VARIATIONS IN GROWTH, AGE AT TRANSFORMATION, AND SEX RATIO OF SEA LAMPREYS REESTABLISHED IN CHEMICALLY TREATED TRIBUTARIES OF THE UPPER GREAT LAKES

by

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TECHNICAL REPORT NO. 35

Great Lakes Fishery Commission
1451 Green Road
Ann Arbor, Michigan 48105

May 1979

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ABSTRACT

Growth and age at metamorphosis were determined for populations of larval sea lampreys that became reestablished after chemical treatments of tributaries of Lakes Superior and Michigan with the selected lampricide, 3-trifluoromethyl-4-nitrophenol. Age at metamorphosis varied from 3 to 7 years. Growth of ammocetes varied considerably from stream to stream and within streams. Mean lengths of ammocetes of age group III in late summer or early fall in different streams ranged from 65 to 144 mm. Ammocetes of the first year class established after a chemical treatment grew faster than those of succeeding year classes. Transformation at an early age usually occurred only among fast-growing larvae in large streams. A reversal of the sex ratio, from predominately male to predominately female, followed the reduction of the adult sea lamprey population. Sex ratios of larval and recently metamorphosed sea lampreys reestablished after chemical treatments rapidly shifted from an excess of males to an excess of females. The shift in sex ratio was related to decreased densities of sea lampreys resulting from treatments.

INTRODUCTION

The selective lampricide, 3-trifluoromethyl-4-nitrophenol (TFM), effectively reduces larval populations of sea lampreys *(Petromyzon* marinus) in streams (Applegate et al. 1961). Continued control of the sea lamprey depends on the re-treatment of streams when new populations become reestablished after chemical treatments. The reestablished sea lampreys must be detected and destroyed before they metamorphose and migrate into the Great Lakes.

Estimates of the age at first metamorphosis of sea lampreys of a given year class in the Great Lakes region have ranged from 3 to 7 years. Several authors have subjectively estimated age at metamorphosis on the basis of length-frequency data. For the Ocqueoc River, a tributary of Lake Huron, the age at metamorphosis was estimated as 3 years by Applegate (1950) and as 5% to 6% years by Hardisty (1961a). For a tributary of Cayuga Lake, New York, the age at metamorphosis was estimated as 4 to 5 years by Gage (1928) and 7 years by Wigley (1959). The variation

1 This study was part of a program conducted by the U.S. Fish and Wildlife Service under contract with the Great Lakes Fishery Commission.

in the estimates indicates the difficulty in accurately determining age at metamorphosis on the basis of length-frequency data.

Efforts to obtain accurate information on larval life history were intensified in 1960. In the first of two studies, ammocetes of known age were established in the Big Garlic River (a tributary of southern Lake Superior) by introducing sexually mature sea lampreys above a dam; the first metamorphosed sea lampreys were collected in an inclined-plane trap at the dam 5 years later (Manion and McLain 1971).

The second study, described here, provides information on growth and age at metamorphosis of reestablished populations of sea lampreys and on the sex ratio of larval and metamorphosed sea lampreys in selected tributaries of the upper Great Lakes (Fig. 1). The duration of larval life must be known to insure that streams are treated before reestablished populations of sea lampreys metamorphose and become parasitic in the Great Lakes.

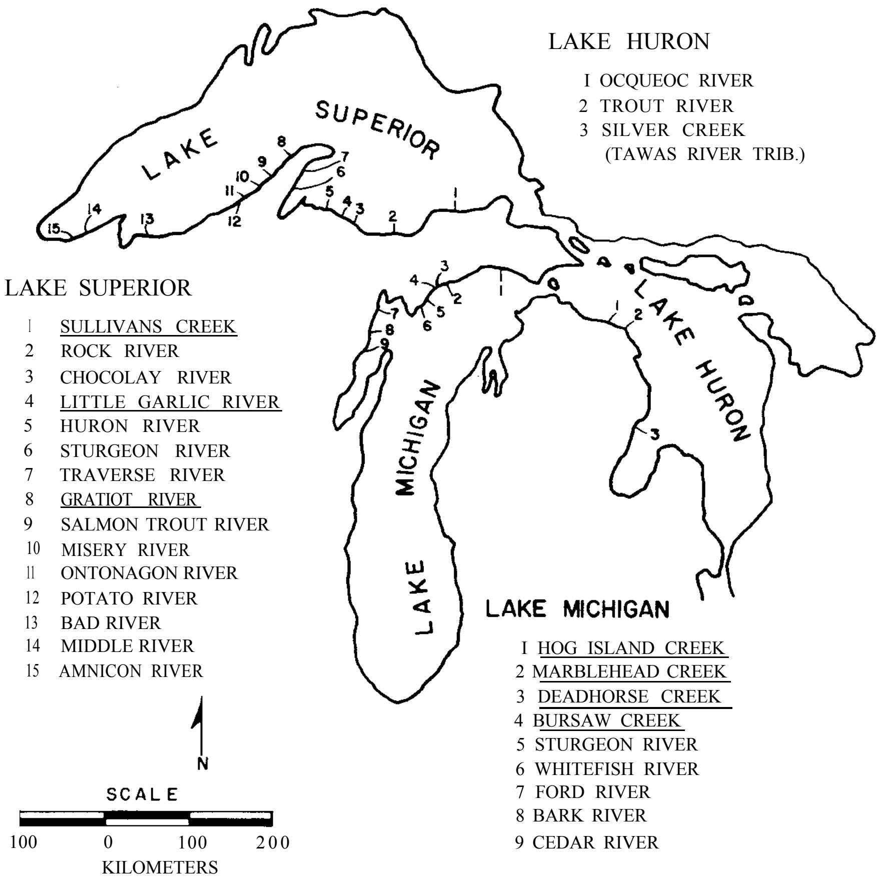

Figure 1. Location of tributary streams of the Upper Great Lakes mentioned in the text. Streams in which growth and duration of larval life of the 1960 year class were studied are underlined.

MATERIALS AND METHODS

The virtual elimination of existing populations of sea lamprey ammocetes by chemical treatment provided an unique opportunity to study growth and age at metamorphosis of reestablished populations. Age of ammocetes was determined or estimated by plotting length frequencies of larvae. The mean length was calculated for year classes between which overlap was slight or absent, and as the overlap increased with age, the modes were used as estimates of average length at each successive age.

Growth was measured easily in streams where ammocetes grew rapidly, or in which year classes preceding and following the one under study were small or missing. Growth was difficult to estimate after the 3rd year in streams where larval growth was slow, and large year classes were recruited annually. More exact data on growth were provided by marking ammocetes over 39 mm long with a subcutaneous injection of an insoluble dye, as described by Wigley (1952), Smith and McLain (1962), and Hansen and Stauffer (1964).

A study of growth and duration of larval life of the 1960 year class of sea lampreys was initiated in four tributaries of northern Lake Michigan and three tributaries of Lake Superior (Table 1). To obtain uniform data, ammocetes were collected with electric shockers at the same locations and usually within the same 10- to 14-day period in May, August, and October. Study areas were selected on each stream near the mouth and below the lowermost spawning site. In addition, treatment of the streams with lampricides also provided samples for analyses. In some streams, large ammocetes (over 139 mm long) collected in the spring were confined in cages and monitored throughout the summer for evidence of transformation. Also, each year samples were collected at index stations on all lamprey-producing tributaries of the United States waters of Lake Superior to provide additional data on growth and duration of larval life. Larvae were preserved in 5% formalin and later measured (total length) to the nearest millimeter.

Table 1. Physical features of seven streams and lengths of stream sections inhabited by sea lamprey ammocetes.

Lake and stream[a]	Average width (m)	Average depth (cm)	Summer flow (m^3/s)	Length of stream inhabited by ammocetes (km)
Lake Michigan				
Marblehead Creek	4.6	25.4	0.2	4.8
Bursaw Creek	3.0	20.3	0.1	4.0
Deadhorse Creek	3.7	25.4	0.1	2.4
Hog Island Creek	4.6	15.2	0.1	4.8
Lake Superior				
Little Garlic River	4.6	25.4	0.2	4.8
Gratiot River	3.7	30.4	0.1	1.1
Sullivans Creek	2.1	12.7	0.1	1.6

a See Figure 1 for locations of streams.

Identification of the various species of ammocetes associated with sea lampreys was based on characteristics described by Vladykov (1960) and Purvis (1970). The sex of transformed lampreys was determined on the basis of criteria described by Applegate and Thomas (1965).

Physical and chemical characteristics of the streams were described by Zimmerman (1968), and the fishes of the Lake Superior streams by Moore and Braem (1965).

The term "residual" in this report refers to sea lampreys that survive chemical treatments, and "isolated population" refers to sea lampreys above falls, dams, and other barriers, where recruitment is sporadic.

The age at transformation of a reestablished population of ammocetes is difficult to determine if residual larvae are also present in the stream. Only a small percentage of a year class may transform during the year metamorphosis begins, and it is often impossible to separate these animals from the small residual population when the length frequencies of the two groups overlap. Residual larvae and transformed lampreys become obscured in the length-frequency data when the reestablished populations attains a mean length of 110-120 mm. Frequent samples provide the necessary data to determine the relative sizes of the residual and reestablished populations.

GROWTH AND DURATION OF LARVAL LIFE OF THE 1960 YEAR CLASS IN SEVEN TRIBUTARY STREAMS OF LAKE MICHIGAN AND LAKE SUPERIOR

Growth of sea lamprey ammocetes of the 1960 year class was monitored in four small tributaries of Lake Michigan (Marblehead, Bursaw, Deadhorse, and Hog Island creeks) and three tributaries of Lake Superior (Little Garlic and Gratiot rivers and Sullivans Creek; Fig. 2). The 1960 year class was established in the four Lake Michigan tributaries by naturally spawning sea lampreys after chemical treatments in May and June 1960 had eradicated existing larval populations. In two Lake Superior tributaries - Sullivans Creek and the Little Garlic River - chemical treatments in August and September 1959 eliminated the existing ammocete populations. In the third, the Gratiot River, the operation of an electrical barrier from 1954 to 1959 prevented the establishment of ammocetes until 1960. Growth of sea lamprey larvae was traced for 5 years in Marblehead and Bursaw creeks and Little Garlic and Gratiot rivers, for 6 years in Sullivans Creek, and for 7 years in Deadhorse and Hog Island creeks (Table 2). A summary of the data on growth and age at metamorphosis for lampreys in each of the seven streams follows.

Lake Michigan

Marblehead Creek

Growth of the 1960 year class of sea lamprey ammocetes could be readily interpreted in Marblehead Creek because the lampreys grew rapidly and few ammocetes of later year classes became established. The greatest annual growth (32 mm) was between October 1963 and October 1964 and the largest seasonal increases in length occurred between May and August each year (Table 2). The annual mean increment in length was 26 mm over the 5-year period, 1960-65.

The first evidence of transformation was noted in August 1965 when seven metamorphosing sea lampreys were recovered. Two of the lampreys had been marked and released as larvae in 1964.

A total of 343 ammocetes were collected during the chemical treat-

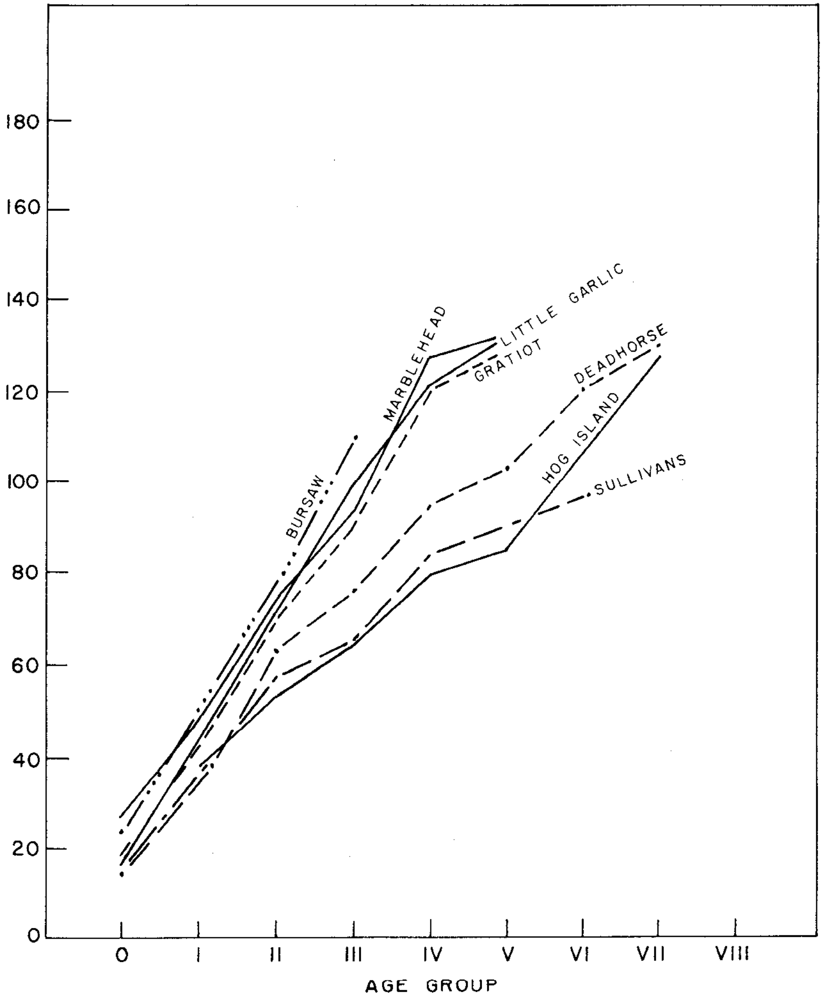

Figure 2. Total length each fall (August-October) during successive years of life of sea lamprey ammocetes of the 1960 year class in seven selected streams. See Fig. 1 for location of streams.

ment of Marblehead Creek in 1965. The length-frequency distribution of the 1960 year class appeared normally distributed, with a modal length of 13 1 mm (Fig. 3), although the frequencies in samples from previous Octobers were bimodal. The 1964 and **1965** samples indicated little growth (3 mm) from October 1964 to August 1965 (Table 2). Ten transformed lampreys (mean length, 146 mm) were collected during chemical treatment, of which three had been marked as larvae in 1964. Length-frequency data indicated that larvae longer than 110 mm probably belonged to the 1960 year class (Fig. 3); if this interpretation is correct, 4.2% (10 of 242) of the lamprey population had metamorphosed. In the August 1965 (pre-treatment) sample, this percentage was about 3 (7 of 237).

Evidence that metamorphosis of the 1960 year class occurred at age

Table 2. Mean total length (mm) of sea lampreys of the 1960 year class at ages 0 to VII in seven streams.
[Numbers of lampreys measured are shown in parentheses; if not indicated, the numbers exceed **19.**]

Age group and date of collection	Lake Michigan				Lake Superior		
	Marblehead Creek	Bursaw Creek	Deadhorse Creek	Hog Island Creek	Little Garlic River	Gratiot River	Sullivans Creek
Age 0							
Oct. 1960	28 (46)	-			16 (73)	18 (94)	16 (38)
Age I							
May 1961	-	-	-	-	23 (59)	18 (50)	21 (31)
Aug. 1961			—		41 (50)	31 (45)	-
Oct. 1961	49(103)	49 (70)	**38 (89)**	37 (49)	45 (35)	44 (12)	
Age II							
May **1962**	57 (55)	55 (83)	42 (82)	37 **(60)**	54 **(46)**	49 (63)	53 (60)
Aug. 1962	67 (75)	70 (98)	61 (65)	52 (91)	69 (33)	60 (57)	—
Oct. 1962	75 (130)	74 **(46)**	62 (161)	54 (88)	71 (43)	69 (4)	56 **(73)**
Age III							
May 1963	79 (137)	87 (70)	65 (147)	57 (90)	81 (57)	79 (39)	56 (130)
Aug. **1963**	95 (106)	95 (154)	68 (103)	62 (90)	95 (70)	91 (23)	59 (151)
Oct. **1963**	96 (130)	108 (60)	76 (113)	65 (83)	98 (56)	91 (11)	65 (107)
Age IV							
May 1964	101 (179)	-	80 (167)	-	103	107 (23)	74 (100)
Aug. 1964	117 (121)	-	86		117	117 (21)	84 (122)
Oct. 1964	128 (178)	-	92	8 0 -	121	-	-
Age V							
May 1965	130(90)	-	95	80	123	124	84
Aug. **1965**	131 (282)	-	101	92	**130**[a]	128	-
Oct. 1965	a	a	101	-	—	a	-
Age VI							
Aug. 1966	—	—	119	-	—	-	**95**[a]
Oct. 1966	—	—	121	-	—	-	-
Age VII							
Aug. 1967	-	-	125		-	-	-
Oct. 1967	-	-	**129**[a]	**122**[a] -	-	-	-

[a]**Stream** treated with TFM.

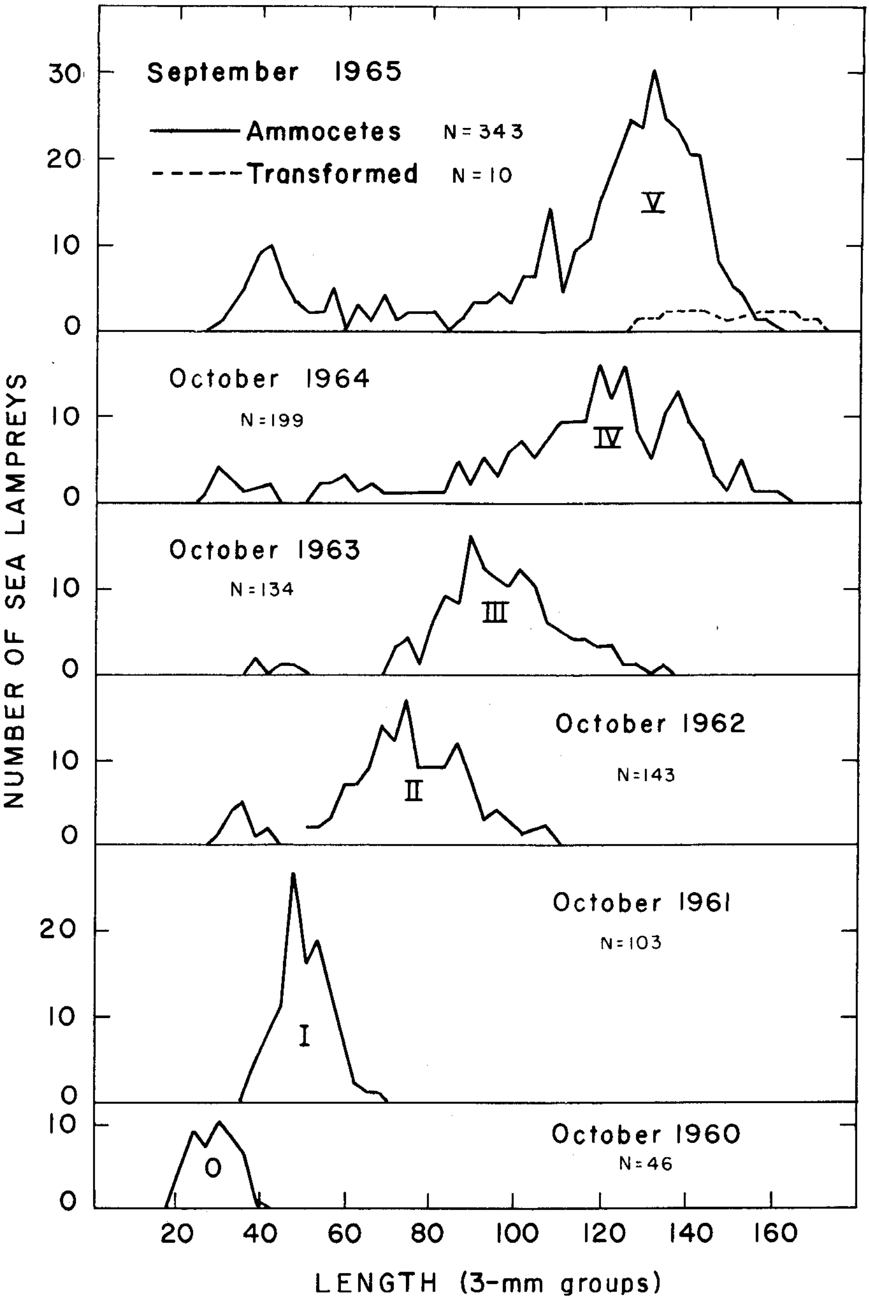

Figure 3. Length distribution of sea lampreys of age groups 0 to V from Marblehead Creek, 1960-65. The September 1965 sample was collected during chemical treatment of the stream.

V in Marblehead Creek is supported by three observations: (1) 17 transformed sea lampreys were collected, of which 5 had previously been marked as larvae; (2) only 2 residual lampreys were taken in 17 collections over a 5-year period after the chemical treatment in 1960; and (3) the lengths of the transforming lampreys coincided with those of larval lampreys of the 1960 year class.

Bursaw Creek

Mean length of the 1960 year class of sea lamprey ammocetes at age III in October 1963 (108 mm) was greater in Bursaw Creek than in the other six streams intensively studied (Table 2). Unfortunately, the 1960 year class virtually disappeared after 1963. In late summer and fall 1963, the stream was reduced by drought to a series of pools which may have contributed to the nearly total loss of the population.

Samples collected during the chemical treatment of the stream in September 1965 confirmed that there were few survivors of the 1960 or 1961 year classes (Fig. 4). Seven transformed sea lampreys (mean length, 162 mm), but no large larvae, were collected. It was impossible to determine whether the transformed lampreys were residual, or remnants of the 1960 year class. The large mean length of the transformed animals and lack of larvae of the 1960 year class preclude assigning a tentative age to the transformed lampreys. Based on the length of the larvae at age III, I would expect first metamorphosis to occur at age V in this population.

Deadhorse Creek

Growth of sea lamprey larvae was monitored in Deadhorse Creek from October 1961 to October 1967 (Table 2, Fig. 5). Increase in length of year classes became difficult to trace by 1964 because length-frequency distributions overlapped. A total of 311 larvae (mean length, 84 mm; range, 60-123) were marked and released in August 1965. From August 1965 to October 1967, the mean lengths of marked larvae increased 3 1 mm (Table 3) and the estimated mean length of the 1960 year class increased 28 mm.

Table 3. Length of marked sea lamprey larvae recovered in various periods from 3 11 larvae (mean length, 84 mm) released in Deadhorse Creek in August 1965.
[Marked larvae recaptured were measured and released.]

Month ofrecovery	Number recovered	Percentage recovered	Mean length (mm)
October 1965	77	25	86
May 1966	32	10	85
August 1966	51	16	94
October 1966	17	5	99
August 1967	13	4	111
October 1967	12	4	115

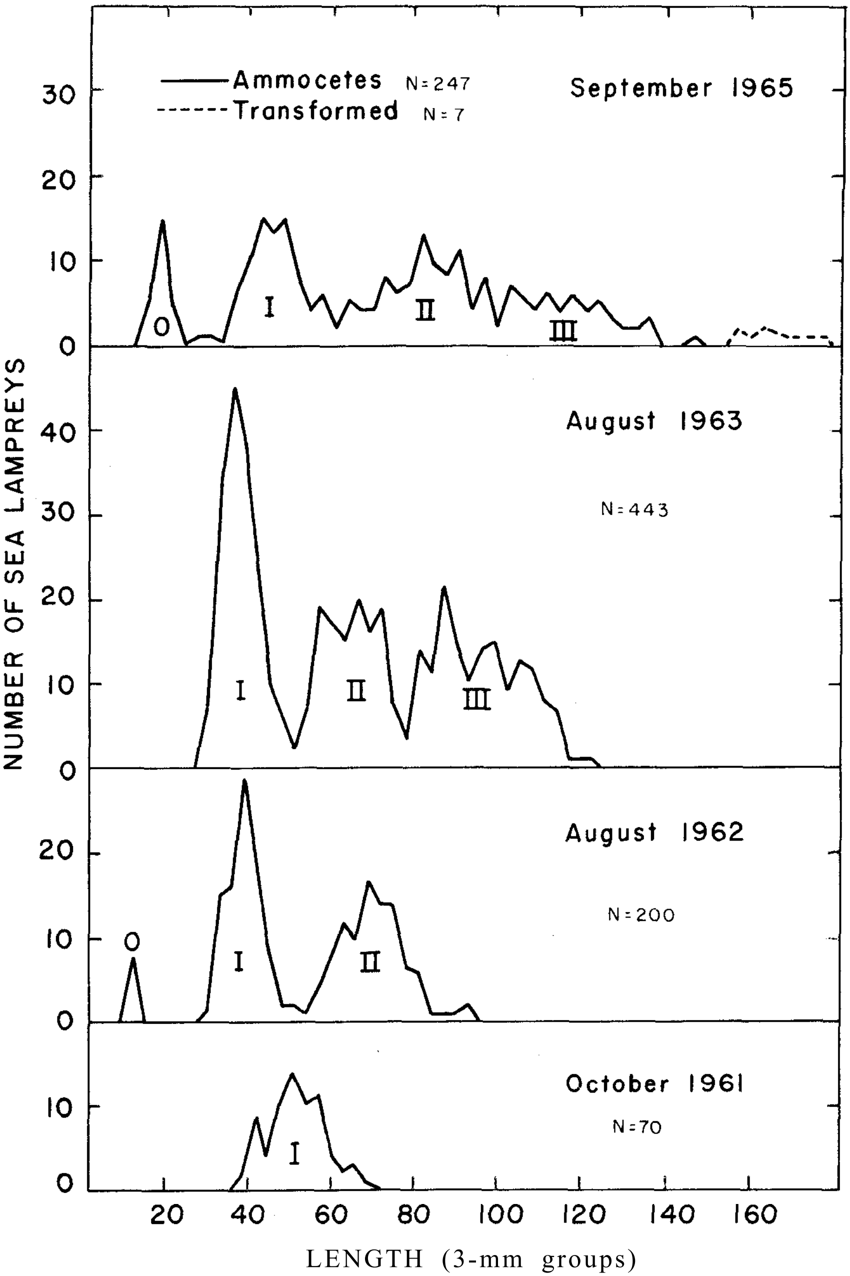

Figure 4. Length distribution of sea lampreys of age group 0 to III from Bursaw Creek, 1961-65.

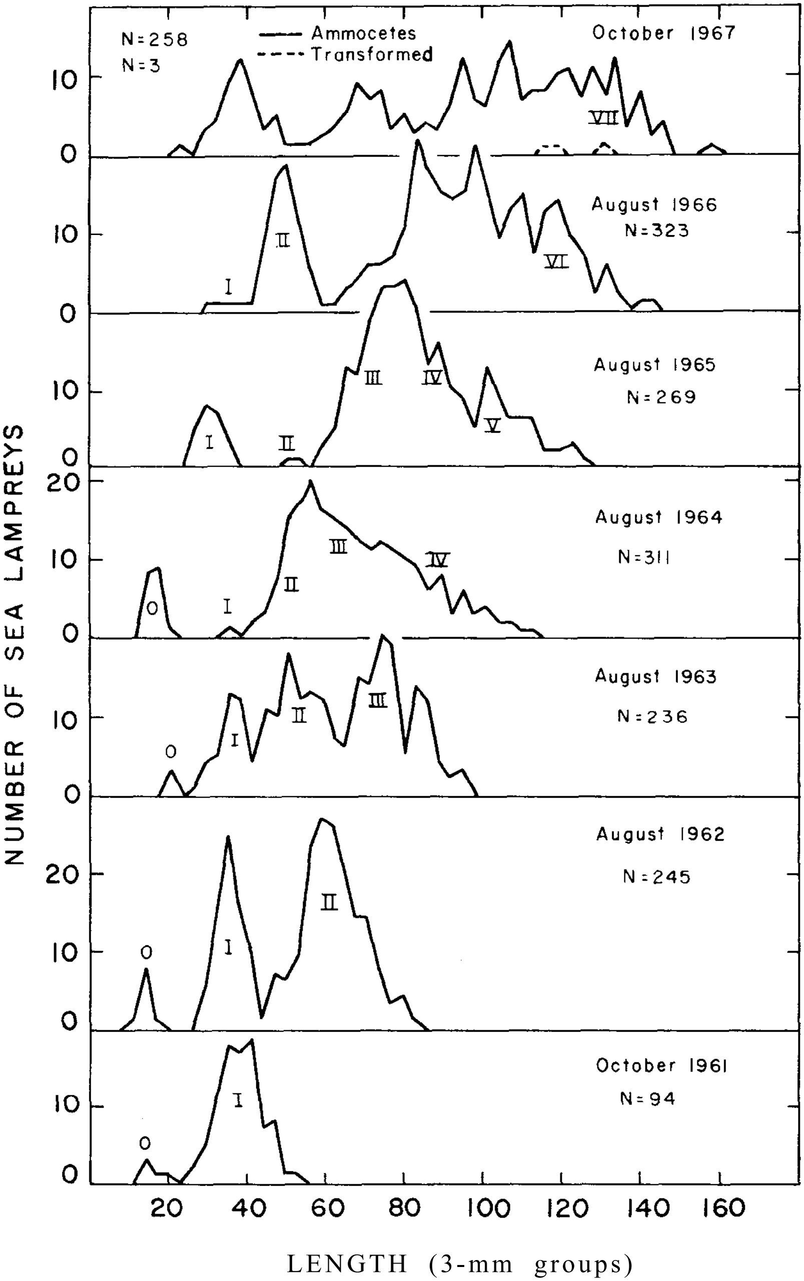

Figure 5. Length distribution of sea lampreys of age groups 0 to VII from Deadhorse Creek, 1961-67.

One transformed lamprey marked as an ammocete in 1965 and collected in August 1967, and 2 transformed lampreys collected when the stream was treated in October 1967 indicated initial metamorphosis occurred at age VII. These 3 transformed lampreys were exceptionally small (115, 120, and 130 mm long), compared with 4 large animals (length range, 152-172 mm) collected from the known-age population in the Big Garlic River (Manion and McLain 1971), the 10 transformed lampreys (mean length, 146 mm) taken in Marblehead Creek, and 209 (mean length, 138 mm) taken in the Little Garlic River, Lake Superior (discussed later). Only 74 larvae 120 mm or longer were collected; the longest was 159 mm.

It should be possible to collect most of the larvae killed in Deadhorse Creek during a chemical treatment because the stream is small and clear. The recovery of only 4% (12 of 3 11) of the marked larvae during the treatment in October 1967 indicates an extremely high loss due to migration or mortality or both in the period from August 1965 to October 1967.

Hog Island Creek

Growth of sea lamprey ammocetes was traced in Hog Island Creek from October 1961 to October 1967 (Table 2, Fig. 6). As in most streams, growth was easily traced through age group III.

In May 1965, 107 ammocetes (mean length, 75 mm; range, 60-100) were marked and released. The number of marked and unmarked larvae recovered with electric shockers after August 1965 was too small to determine accurately the rate of growth.

The mean length (122 mm) of 13 marked larvae (12% of the number marked) recovered during the chemical treatment in October 1967 was similar to that of the modal length of age VII larvae in the treatment collection.

A total of 496 large larvae (length range, 121-161 mm) and 1 transformed sea lamprey (137 mm) were collected during chemical treatment. The recovery of one transformed sea lamprey indicates initial metamorphosis of ammocetes may occur in Hog Island Creek at age VII.

Lake Superior

Little Garlic River

Growth of sea lamprey ammocetes was traced in the Little Garlic River from October 1960 to August 1965 (Table 2, Fig. 7). Maximum growth of the 1960 year class occurred between May and August each year. The largest increments of growth were 18 mm between May and August 1961 and 15 mm between May and August 1962.

By October 1964, few lampreys of the 1960 year class were available in the study area above the estuary. Apparently a large percentage of the 1960 year class had migrated into the estuary during the intervening 5 years, since a sample taken near the mouth in June 1965 included many ammocetes longer than 140 mm. In a selected sample of 114 large am-

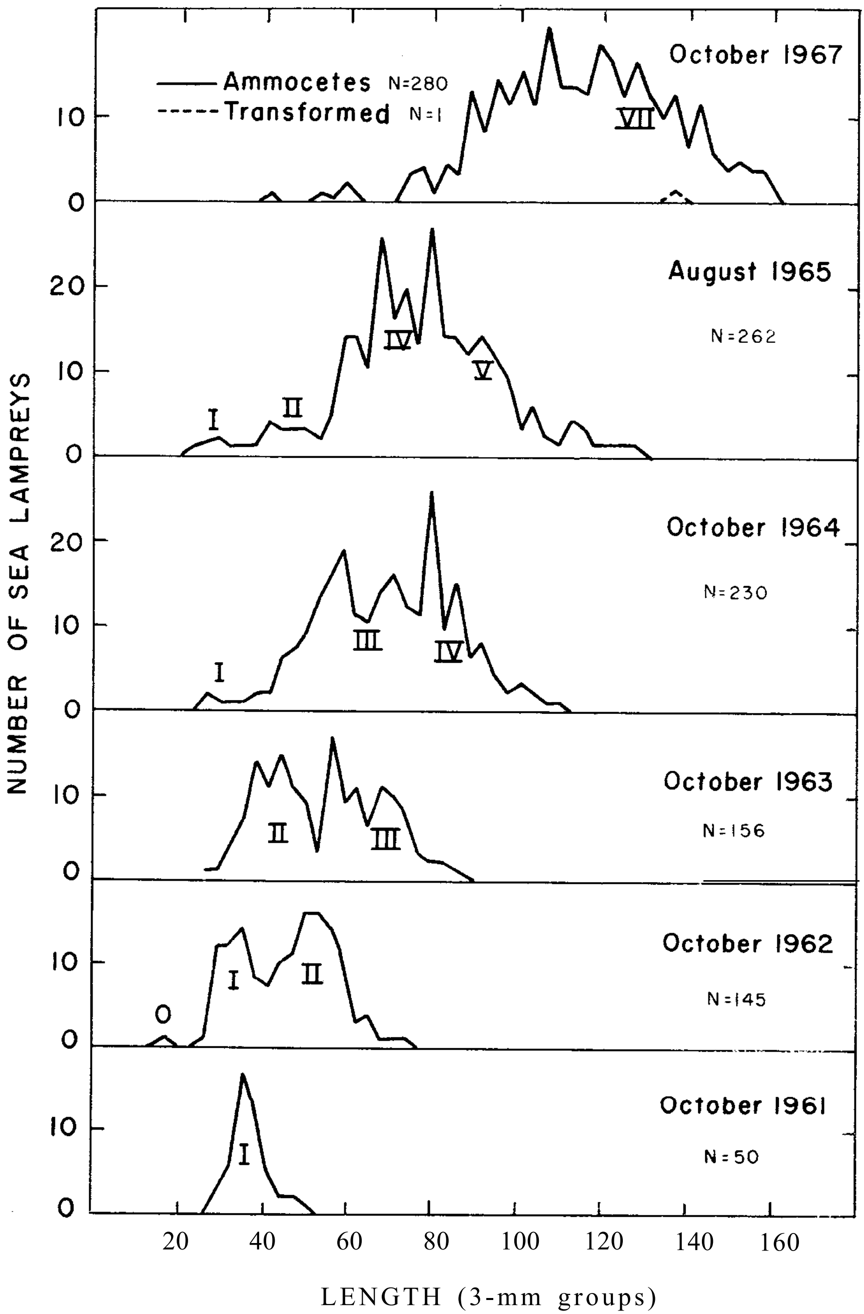

Figure 6. Length distribution of sea lampreys of age groups 0 to VII from Hog Island Creek, 1961–67.

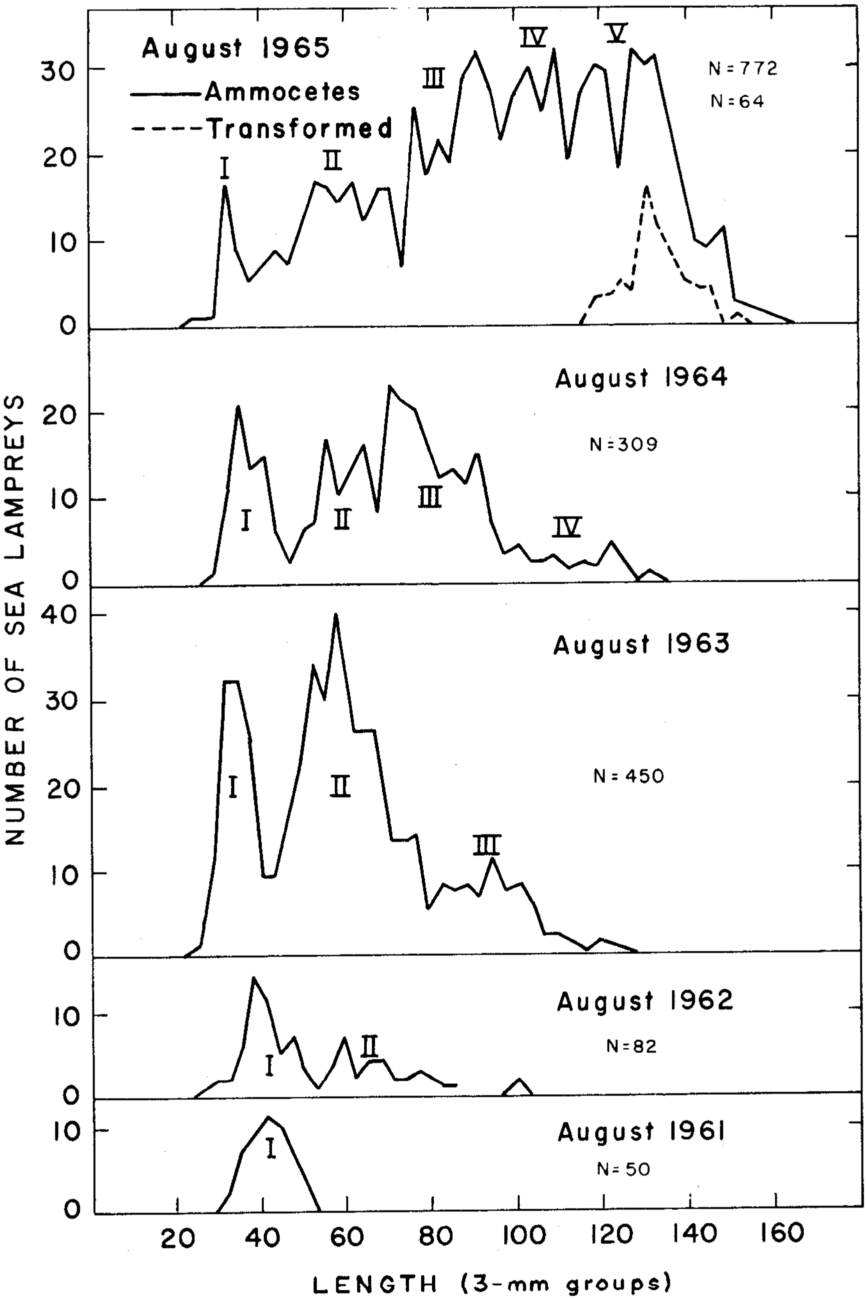

Figure 7. Length distribution of sea lampreys of age groups I to V from the Little Garlic River, 1961–65.

Table 4. Sex ratio of sea lamprey ammocetes collected at three locations in the Little Garlic River.

Location	Number	Percentage males
Mouth	372	17
450 m above mouth	120	34
1.6 km above mouth	152	30
Total	644	23

mocetes (mean length, 152 mm; range, 140-173) held in cages and monitored for transformation, 17% (20) with a mean length of 142 mm had transformed by August 10, 1965—thus establishing initial metamorphosis at age V. (The average length of the remaining 95 larvae had shrunk to 142 mm.)

Sex ratios of larvae varied in different areas of the stream (Table 4). The percentage of males collected near the mouth was about one-half that found upstream. In contrast, in Shelter Valley Creek, a tributary of Lake Ontario, Lowe (1972) found a much higher proportion of males near the mouth (53%) than in the upper reaches of the stream (11%). Additional data are needed to determine whether variations in larval sex ratios within streams are common and what factors influence the differential sex ratios.

Most of the transformed sea lampreys were taken in the lowermost area of the Little Garlic River. Of the 209 transformed lampreys collected during chemical treatment, 177 were in the estuary and 32 were in a 4.2-km section above the estuary. In the Big Garlic River transformed lampreys also accumulated in the lower reaches (Manion and Smith 1978).

Although the sex ratio of the larvae in the Little Garlic River was 23% males, 44% of the transforming lampreys were males-strongly suggesting a tendency for males to metamorphose before females in this stream.

Gratiot River

Length of sea lamprey ammocetes in the Gratiot River (Fig. 8) at most ages was similar to that in Marblehead Creek and the Little Garlic River (Table 2). Although larvae transformed at age V in those two streams, no transformed lampreys of that age were recovered in the Gratiot River. In 1965, a total of 213 age V larvae (120 mm or longer) collected during the time of year when metamorphosis occurs (August to October) showed no evidence of transformation. In addition, none of six large ammocetes (141-162 mm long) placed in cages in May 1965 metamorphosed.

The stream was treated in October 1965 because the growth rate of larvae was similar to that in other streams that produced metamorphosed lampreys at age V. About 31% of the 171 marked ammocetes released in June 1965 were recovered during the chemical treatment. This high recovery rate of marked larvae and the absence of any transformed lampreys in the collections make it improbable that transformed lampreys

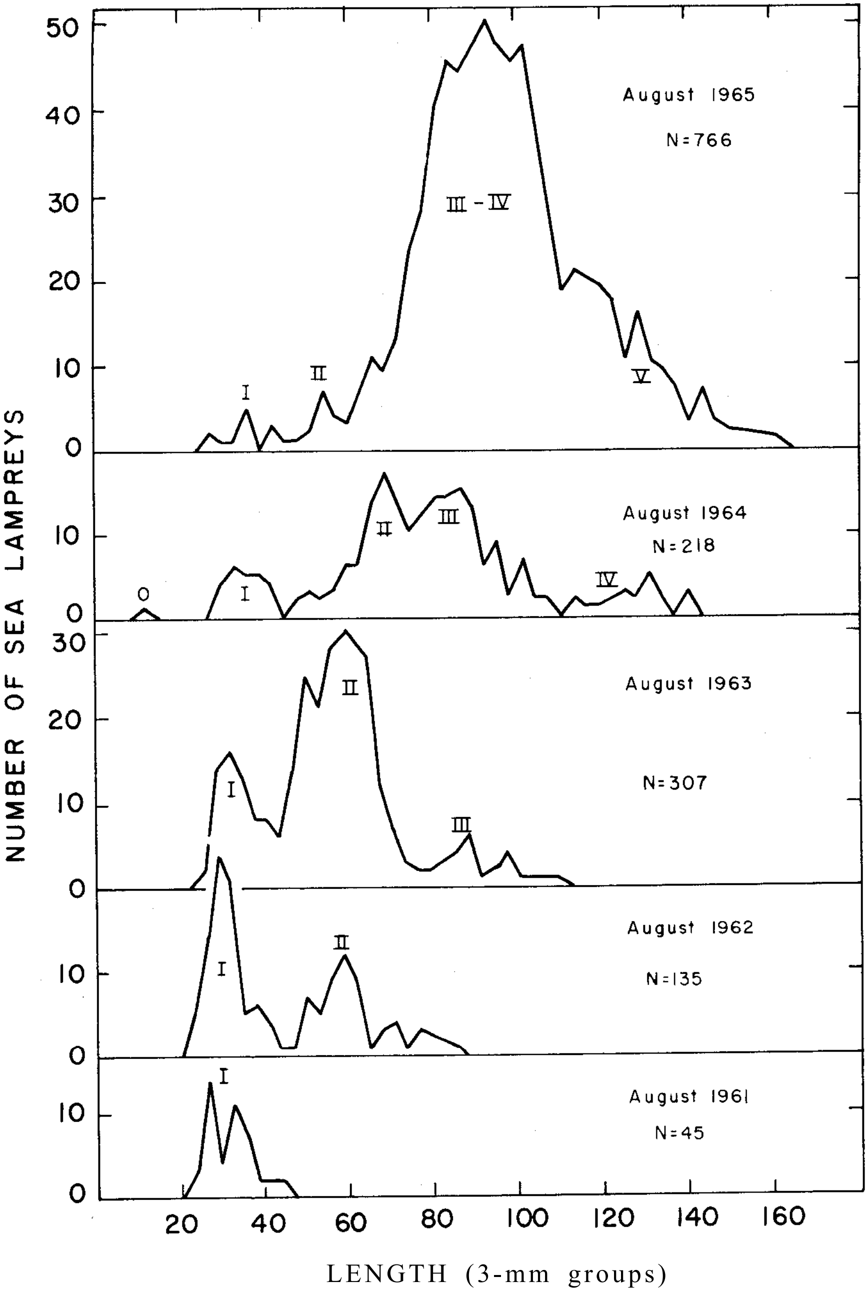

Figure 8. Length distribution of sea lamprey ammocetes of age group 0 to V from the Gratiot River, 1961–65.

were present. The mean length of the marked larvae increased 4 mm from June 9 to October 21, 1965. Some lampreys in this stream would probably have transformed during the following year, at age VI.

Even though new year classes of lampreys were established in the Gratiot River each year from 1960 to 1965, only one year class (1968) was established during the 4 years (1966-69) following chemical treatment.

Sullivans Creek

Growth of sea lamprey ammocetes in Sullivans Creek was monitored from October 1960 to August 1966 (Table 2, Fig. 9). A total of 3,355 ammocetes were collected and measured, of which 661 were taken during chemical treatment on August 30, 1966. By May 1964, lampreys of the 1960 and 1961 year classes merged into a single length-frequency group. When the stream was treated only 10 larvae longer than 120 mm were collected, none of which had transformed.

Sullivans Creek is a marginal producer of lampreys because of its limited ammocete habitat, cold water temperatures, slow growth of larvae, and moderately steep gradient where ammocetes are likely to drift downstream. Such streams offer limited potential for producing parasitic-phase sea lampreys unless ammocetes that drift into Lake Superior along the wave-swept shoreline can survive and metamorphose.

GROWTH VARIATIONS WITHIN THREE LAKE SUPERIOR TRIBUTARIES

Length-frequency distributions show growth of ammocetes vary widely within and between streams. Differential growth rates of ammocetes within streams were also reported by Hardisty (1944) and Manion and McLain (1971). Variations in growth within streams were particularly pronounced in three tributaries of Lake Superior-the Traverse, Sturgeon, and Ontonagon rivers.

Traverse River

The Traverse River (Fig. 1) is 6 to 9 m wide and has summer flows of 0.14 to 0.28 m^3/s. The stream is characterized by beaver ponds connected by stretches of stream with gravel bottoms suitable for lamprey spawning. Silver Creek, the only tributary infested with sea lampreys, joins the Traverse River about 5.6 km above the mouth. The population of sea lamprey larvae in Traverse River has sometimes been extremely dense. On one occasion, 1,075 larvae were collected in a 93 m^2 area.

The ammocete population in the Traverse River best illustrates the extreme variations in growth of larvae that may occur within a stream. Ammocetes were reestablished after the first chemical treatment in 1959. During the chemical re-treatment of the river in 1963, ammocetes were collected in seven areas over a 3. l-km section of the river extending from

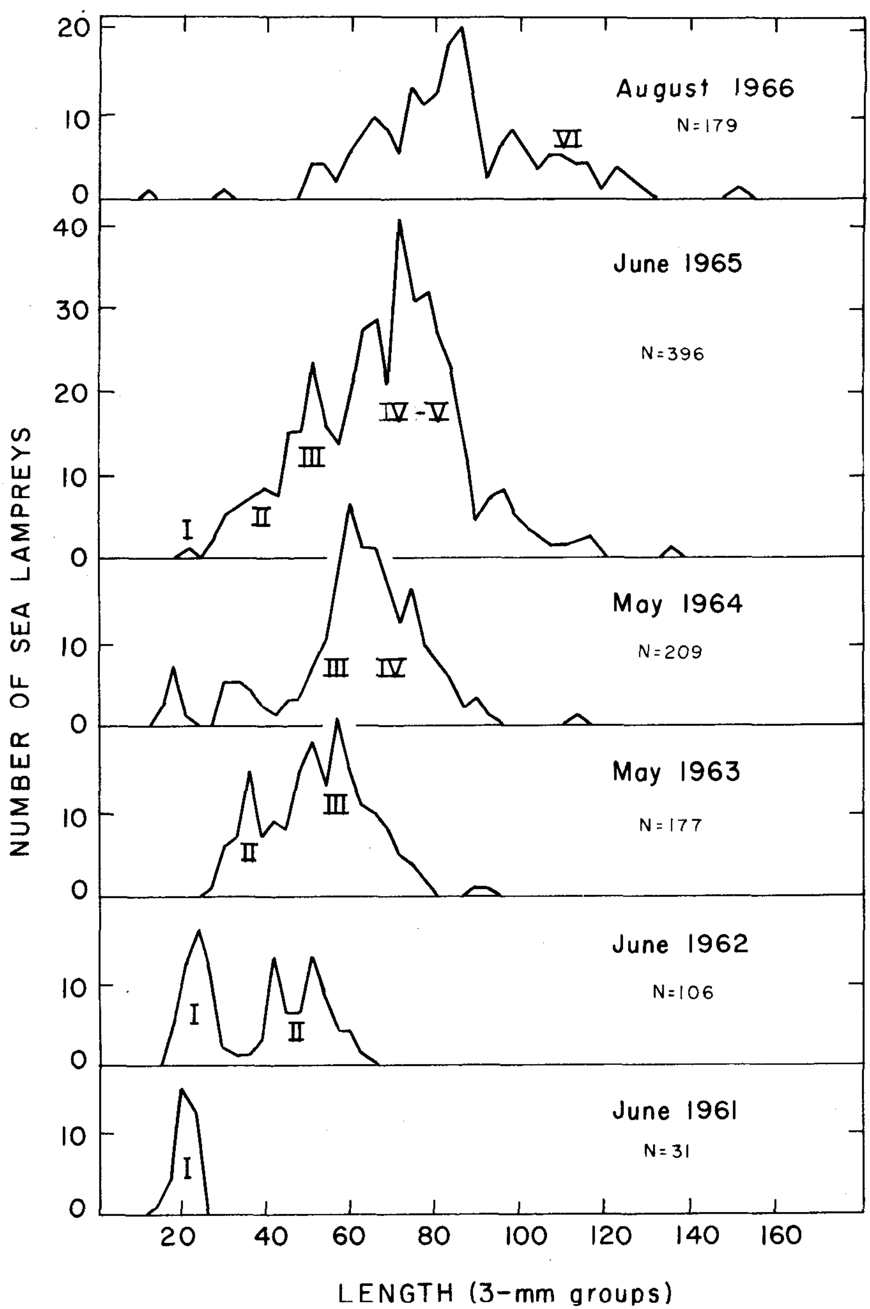

Figure 9. Length distribution of sea lamprey ammocetes of age groups I to VI from Sullivans Creek, 1961–66.

Table 5. Mean length (mm) of age groups I to IV of sea lamprey ammocetes collected at different localities in the Traverse River.
[Number of ammocetes measured are shown in parentheses.]

Date and station number	Location	Distance above mouth (km)	Age group I	II	III	IV
August 1963						
1	Traverse River above Silver Creek	5.8	32 (28)	59 (179)	83 (57)	-
2	Silver Creek	5.8	35 (86)	62 (560)	-	-
3	Junction with Silver Creek	5.6	32 (144)	50 (292)	80 (534)	119 (170)
4	Below Silver Creek	4.8	32 (84)	47 (83)	74 (145)	-
5	Above Gay Bridge	4.3	32 (44)	44 (174)	89 (236)	-
6	Gay Bridge	3.5	32 (82)	59 (384)	98 (169)	-
7	Below Gay Bridge	2.7	29 (14)	41 (167)	77 (334)	-
August 1967						
1A	Junction with Silver Creek	5.6	35 (52)	53 (192)	71 (264)	-
2A	Head of estuary	1.2	35 (13)	68 (190)	100 (46)	-

Silver Creek to a point 0.8 km below Gay Bridge (a country-road bridge that crosses the stream 3.5 km above the mouth).

The collection of 3,966 ammocetes in the seven areas produced prominent length-frequency modes. Modal lengths in different areas differed little at age I (28 to 35 mm), but modal lengths ranged from 41 to 62 mm at age II and from 74 to 98 mm at age III (Table 5). The III group was 45 mm longer than the II group at a point 4.3 km above the mouth, but only 27 mm longer at a collecting station 0.5 km farther upstream. Small numbers of IV group larvae, hatched in Silver Creek, were recovered within 275 m downstream from the mouth of this creek. Evidently the complex of beaver dams restricted the downstream movement of the small numbers of the IV group.

New year classes of sea lamprey larvae established after the 1963 treatment provided additional data on variation in growth in two areas (Table 5, Fig. 10). In August 1967 the II group ammocetes found at the head of the estuary were nearly as long (68 mm) as the III group (71 mm) collected from the upstream area at the junction with Silver Creek.

The factors that influence growth of ammocetes are complex and interrelated and probably vary from stream to stream. Two factors probably contributed heavily to the wide variations in growth in the Traverse River: (1) the habitats provided by the beaver ponds, which in turn influence bottom type and food supply, and (2) the density of the ammocetes. Generally, the length of ammocetes is smaller in areas close to spawning sites than in areas farther downstream.

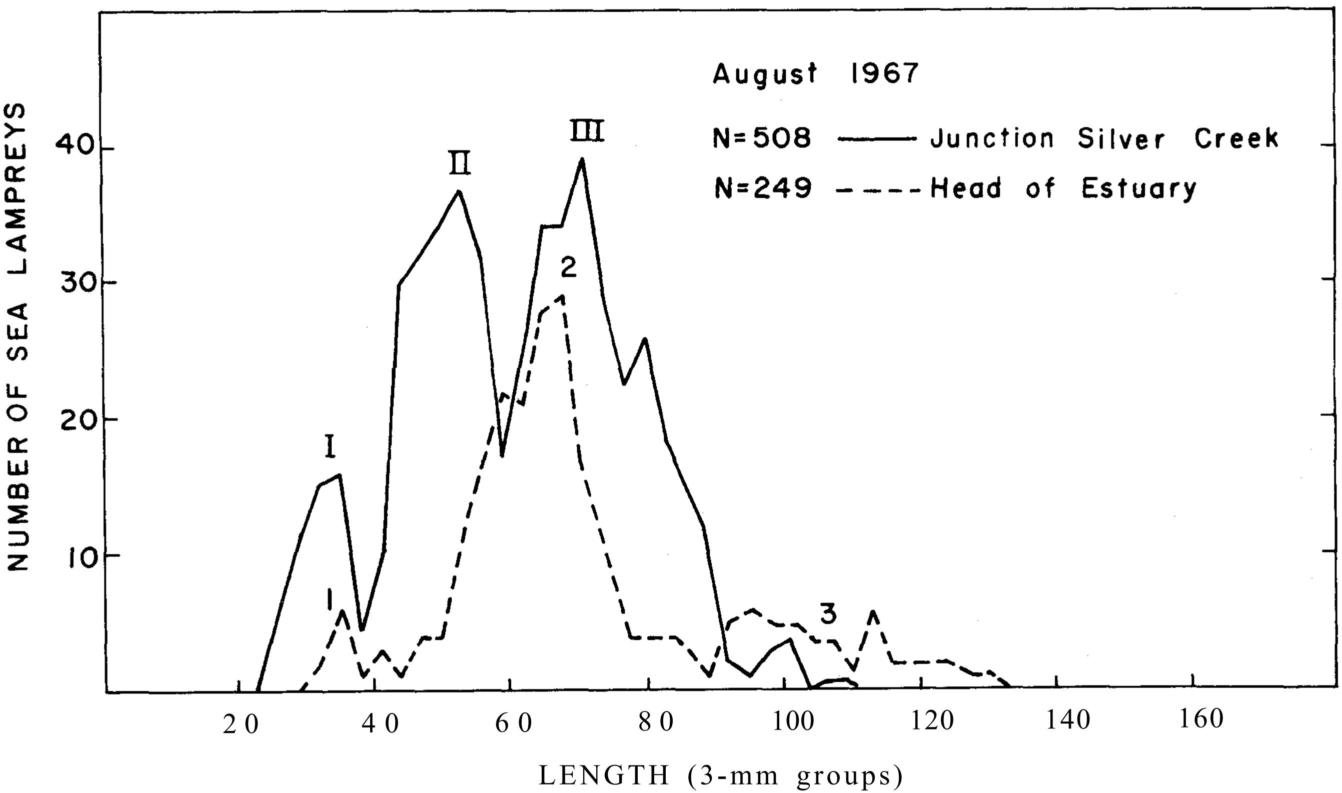

Figure 10. Growth of sea lampreys of age groups I to III in two areas of the Traverse River, August 1967.

Sturgeon River

Distribution of sea lampreys in the Sturgeon River is limited by a hydroelectric dam 72 km above the mouth. The river at state highway M-35, 19 km below the dam, is 18-27 m wide. Water flow is controlled by the dam and fluctuates between 0.9 and 20 m^3/s from mid-May to October.

A mark-recapture study was conducted to determine if the increased length of sea lamprey ammocetes observed several kilometers below the lowest spawning area was due to increased growth or to earlier downstream migration of the larger, faster-growing larvae of a year class. Previous information (unpublished) showed strikingly different growth rates of larvae between the spawning area at state highway M-35 and an area 13 km downstream.

Two groups of larvae of the 1967 year class (established after the chemical treatment of the river in 1966) were collected at M-35, marked, and released 13 km downstream: one group of 897 larvae with a mean length of 60 mm (range, 41-88) was marked and released on August 28, 1968, and a second group of 246 with a mean length of 78 mm (range, 60-115) was marked and released on June 3, 1969.

Marked larvae were recovered on August 2 1, 1969, about 1 year after the release of the first group and 2½ months after the release of the second. Mean lengths of the transplanted larvae and the natural population at M-35 (Table 6) differed significantly ($P < 0.01$). The mean length of larvae that were transplanted in 1968 had increased 44 mm (to 104 mm), compared with an increase of 28 mm for larvae at the M-35 bridge. Even

Table 6. Growth of sea lamprey ammocetes in the Sturgeon River at state highway M-35 and ammocetes transplanted 13 km downstream.

Location of collection	Date	Number	Length (mm) Mean	Length (mm) Range	Length (mm) Increment	Percentage growth increment	Percentage of marked larvae recaptured
Group 1							
M-35	8/28/68	897[a]	60	41-88	-	-	-
M-35	8/18/69	120	88	73-123	28	47	-
Downstream 13 km from M-35	8/21/69	87[b]	104	W-132	44	73	10
Group 2							
M-35	6/3/69	246[a]	78	60-115	-		-
M-35	8/18/69	120	88	73-123	10	13	-
Downstream 13 km from M-35	8/21/69	47[c]	98	81-116	20	26	19

[a]Marked and released 13 km downstream from M-35.
b Recaptures from 897 ammocetes marked and released on August 28, 1968.
[c]Recaptures from 246 ammocetes marked and released on June 3, 1969.

larvae that had been transplanted downstream only 2½ months earlier were 10 mm (11%) longer in the downstream area.

A sample of 239 unmarked sea lampreys that had drifted into the downstream area also had a mean length of 104 mm (range, 80-140). After 1 year, larvae that had been transplanted to the downstream area, and larvae that had drifted downstream naturally, had reached the same size and were 16 mm longer (18%) than larvae in the upstream population.

The larger size of the age II ammocetes downstream was thus not a result of migration of the larger, faster-growing segment of the upstream population, but was probably due to better growing conditions because of a lower density of ammocetes or the presence of more favorable habitat, or both, in the downstream area. Other studies indicate that large ammocetes move downstream faster or are more likely to migrate than small larvae (Hansen and Stauffer 1964; Manion and Smith 1978). However, the ammocetes in those studies were of an older age and larger size than in the present study.

Ontonagon River

In contrast to the diverse growth rates of sea lamprey ammocetes in the 3.1-km section of the Traverse River, the growth was more uniform over long reaches of the Ontonagon River. This river, which has summer flows of about 20 m^3/s, is one of the largest streams infested with sea lampreys along the south shore of Lake Superior. The Ontonagon River divides into the East and Middle Branches about 39 km above the mouth. The summer flow in the East Branch averages about 3.7 m^3/s and 2.7 m^3/s in the Middle Branch.

When the Ontonagon River was chemically treated in July 1963, 1,063 sea lamprey larvae of age groups I and II were collected at seven locations (Table 7). At two stations in the East Branch, which are 20 km apart, age II ammocetes were of similar mean lengths (76 and 74 mm). The mean lengths of larvae of ages I (47 mm) and II (83 mm) in the Middle

Table 7. Mean length (mm) of age groups I and II of sea lamprey ammocetes in the Ontonagon River, July 1963.
[Numbers of ammocetes measured are shown in parentheses.]

Station number	Kilometers above mouth	Age I	Age II
East Branch			
1	68		76 (46)
2	48	38(20)	74 (94)
Middle Branch			
3	42	47 (5)	83 (45)
Main stream	32		
4 (Victoria Bridge)	24	50 (27)	83 (124)
5 (Grand Rapids)		47 (36)	83 (397)
6 (Junction Mill Creek)	8	47 (66)	81 (104)
7 (2-Mile Boom)	3	-	92 (99)

Branch, about 3.2 km above the confluence with the main river, were similar to those of larvae at stations 4,5, and 6 in the main river, 8 to 32 km above the mouth. However, average length at age II was markedly less in the East Branch (76 mm) than at a location 3 km above the mouth in the main stream (92 mm). Thus, although growth of ammocetes was similar over long stretches of the river, it was far from uniform throughout all parts of the stream.

GROWTH VARIATIONS BETWEEN YEAR CLASSES

Along with variation in growth of sea lamprey ammocetes between and within streams, growth varies between year classes. The first year class of ammocetes established after a chemical treatment grows at a significantly faster rate than succeeding year classes. As ammocete abundance increases, the growth of each year class is usually slower than that of all previous year classes. For example, in the Traverse River (Table 8, Fig. 1 1), the mean length at age I was 47 mm for the 1964 year class, 35 mm for the 1965 year class, and 32 mm for the 1966 year class. At age II the mean length of the 1965 year class was 20 mm shorter than that of the 1964 year class at the same age. Slower growth of successive year classes is also evident for many year classes in Figures 4–9.

The increased density of larvae that results from the recruitment of successive year classes probably depresses the growth rate of all year classes and serves as a self-regulating mechanism in determining the percentage of larvae that metamorphose from a population at any given age. If the density of a population decreases, accelerated growth should increase the percentage of ammocetes that could transform at an earlier age.

AMMOCETE POPULATIONS WITH RAPID GROWTH AND EARLY TRANSFORMATION

Analysis of length frequencies of ammocetes from many tributaries of Lake Superior indicates transformation will occur after 5 or more years

Table 8. Mean length (mm) at different ages of the 1964 to 1967 year classes of sea lamprey ammocetes collected in October in the Traverse River.
[Numbers of lampreys measured are shown in parentheses; if not indicated, the numbers exceed 19.]

Year class	Age group			
	0	I	II	III
1964	19 (62)	47 (56)	67 (51)	80
1965	17 (39)	35 (52)	47	-
1966	17 (30)	32	-	-
1967	14 (49)	-	-	-

of larval life. In six streams, however, ammocetes grew much more rapidly and probably transformed earlier (Table 9). Although conclusive evidence is lacking, the recovery of transforming sea lampreys with lengths similar to those of age III larvae strongly suggests that initial transformation occurred at age III in the Sturgeon, Ontonagon, Bad, and Amnicon rivers and at age IV in the Salmon Trout and Potato rivers.

Manion and McLain (197 1) reported ammocetes grew faster in large (>1.4 m^3/s) and medium (0.6-1.4 $^3/s$) streams than in small (<0.6 m^3/s). Consequently, a higher percentage of ammocetes would be expected to attain the minimum length (120 mm) necessary for transformation at a younger age in large and medium streams than in small streams.

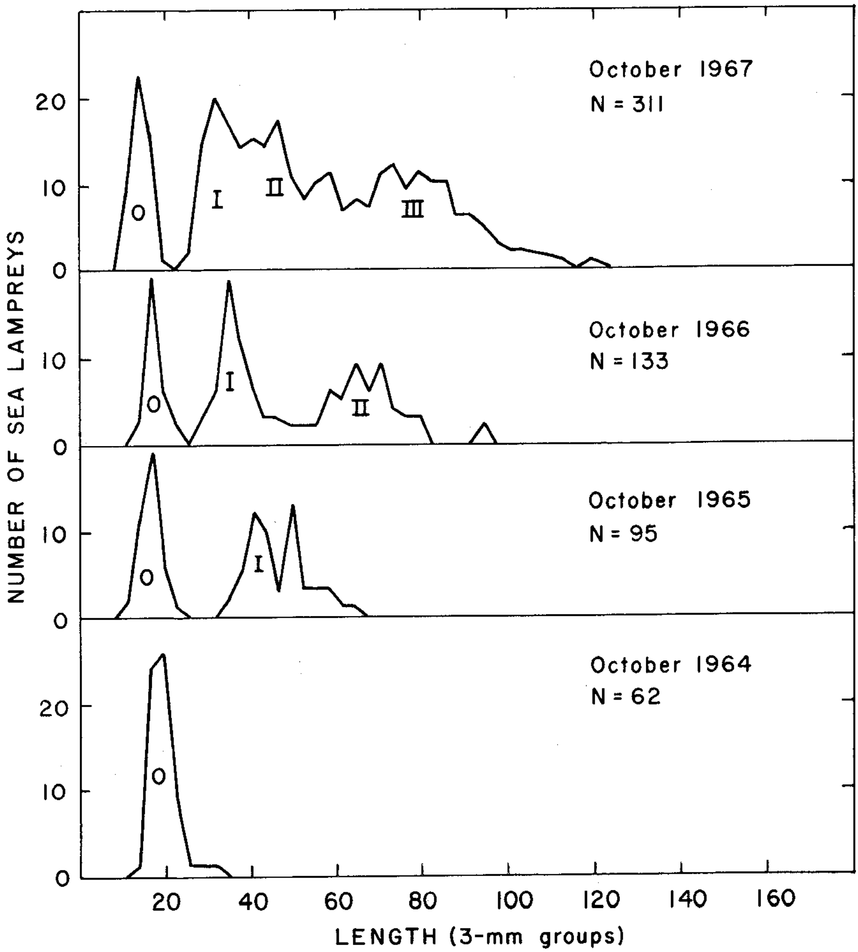

Figure 11. Length distribution of the 1964 year class of sea lamprey ammocetes at ages 0 to III in the Traverse River and of succeeding year classes at ages 0 to II.

Table 9. Estimated age at earliest metamorphosis and mean length (mm) of sea lamprey ammocetes collected in late summer or fall in six tributaries of Lake Superior. [Numbers of ammocetes measured are given in parentheses. Location of streams is shown in Figure 1.]

Stream	Estimated age at metamorphosis	Age I	Age II	Age III	Age IV
Sturgeon River	III	60 (417)	88 (120)	125 (471)	-
Salmon Trout River (Houghton County)	IV	61 (37)	—	144 (130)	-
Ontonagon River	III	59 (61)	95 (523)	125 (356)	-
Potato River	IV	61(2)	112 (23)	139 (42)	157 (363)
Bad River	III	53 (114)	105 (123)	119 (492)	-
Amnicon River	III	45 (29)	74 (59)	113 (347)	-

Estimates of the age at metamorphosis in the Ontonagon, Bad, and Amnicon rivers were based on the recovery of transformed lampreys with lengths similar to the lengths of age III larvae reestablished after chemical treatments. In three streams, the Sturgeon, Salmon Trout, and Potato rivers (classified as large, medium, and small, respectively, based on stream flow), the growth of ammocetes was monitored closely to determine whether fast growth would result in transformation in less than 5 years.

Sturgeon River

Growth of ammocetes of the 1967 year class was monitored for 3 years after the eradication of the ammocete population in a chemical treatment of the river in 1966. A total of 631 larvae and 32 transformed sea lampreys were collected in a 2.4-km section of the river during a partial treatment in August 1970 (Fig. 12). The three following factors suggest that at least some of the transformed lampreys were age group III and originated from the 1967 year class.

First, in the interval between the chemical treatment in 1966 and the experimental treatment in 1970, a total of about 6,160 m^2 of habitat were surveyed in 48.5 hours of electrofishing. Of the 2,385 sea lamprey larvae collected, only 6 were considered survivors of the 1966 treatment. Thus the residual population must have been small, and it is unlikely that the treated area would produce 32 transformed lampreys that survived the 1966 treatment.

Second, 20 of the transformed lampreys, 132-149 mm long, fell within the range of lengths of age III larvae (Fig. 12).

Third, a sample of 394 ammocetes longer than 119 mm was composed of 29% males, whereas the transformed group was composed of 53% males. This is similar to the ratio of male larvae to male transformed lampreys in the Little Garlic River-23% male larvae and 44% male transformed lampreys. Data (presented later in this report) show that larvae

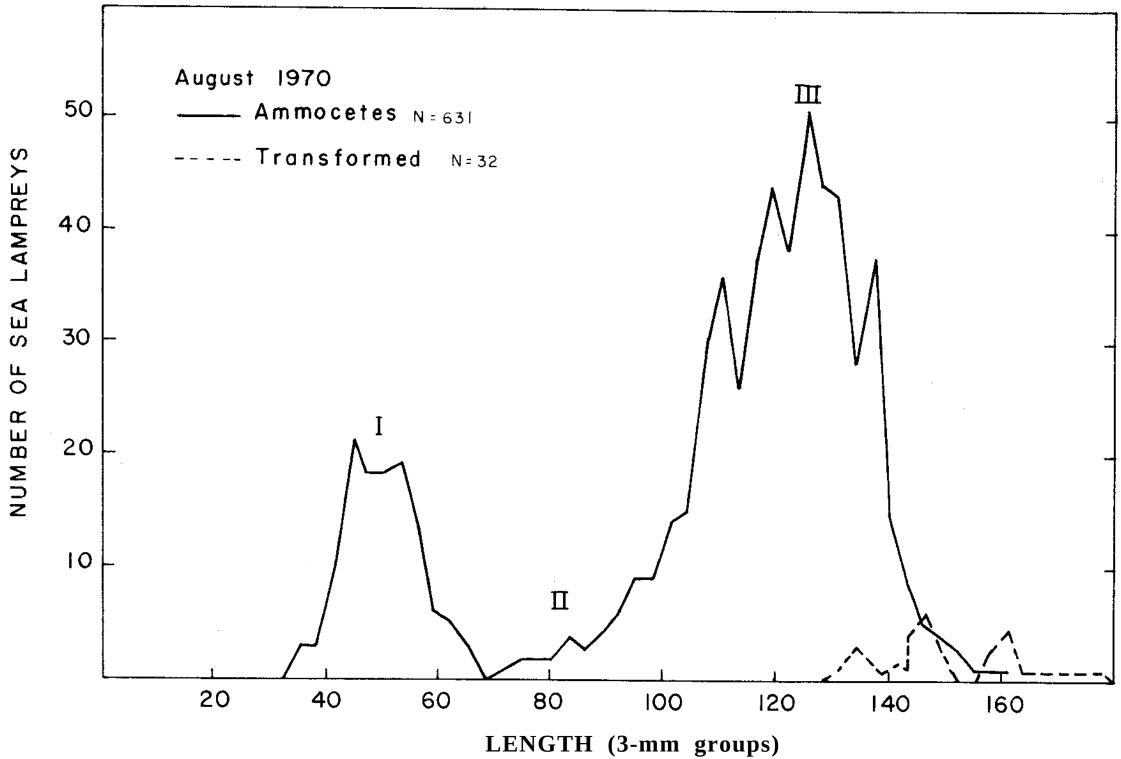

Figure 12. Length distribution of age groups I to III of sea lampreys from the Sturgeon River.

that survive chemical treatments and are later collected as transformed lampreys are predominantely female.

Salmon Trout River

The fastest growth of sea lamprey ammocetes in a Lake Superior stream was observed in the Salmon Trout River. The stream is about 7.6 m wide and has an average summer flow of 1 m^3/s. A dam limits sea lamprey distribution to the 0.6 km of stream below it; most of the population is confined to one large pool.

A total of 37 sea lampreys were marked in May 1966 as age II larvae, and 20 (54%) were recovered during the chemical treatment in August 1967 as age III larvae-all within 30 m or less downstream from the release site. The mean length of the larvae increased from 80 mm (range, 61-100) to 144 mm (range, 127-160; Fig. 13). The mean length of unmarked lampreys was similar. The annual growth of the ammocetes averaged 48 mm for the 3-year period. Although these ammocetes were in the length range and captured at the time of year at which metamorphosis takes place, no metamorphosed lampreys were collected. Because nearly all of the ammocetes were of transformation size (>120 mm long), I would expect some larvae to metamorphose the following year, at age IV.

Potato River

Although growth of sea lamprey ammocetes is usually slow in small streams, the Potato River was an exception. In some years the flow dwindles to trickles of water connecting a series of pools. The average lengths of year classes at various ages were determined from length-frequency data (Table 10). A total of 2,176 larvae and 190 transformed sea lampreys were collected during 1966-69.

Growth of ammocetes of the 1965 year class was monitored from 1966 to 1969 after chemical treatment of the river in 1964. Analysis of growth of the 1965 year class was facilitated by the absence of the 1966 year class. Absence of year classes of ammocetes is not uncommon in small streams in which sand bars may block the mouth of the stream during some spawning seasons.

In September 1966, two larvae (60 and 62 mm long) representing the 1965 year class were collected. Migration of lampreys of this year class from an upstream spawning area was apparently slow; substantial numbers of young-of-the-year and-yearling ammocetes of other year classes were previously collected at this site. The assumption that the two larvae collected in September 1966 were age group I was supported by the collection there of considerable numbers of larvae of the 1967 year class as age I ammocetes in August 1968 (Table 10). The range in length of these larvae was 39-76 mm (mean, 56).

At age III, in 1968, lampreys of the 1965 year class attained a mean length of 139 mm (range, 113-166), and 50% of the larvae were as long as

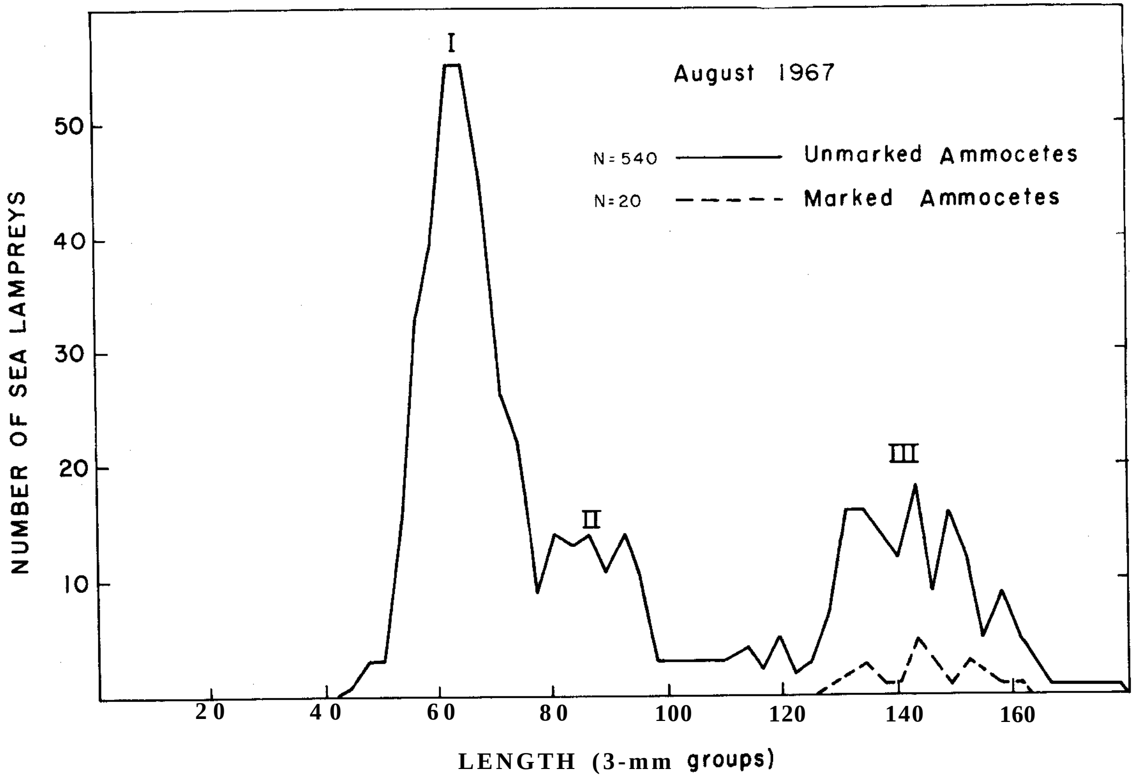

Figure 13. Length distribution of age groups I to III of sea lamprey ammocetes from the Salmon Trout River (Houghton County).

Table 10. Length distribution of sea lampreys of the 1965, 1967, and 1968 year classes from the Potato River, 1966-69.

Length interval	Ammocetes						Metamorphosed lampreys	
	1966	1967	1968	1969			1969	
(mm)	Sept. 12	Oct. 4	Aug. 16	June 4	July 31	Sept.4	July 31	Sept. 4
13- 18		16				1		
19- 24		14						
25- 30				5	1			
31- 36				15	9	1		
37- 42			6	5	41	31		
43- 48			20		56	87		
49- 54			39	1	20	143		
55- 60	1		71	4	5	101		
61- 66	1		30	7	7	46		
67- 72			6	15	21	15		
73- 78			2	18	66	19		
79- 84		1		13	101	36		
85- 90				5	128	66		
91- 96				1	82	91		
97-102				1	36	92		
103-108		9			23	61		
109-114		3	1		2	38		
115-120		4	3			15		
121-126		2	4			4		
127-132		1	7		3	2		
133-138		2	6	1	4	2		
139-144			6		19	6	3	2
145-150			8	2	41	11	31	16
151-156			2	1	50	20	27	33
157-162			3	1	73	31	18	29
163-168			2	2	44	21	9	16
169-174					19	7	1	4
175-180					7	3		1
Total	2	53	216	97	858	950	89	101

metamorphosing lampreys taken in this stream in 1969. Possibly a small percentage of lampreys transformed at age III, though none were collected.

An experimental treatment of the study area with TFM on July 31 provided a sample of 349 lampreys of age group IV of which 89 were transforming. The length of the IV and II group ammocetes did not overlap. Chemical treatment of the entire stream in September provided an additional sample of 204 sea lampreys of age group IV, of which 101 had transformed. The two collections of IV group lampreys were combined for analysis because of their nearly identical mean lengths. Because of the missing 1966 year class and the lack of overlap with larvae of age II, certain statistics were available that are not normally available for older age groups (Table 11).

Table 11. Mean length and percentage males of age IV larval and transformed sea lampreys in the Potato River.

Stage	Number collected	Percentage males	Mean length (mm)[a]		SD[b]	SE of mean[b]
			Males	Females		
Larvae	363	21.5	158 (129–178)	157 (129-178)	9.4	0.49
Transformed	190	28.9	154 (141-168)	156 (140-180)	6.9	0.50

a Ranges in parentheses.
b Sexes combined.

Mean lengths of the sexes among larval and transformed lampreys in the Potato River were closely similar. Applegate and Thomas (1965) reported female transformed sea lampreys were 2-3 mm longer than males in two tributaries of Lake Michigan. However, data from other Lake Michigan streams did not show this close similarity in length between the sexes in transformed lampreys. Female transformed lampreys were as much as 15 mm longer than males in the Ford River, 12 mm in the Cedar River, and 11 mm in the Whitefish River (Table 12).

The high percentage (34.4) of sea lampreys of known age (IV) that metamorphosed in the Potato River in the first year in which transformation is known to have occurred was much greater than that in any other river studied to date. Although the rapid growth was probably a dominant factor, other populations of ammocetes with large mean lengths did not produce such high percentages of transformed lampreys in the first year of metamorphosis.

Table 12. Number, percentage males, and mean length of transformed sea lampreys captured in fyke nets in tributaries of Lake Michigan.

Stream and date of chemical treatment	Year of collection	Number	Percentage males	Mean length (mm)		
				Males	Females	Sexes combined
Sturgeon River	1961	266	61	137	142	139
5/1/63	1962	382	66	138	142	140
	1963	30	70	140	140	140
Ford River	1961	476	76	134	149	138
6/15/64	1962	56	75	133	137	134
	1963	13	69	135	141	137
Cedar River	1961	343	52	145	155	150
8/12/64	1962	86	55	138	150	144
Whitefish River	1961	56	50	134	144	139
10/10/62	1962	174	67	134	145	138
6/3/65	1963	685	54	147	156	151
	1964	269	A7	157	162	160
	1966	22	9	146	164	163
Bark River 9/9/62	1961	511	39	150	154	152

SEX RATIO AND LENGTH OF LARVAL AND TRANSFORMED SEA LAMPREYS IN ORIGINAL AND RESIDUAL POPULATIONS IN STREAMS

Spawning populations of parasitic and nonparasitic species of lampreys are normally characterized by an excess number of males (Schultz 1930; Applegate 1950; Wigley 1959; Hardisty 1961b; Purvis 1970; Smith 1971). Some authors have reported an increase in the percentage of males as the population increased. A preponderance of females in spawning populations of lampreys is rare.

During the increase in the sea lamprey population of Lake Superior in the 1950's, the percentage of males among adults remained remarkably stable. In 5 of the 6 years from 1954 to 1959, the percentage of adult males collected at electric barriers varied slightly over 1 percentage point, from 57.4 to 58.7 (Smith 1971). In 1960 the percentage of males increased to 69.2 and ranged from 67.1 to 69.6 for the next 3 years. The increase coincided with the peak population of adults captured at Lake Superior electric barriers in 1961 (69,584) and persisted for 2 years (1962-63) after the adult population declined by 87% as a direct result of the chemical treatments that were begun in 1958. The percentage of males then began to decline steadily, from 54.8 in 1964 to 26.7 in 1969. For the 8-year period, 1971-78, the percentage of males in the adult population stabilized at 29 to 31.

Similar declines were observed in the percentage of adult males in Lakes Michigan and Huron as chemical control measures became effective. For example, the percentage of males collected in Lake Michigan tributaries averaged 68 (range, 64-70) from 1963 to 1965 (Smith 1971), but only 35 (range, 2144) in 1972-78. In Lake Huron, males declined from an average of 58% (range, 54-62) in 1960-62 to 37% (range, 31-39) in 1973-78.

The sex ratio of larval and transformed sea lampreys collected in streams was examined because the shift in the sex ratio of adults from a preponderance of males to females probably originated in tributary streams. Sex ratios of transformed sea lampreys collected during the first chemical treatments in Lake Superior showed high percentages of males in the Huron (64), Ontonagon (69), and Middle (73) rivers (Table 13). In contrast, only 4% of the metamorphosed lampreys collected in the Rock River were males. Apparently, a wide range in sex ratios occurred in Lake Superior tributaries during the period of maximum abundance of adults in the lake.

Mean length of transformed lampreys collected during the initial treatments of six streams was 140 mm (range, 133-147; Table 13). The mean length of larvae that survived the original treatments and were collected as transformed lampreys in later treatments was 166 mm (range, 160-173), a 19% increase. The length of residual transformed lampreys collected in a third treatment of the Huron River increased an additional 9%.

Table 13. Mean length and percentage males of transformed sea lampreys collected during initial chemical treatment and subsequent retreatments in tributaries of Lake Superior. [Numbers of lampreys measured or sexed are shown in parentheses.]

Stream and date of collection	Length (mm) Range	Mean	Mean increment	Percentage increase in length	Percentage males
Huron River					
9/7/58	118-156 (79)	138	-	-	64 (25)
10/4/61	132-190 (98)	163	25	18	48 (42)
10/20/65	167-195 (38)	177	14	9	16 (38)
Middle River					
9/28/58	112-152 (92)	133	-	-	73 (56)
7/17/62	142-175 (22)	160	27	20	18 (22)
Chocolay River					
10/29/58	121-183 (214)	147	-	-	—
10/24/61	144-203 (55)	173	26	18	29 (34)
Rock River					
10/26/58	126162 (56)	144	-	-	4 (24)
9/20/61	145-188 (95)	171	27	19	12 (52)
Misery River					
10/3/59	124-143 (8)	134	-	-	-
9/30/62	154–177 (15)	164	30	22	—
Ontonagon River 7/23/60	120-183 (126)	145	-	-	69 (32)

The increased length of residual transformed lampreys-probably largely a result of decreased population density-was accompanied by a decline in the percentage of males in the Huron and Middle rivers. In the Huron River, males declined from 64% in 1958 to 48% in 1961 and 16% in 1965; and in the Middle River, males declined form 73% in 1958 to 18% in 1962.

Larger samples of transformed sea lampreys and more continuous data were collected in fyke nets fished in five tributaries of northern Lake Michigan (Table 12). Transformed male lampreys predominated in four of the five streams before chemical treatments began. Although the percentage of males fluctuated from year to year, the mean lengths of transformed lampreys showed little change.

After the chemical treatment of the Whitefish River in 1962 (Table 12), the mean length of transformed sea lampreys steadily increased and the percentage of males decreased. Four years after the first chemical treatment, metamorphosed lampreys had increased about 20% in length and the sex ratio had declined from 67% in 1962 to 9% in 1966. The annual average lengths of transformed sea lampreys collected in the Pere Marquette River (Lake Michigan) ranged from 134 to 142 mm for a 3-year period before the chemical treatment, then increased to 153-164 mm in the 5 years after treatment (Hodges 1972).

With few exceptions, sea lamprey ammocetes that survive chemical treatments and are collected during later treatments as transformed lampreys are larger than the lampreys in the original population and are predominantly female.

Populations of larval and transformed sea lampreys isolated for a number of years above falls and dams are also predominantly female. Metamorphosed sea lampreys recovered above the falls in the Ocqueoc River (Lake Huron) during the initial chemical treatment in 1968 had a mean length of 161 mm and were 82% female, whereas below the falls, where annual recruitment was likely, transformed lampreys has a mean length of 135 mm and were 48% female (Table 14). A study of the sex ratio of transformed and larval sea lampreys in the Ocqueoc River a few years earlier (Hardisty 1965) showed percentages of females to be closely similar to that below the falls. The earlier study showed that female transformed and larval sea lampreys made up 47 and 52% of the population, respectively. By 1973, a sample of 162 residual larvae collected below the falls consisted of 78% females.

Similar observations have been made elsewhere. Ammocetes recovered in 1969 from an isolated population above a lamprey-proof dam constructed in 1958 on Silver Creek, a tributary of the Tawas River (Lake Huron), had a mean length of 130 mm (range, 103-158) and were 83% females. Ammocetes similarly isolated above a dam on Trout River (Lake

Table 14. Sex ratio and mean length of sea lampreys from two locations in the Ocqueoc River, 1968.

Location, stage, and sex	Number collected	Percentage	Mean length (mm)
Below falls			
Ammocetes			
Males	238	45	130
Females	287	55	131
Transformed			
Males	517	52	132
Females	478	48	137
Above falls			
Ammocetes			
Males	29	24	146
Females	91	76	151
Transformed			
Males	15	18	159
Females	69	82	161

Huron) were 92% female and averaged 165 mm (range, 133-188). A residual population of 144 ammocetes collected in a small tributary of the Chocolay River (Lake Superior) had a mean length of 165 mm (range, 142-191) and consisted of 96% females. An increase in the percentage of transformed females (from 46 to 85) over 7 years (1966-72) was also noted in an isolated population of sea lampreys in the Big Garlic River (Manion and Smith 1978). They suggested, "Several factors possibly influence changes in the sex composition of a sea lamprey population: increase in the number of females in the ammocete population because males tend to transform earlier; differential mortality during metamorphosis; or perhaps changes or reversals of sex in individuals."

The high percentage of female larvae recovered in populations of residual larvae apparently was not the result of a differential sex mortality caused by TFM: Because persistent seiche action in the lower 180 m of the Little Garlic River during a chemical treatment prevented a complete kill of ammocetes, this area was re-treated within 2 months. The percentage of male larvae recovered in the second treatment (14.8) was similar to that in the first treatment (17.2), indicating little, if any, differential mortality.

One exception to the high percentage of females found in streams where recruitment was prevented or limited was reported in Carp Lake River, Lake Michigan, by Applegate and Thomas (1965), who noted that the percentage of females decreased from 54 to 24 in a 5-year period when recruitment above a dam was prevented. From these data they postulated that "females transform at an earlier age than do males." Their examination of sex ratios of recently transformed sea lampreys in three Lake Michigan tributaries and one Lake Huron tributary showed a preponderance of females, and they concluded that "populations of recently transformed sea lampreys in Great Lakes streams are normally characterized by a small but variable preponderance of females."

If female lampreys tend to transform at an earlier age than males, and females predominated in tributary streams of the Great Lakes before chemical control measures, one would expect to find a high percentage of females in the adult population. However, this was not the case (Smith 1971).

Data in the present paper show that male larval and recently metamorphosed sea lampreys predominated in some tributaries of Lakes Superior and Michigan and coincided with the dominance of males in the adult population before chemical controls.

In Lake Superior, following chemical control measures, the ratio of male to female adult sea lampreys completely reversed, from 2.3 males per female in 1962 to 2.7 females per male by 1969-a sixfold increase in the ratio of females to males. The high percentage of female lampreys collected in residual populations, isolated populations, and reestablished populations have combined to produce highly female populations of adults in the upper Great Lakes.

Although the exact mechanism that causes the preponderance of females is unknown, a common factor among these populations is the low density of larvae which results from either chemical treatments, or natural and artificial barriers preventing recruitment. Evidently, density-dependent factors in the stream environment regulate the sex ratio of the population. The sea lamprey is a highly adaptable species and apparently responds to decreased numbers by producing more females.

SUMMARY AND CONCLUSIONS

Control of the sea lamprey now depends on the chemical treatment of tributaries before ammocetes metamorphose and migrate into the Great Lakes. Scales, otoliths, and other bony structures commonly used to age fish are not present in sea lampreys. Thus, the exact age at metamorphosis of ammocetes is difficult to determine.

The present study of the growth and age at metamorphosis of sea lamprey ammocetes established after chemical treatments shows pronounced variations in growth and age at metamorphosis. The results of this study and others (Manion and McLain 1971; Manion and Smith 1978) show that neither age nor length are critical factors for metamorphosis. Where a single year class was monitored for a period of 17 years, transformation began at age V and continued for a period of 13 years (Manion and Smith 1978). Nine transforming sea lampreys were collected in the Salmon Trout River (Houghton County, Michigan) during a chemical treatment on October 11, 1978; evidence strongly suggested that they originated from the III group established in 1975. Although earlier data (Fig. 13) showed no evidence of transformation among III group ammocetes in the Salmon Trout River in 1967, the mean length of age III ammocetes in the Salmon Trout River was closely similar (about 144 mm) in both years.

Distinct variations in growth among reestablished and residual populations of sea lamprey ammocetes emphasize the need for close surveillance and frequent monitoring of larval populations in all lamprey-producing streams to determine the age at metamorphosis and the optimum interval between chemical treatments.

Sex ratios of larval and transformed sea lampreys before chemical control showed the sex composition varied from stream to stream. A predominance of transformed male sea lampreys in some densely populated streams, along with a tendency for males to transform before females, would result in the predominance of males in the adult population.

The high percentage of female larval and transformed sea lampreys collected in reestablished and residual populations after chemical treatments indicates density-dependent factors were responsible for the shift in the sex ratio of adults.

ACKNOWLEDGMENTS

I thank Betty J. McEachern, who reviewed the manuscript and offered many suggestions, and Albert W. Bowers who prepared the figures.

REFERENCES

APPLEGATE, V. C.

1950. Natural history of the sea lamprey (Petromyzon *marinus)* in Michigan. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 55, 237 pp.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, and M. A. SMITH.

1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1. 35 pp.

APPLEGATE, V. C., and M. L. H. THOMAS.

1965. Sex ratios and sexual dimorphism among recently transformed sea lampreys, *Petromyzon marinus* Linnaeus. J. Fish. Res. Board Can. 22:695–711.

GAGE, S. H.

1928. The lampreys of New York State-life history and economics. Pages 158-191 *in* Biological survey of the Oswego River system. N.Y. Conserv. Dep. Suppl. 17th Annu. Rep. (1927).

HANSEN, M. J., AND T. M. STAUFFER.

1964. Cadmium sulfide and mercuric sulfide for marking sea lamprey larvae. Trans. Am. Fish. Soc. 93:21-26.

HARDISTY, M. W.

1944. The life history and growth of the brook lamprey *(Lampetra planeri).* J. Anim. Ecol. 13:110-122.

1961a. The growth of larval lampreys. J. Anim. Ecol. 30:357-371.

1961b. Sex composition of lamprey populations. Nature 191: 1116-l 117.

1965. Sex differentiation and gonadogenesis in lampreys. (Part II). J. Zool. 146, Part 3:346–387.

HODGES, J. W.

1972. Downstream migration of recently transformed sea lampreys before and after treatment of a Lake Michigan tributary with a lampricide. J. Fish. Res. Board Can. 29:1237-1240.

LOWE, D. R.

1972. Variations in body composition of pre-adult landlocked sea lamprey, *Petromyzon marinus* L. in relation to size and season. M.S. thesis. Univ. of Guelph, Guelph, Ontario. 81 pp.

MANION, P.J., and A. L. MCLAIN.

1971. Biology of *larval* sea lampreys *(Petromyzon marinus)* of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960-65. Great Lakes Fish. Comm. Tech. Rep. 16. 35 pp.

MANION, P.J., and B. R. SMITH.

1978. Biology of larval and metamorphosing sea lampreys. *Petromyzon marinus,* of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966-72. Great Lakes Fish.-Comm. Tech. Rep. 30. 35 pp. -

MOORE, H. H., AND R. A. BRAEM.

1965. Distribution of fishes in U.S. streams tributary to Lake Superior. U.S. Fish Wildl. Ser., Spec. Sci. Rep. Fish. 516. 61 pp.

PURVIS, H. A.

1970. Growth, age at metamorphosis, and sex ratio of northern brook lamprey in a tributary of southern Lake Superior. Copeia 1970:326-332.

SCHULTZ, L. P.

1930. The life history of *Lampetra planeri* Bloch, with a statistical analysis of the rate of growth of the larvae from western Washington. Occas. Pap. Mus. Zool. Univ. Mich. No. 221. 35 pp.

SMITH, B. R.

1971. Sea lampreys in the Great Lakes of North America. Pages 207-247 in M. W. Hardisty and I. C. Potter, eds. The biology of lampreys, vol. 1. Academic Press, London.

SMITH, B. R., and A. L. McLAIN.
1962. Estimation of the brook and sea lamprey ammocete populations of three streams. Great Lakes Fish. Comm. Tech. Rep. 4:1-18.

VLADYKOV, V. D.
1960. Description of young ammocoetes belonging to two species of lampreys: *Petromyzon marinus* and *Entosphenus lamottenii*. J. Fish. Res. Board Can. 17:267-288.

WIGLEY, R. L.
1952. A method of marking larval lampreys. Copeia 1952:203-204.
1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish Wildl. Serv., Fish. Bull. 59:561–617.

ZIMMERMAN, J. W.
1968. Water quality of streams tributary to Lakes Superior and Michigan. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 559. 41 pp.