumulated over the years, had a higher rate of occurrence: 82 percent in 1949, 60 in 1950, and 65 in 1951.

Lake trout in Cayuga Lake suffered a loss in weight that was directly related to the number of lamprey attacks and inversely related to the size of trout. Size of lamprey as well as of host fish is of great importance in determining damage by the sea lamprey. Also, mortality from lamprey attacks appears to be higher among small fish than among large ones. Incidence of lamprey wounds on lake trout from Cayuga Lake in July and August was greater in deepwater areas in which the trout concentrate in summer. Feeding activity of parasitic-phase lampreys reached a peak in August. Attachments of lampreys on lake trout were most numerous in the ventral half of the body, between the pectoral fin and the anus. The area immediately posterior to the pectoral fin was especially favored.

Lake trout are attacked much more frequently by sea lampreys in Cayuga Lake than in Seneca Lake. Evidence exists that the ratio of the number of lampreys to lake trout is 3 to 5 times higher in Cayuga Lake than in Seneca Lake.

White suckers from a tributary of Cayuga Inlet exhibited a 26-percent incidence of lamprey attacks in 1951, and a 29-percent incidence in 1952.

Numerous leeches, *Pisicola zebra* Moore, were attached to spawning-run lampreys in Cayuga Inlet in 1951 and 1952. An acanthocephalan was the only other parasite found in adult lampreys.

The only important predators on the sea lamprey in the Cayuga Lake basin are the minnows *Rhinichthys a. atratulus* and *Notropis c. cornutus*, which feed on lamprey eggs.

Control of the sea lamprey in Cayuga Lake could be accomplished at a moderate cost. Three control methods appear to be practical: barrier dam, electromechanical weir and trap, and mechanical trap.

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