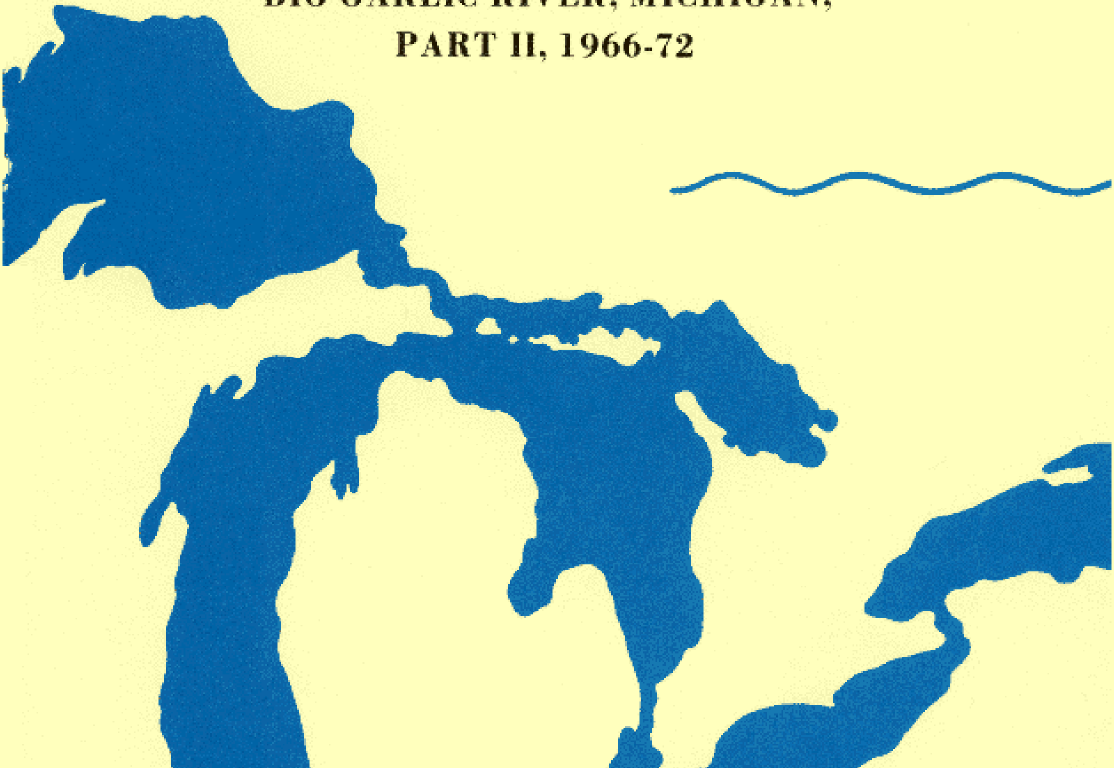
BIOLOGY OF LARVAL AND METAMORPHOSING SEA LAMPREYS, *PETROMYZON MARINUS*, OF THE 1960 YEAR CLASS IN THE BIG GARLIC RIVER, MICHIGAN, PART II, 1966-72



Great Lakes Fishery Commission

TECHNICAL REPORT No. 30

The Great Lakes Fishery Commission was established by the Convention on Great Lakes Fisheries, between Canada and the United States, ratified on October 11, 1955. It was organized in April 1956 and assumed its duties as set forth in the Convention on July 1, 1956. The Commission has two major responsibilities: the first, to develop coordinated programs of research in the Great Lakes and, on the basis of the findings, recommend measures which will permit the maximum sustained productivity of stocks of fish of common concern; the second, to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes. The Commission is also required to publish or authorize the publication of scientific or other information obtained in the performance of its duties.

BIOLOGY OF LARVAL AND METAMORPHOSING SEA LAMPREYS, PETROMYZON MARINUS, OF THE 1960 YEAR CLASS IN THE BIG GARLIC RIVER, MICHIGAN, PART II, 1966-72

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CONTENTS

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by

Patrick J. Manion and Bernard R. Smith

ABSTRACT

The 1960 year class of sea lampreys, *Petromyzon marinus,* isolated in a tributary of southern Lake Superior continued to yield information on the early life history of the sea lamprey. The larval population persisted and newly metamorphosed individuals were captured from 1966 until the study was terminated in 1972. The average lengths of larvae collected in October (when yearly growth is nearly complete) in successive years from 1966 to 1972 were 111, 113, 112, 114, 121, 128, and 129 mm. The average lengths of transforming lampreys during the same years were 1.50, 151, 145, 143, 144, 148, and 156 mm.

A gradual downstream shift of the population took place. Catches in an inclined-plane trap at the lower end of the study area increased to a peak of 13,244 in the 1968-69 migration year (September 1-August 31), and then steadily decreased. As the number of lampreys decreased in the upper sections and increased in the lower ones, the changes in density were reflected in changes in growth rates. Although the mean length of ammocetes throughout the stream was 111 mm in 1966, it had increased by 1971 to 151 and 143 mm in the upstream sections (IV and V), but to only 115 mm in the densely populated area immediately above the trap.

Of a total of 9,889 larvae marked in 196268 to study movement and distribution, 2,045 were recovered as larvae and 1,396 as newly transformed adults. Major downstream movements of larvae occurred during high water in April and May, and of transformed lampreys in mid-October through November. Each year about 40% (range, 30-68) of the annual production of transformed lampreys migrated from the Big Garlic River system in one 12-hour period, and 82% by the end of October.

The Big Garlic River study proved conclusively that metamorphosis of a single year class occurs over a considerable numbers of years. Newly metamorphosed individuals were captured in almost steadily increasing numbers from 1965 (age V) to the termination of the study in 1972 (age XII). Many large ammocetes were still present in the study area in 1972, and it can safely be assumed that they would have continued to metamorphose for several more years.

1 Contribution 537 of the U.S. Fish and Wildlife Service, Great Lakes Fishery Laboratory, Ann Arbor, Michigan 48105. This study is part of a program conducted by the Service under contract with the Great Lakes Fishery Commission. The authors were on the staff of the Laboratory until October 1, 1970.

INTRODUCTION

A study of the larval life history of the sea lamprey, *Petromyzon marinus,* began in the spring of 1960 when sea lampreys nearing spawning condition were introduced into a portion of the Big Garlic River, a tributary of southern Lake Superior in which no lampreys were present because physical barriers prevented their upstream migration. Manion and McLain (1971) described the introduction and biological characteristics of the spawning adults and presented information on the development, behavior, and growth of their progeny from hatching (July 1960) to the first capture of metamorphosed individuals (October 1965). All references to larval life history in this paper are from this work unless otherwise indicated.

Their study provided important knowledge of larval life history and precise information on the earliest age at which sea lamprey ammocetes of the Big Garlic River metamorphosed to the adult stage and migrated to the lakes. Such information is essential to the establishment of frequency and time of chemical treatments of streams with lampricides.

In the Big Garlic River, the minimum age at transformation for the isolated 1960 year class of sea lampreys was 5 years. A large population of known-age larvae (length range, 65-176 mm) remained in the river after the first metamorphosed individuals were observed in 1965. In fact, only four transformed individuals were captured in that year, from a total population of many thousand larvae, clearly revealing that metamorphosis by members of this single year class takes place over more than 1 year. Inasmuch as the application of 3-trifluoromethyl-4-nitrophenol (TFM) to control sea lampreys in the Great Lakes is directed at the larval lampreys (Applegate et al. 1961) and more information was needed on the longevity and life history of the larvae, the Big Garlic River study was continued.

Equally important was the need for more precise knowledge of metamorphosing lampreys, including their distribution, habitat preference, movement, growth, and behavior. Such information is valuable in developing other methods of control, as well as in providing a better basis for establishing the frequency of chemical treatments of streams more efficiently.

We describe the continuing life history of larvae and metamorphosed lampreys of the 1960 year class and present information on growth, movement, and sex composition after the first capture of newly metamorphosed individuals in 1965 until the lower section of the study area was treated with lampricides on September 6-7, 1972.

LARVAL SEA LAMPREYS

Behavior and Movement

During the first 2 years of life, larvae were concentrated in sand-silt habitats in shallow water. At ages II and III, the larger ammocetes (longer than 80 mm) tended to move to deeper water. This segregation by length within the river became more pronounced from 1966 to 1972 and only occasional large lampreys were collected in shallow water near the edge of the river. Almost all larvae were in the deeper water in areas where velocity was reduced (in eddies, behind logs or rocks, and in other similar locations) and loose materials (silt and detritus) had settled to the bottom. Larvae were most plentiful in silt and detritus deposits in the upper four sections (II-V) of the study area (see Fig. 1 for locations of sections), but among aquatic plants in the lowest section (I). Depth of water and particle size of bottom material were important factors in the use of habitat by sea lamprey larvae. Generally, however, at least some larvae were found throughout the river in what appeared to be unfavorable areas.

An inclined-plane trap at the lower end of section I captured lampreys moving out of the study area and permitted observation of the time and magnitude of their downstream movement (McLain and Manion 1967). The trap was operated throughout the year and was efficient at water discharges that occasionally exceeded 6 m^3/s. A plastic enclosure heated with a propane stove allowed ice-free operation at temperatures as low as -34°C during the

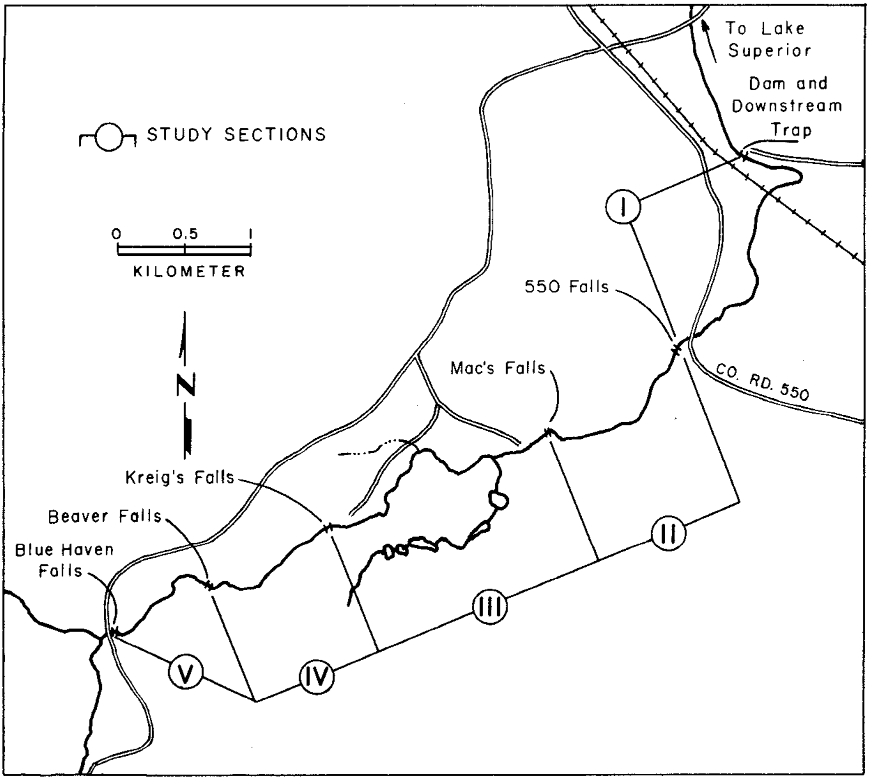

Figure 1. Big Garlic River, Marquette County, Michigan, showing locations of the various study sections and the downstream trap.

winter (Fig. 2). Larvae were also collected with electric shockers throughout the study area in October each year.

The annual shocker collections demonstrated a gradual downstream shift of the population. The numbers of larvae collected decreased in section IV from $4.3/m^2$ in 1966 to none in 1972, and increased in section I from $3.7/m^2$ in 1966 to 5.4 in 1968 and then declined to $3.0/m^2$ in 1972.

The extent of the downstream movement also was shown by the catches of larvae in the trap at the lower end of the study area, which were tabulated by migration year (September l-August 31). Growth of larval lampreys was almost complete by fall, and metamorphosis of those reaching the parasitic phase in a given year was well under way by September; therefore, arbitrary limits for the migration year were selected that would reflect the total year's growth of larvae as well as the total numbers that reached the adult stage in the one time period.

Movement of larvae to the trap increased from 365 in 1962-63 to a peak of 13,244 in 196869, and then decreased progressively each year to 3,062 in 1971-72 (Table 1). The increase in numbers caught between 1962-63 and 1968-69 averaged 2,146; the largest annual increase (3,437) was in 1965-66 and the smallest (247) in 1966-67. After the peak in 1968-69, the catch in the next 3 years decreased successively by 7,149, 2,336, and 697.

After 1970, most of the ammocetes remaining in the river were in sections I and II. Some larvae were near the original spawning sites until 197 1. Apparently a few larvae remained in the two uppermost sections (IV and V) after 1971, but none were collected during the annual collections with an electric shocker in 1972.

The downstream drift of ammocetes was seasonal; movement, as indicated by trap catches was heaviest in May, except in 1962-63, 1967-68, and 1970-71, when the yearly peak was in April (Table 1). Earlier-than-usual spring floods in those 3 years provided the stimulus for earlier migration. For the combined years of trap operation (1962-72), about 92% of the annual catch was made from March 1 to June 30. A minor peak occurred in September-October (3% of the total catch), and the remaining 5% was distributed throughout the other 6 months. The least movement was in February.

In the early years (1960-65) of the study, it was observed that larvae were inactive at water temperatures below 4.4°C. Many more observations in 1966-72 permitted more definitive interpretations of the influence of water temperature and water flow on larval movement. Generally, the number of larvae appearing at the trap increased as winter temperatures increased from 0°C in the spring (Fig. 3). This trend of rising temperature and increased movement continued until water temperatures exceeded 10°C, usually in mid-May (Table 2); the temperature then continued to increase to, and fluctuate within, the normal summer range of 11 to 19°C, while the number of ammocetes captured at the trap dropped rapidly to almost nil by early June.

The influence of water levels on movement of ammocetes is more difficult to document. The first significant catches of larvae for the year were concurrent with the spring runoff in late March or early April. Flows tended

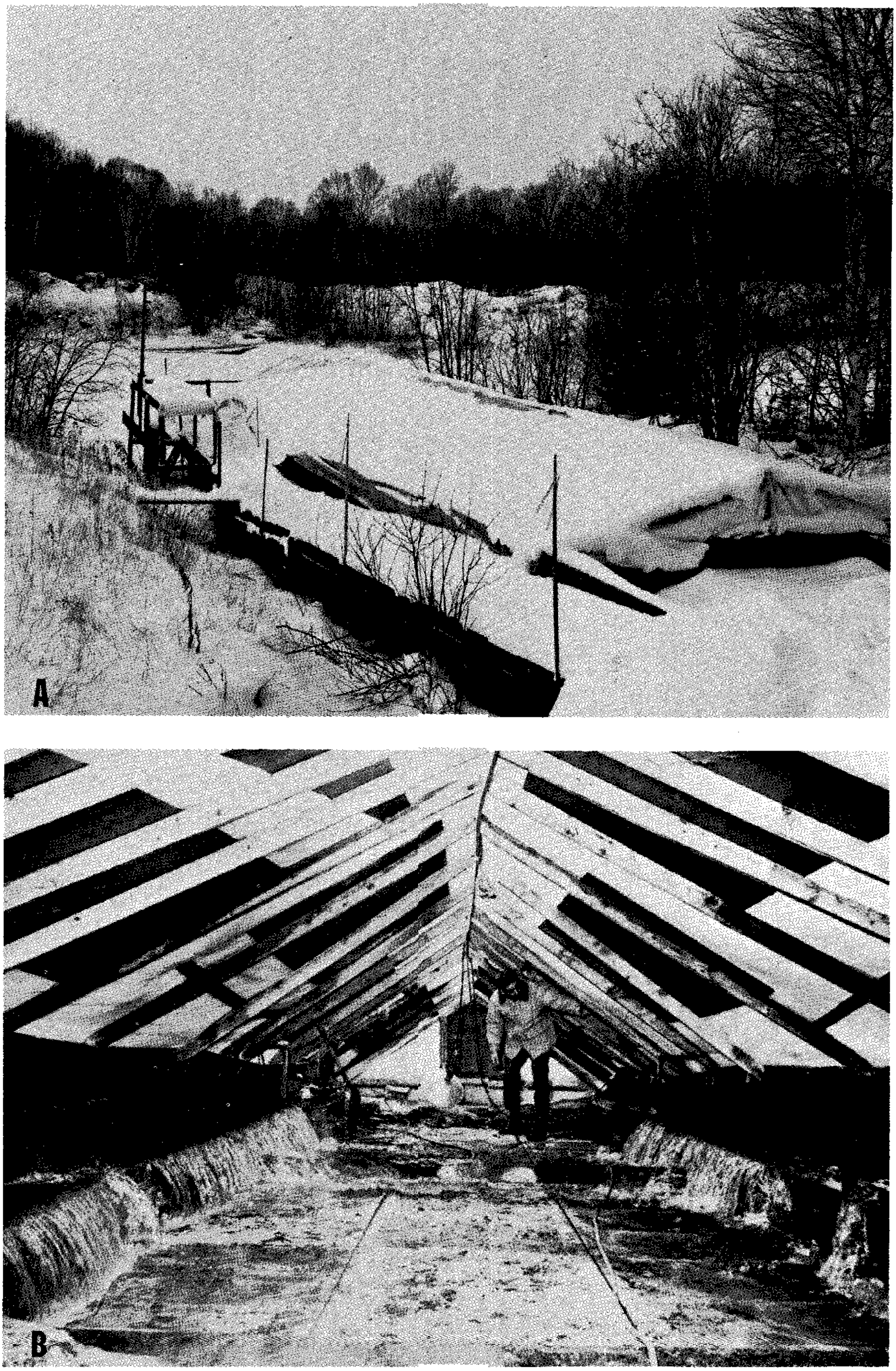

Figure 2. Heated enclosure on the downstream trap of the Big Garlic River, as seen from outside (A) and inside (B). Construction details were given by McLain and Manion (1967).

Table 1. Number of sea lamprey ammocetes captured at the downstream trap by month and migration year (September l-August 31) in the Big Garlic River, 1962-72.

	Migration year									
Month	1962-63	1963-64	1964-65	1965-66	1966-67	1967-68	1968-69	1969-70	1970-71	1971-72
Sept.	1	1	13	40	56	46	560	128	139	19
Oct.	0	2	10	29	80	208	73	175	158	49
Nov.	0	2	4	14	56	46	40	46	12	34
Dec.	0	1	4	37	169	2	68	32	12	6
Jan.	0	1	0	4	15	0	152	10	18	1
Feb.	0	0	2	4	18	0	40	4	14	0
Mar.	1	0	2	89	1,183	552	32	12	65	45
Apr.	351	376	1,249	1,722	2,593	5,903	3,038	2,546	2,605	537
May	7	1,389	2,510	4,684	2,862	3,058	8,762	2,786	682	2,296
June	3	713	286	745	416	610	179	295	48	34
July	0	282		291	247	150	113	53	4	17
Aug.	2	55	96	25	236	154	187	8	2	24
Total	365	2,822	4,247	7,684	7,931	10,729	13,244	6,095	3,759	3,062

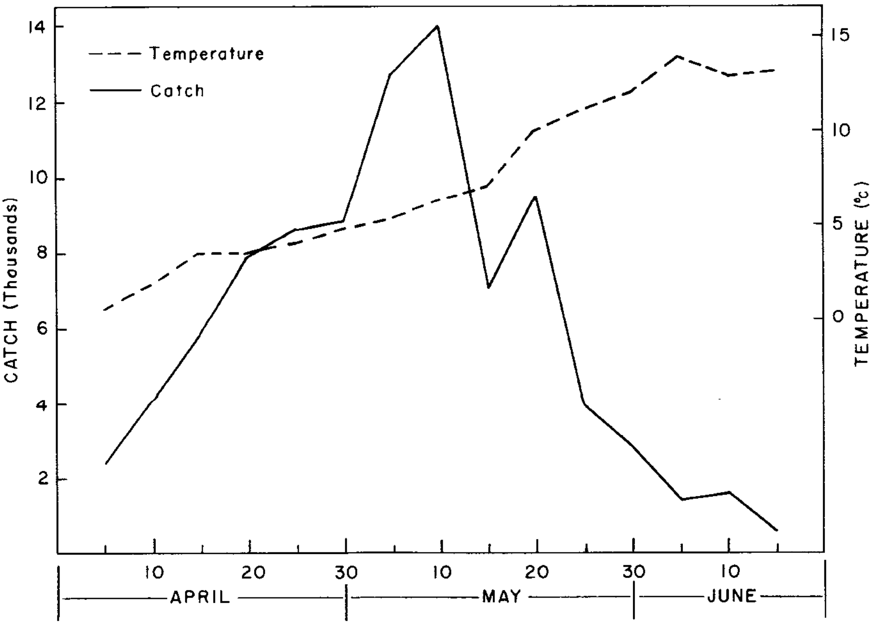

Figure 3. Daily water temperatures and numbers of larval lampreys captured at the downstream trap in the Big Garlic River, 1966-72.

Table 2. Average water temperature (°C) by 10- or 11-day periods in the Big Garlic River in April-November, 1966-72.

Period	1966	1961	1968	1969	1970	1971	1972
April							
1-10		1.7	1.7	0.0	0.6	–	-
11-20	2.2	3.9	6.1	2.8	2.8	3.3	0.0
21-30	4.4	6.1	5.0	3.9	6.7	3.3	1.1
May							
1-10	5.0	6.1	6.7	8.3	7.2	6.1	2.2
11-20	8.9	7.8	10.0	8.9	7.8	8.3	5.0
21-31	12.2	11.7	10.0	12.8	11.1	8.9	14.4
June							
1-10	11.7	13.9	13.9	11.1	15.0	12.8	13.3
11-20	13.9	13.3	12.8	11.7	14.4	15.0	12.2
21-30	18.9	14.4	11.1	12.8	15.0	15.0	13.3
July							
1-10	19.4	-	14.4	12.8	17.2	16.7	13.3
11-20	18.9	18.3	16.7	18.3	16.7	14.4	16.7
21-31	17.2	16.1	15.6	16.7	18.3	14.4	15.6
August							
1-10	16.1	16.7	16.1	17.2	17.8	15.0	13.3
11-20	14.4	14.4	14.4	17.2	18.9	15.6	15.6
21-31	14.4	13.3	13.9	17.2	15.6	13.3	15.6
September							
1-10	15.0	13.9	12.2	15.0	16.1	17.8	12.2
11-20	12.2	13.9	13.3	13.3	12.2	12.2	11.7
21-30	7.8	10.0	11.1	10.6	11.7	10.0	8.3
October							
1-10	7.8	8.3	9.4	10.0	10.6	11.1	8.9
1 l-20	5.6	6.1	11.7	6.1	7.8	8.9	6.7
21-31	2.2	5.0	4.4	3.3	8.9	10.0	5.6
November							
1-10	-	-	2.8	4.4	4.4	2.8	5.6
1 l-20	-	-	-	2.2	-	-	0.6
21-30	-	-	-	-	-	-	1.7

to remain high through April and May, but with a downward trend toward stable flows, while trap catches continued to increase. However, it was observed that within these trends, each time flow increased significantly, the number of ammocetes also increased, indicating that rises in water level triggered or induced downstream movement. Even slight increases in water levels (as little as 6 cm on a staff gauge) resulted in downstream movement of larvae-sometimes in large numbers.

Although movement of larvae was related directly to high water and rising temperatures, it did not appear to be entirely lethargic or passive. Normally, larvae remained in their burrows during daylight and emerged only at night. Average daytime movement of about 18% of the total number caught during the first high water, as opposed to about 0.5% after floods subsided, suggests that initial movement of larvae in early spring was caused partly by the scouring of the substrate by flood waters.

The below-average size of the early migrants suggested that these larvae were weaker and less able than the large ones to resist the floods when they left their burrows. Even though some ammocetes were probably forced from their normal habitats by flood waters, most appeared to be actively seeking better locations by leaving their burrows at night and swimming about for extended periods. Larvae observed at night almost always swam with the head upstream, even though they might be drifting downstream. Active movement was also apparent from the occurrence of major migrations of larvae in the spring after water levels had receded to almost normal flows. If ammocetes were stimulated only by high water and movement was entirely passive, the magnitude of migration should have been as great in the fall (when water levels were often as high as in the spring)-or at least higher than only 3% of the total annual catch.

There were indications that other factors also caused larvae to -become more active and move downstream. Some marked ammocetes released in 1963 in sections II and III, which were densely populated, were captured in the trap within 7 months, whereas marked larvae released in the areas of low density (sections IV and V) were captured In significant numbers only after about 2 years. These data suggest that the stress of density stimulated downstream movement. Similarly, collections of ammocetes in the area above the trap with backpack shockers in 1966 and 1972 caused larvae to appear at the trap, some 275 m downstream almost immediately-indicating that external disturbances also induced downstream movement.

The release of marked ammocetes in the upper sections of the study area and their recapture downstream provided additional information on movement. Ammocetes were collected in the spring at the downstream trap and marked by subcutaneous injection of an insoluble dye (Wigley 1952). They were then released upstream in the five areas. The color of the dye and the location of marks on the body of the ammocete identified the date and location of release.

A total of 4,915 ammocetes collected at the trap were marked from 1966 to 1972, in addition to 5,642 marked by Manion and McLain (1971) from 1962 to 1965. The chrome green dye used to mark 668 larvae in October 1964 and 1965 either leached out or was absorbed and became indiscernible shortly after marking. Therefore lampreys marked with that dye were deleted from all totals.

Retention of the other marks was good until 1972, when some larvae were observed to have lost all except a trace of dye. The location of the mark on these animals was identified by an increase in pigmentation along the entry path of the marking needle. Trace marks were verified under a microscope.

The revised total of 4,974 larvae marked from 1962 to 1965 yielded a combined total of 9,889 for 1962.72. Of these, 2,045 (21%) were recovered as larvae-l,337 at the downstream trap and 708 with electric shockers (Table 3)-and 1,396 marked as larvae were captured in the trap as newly metamorphosed individuals.

In the first 2 years, marked individuals were released in all sections of the study area except the uppermost (V). Larvae from the group marked in 1962 appeared at the trap in 1965 and those from the group marked In 1963 appeared in 1964. Both groups continued to contribute to the trap catch throughout the study period; a total of 9% of those released in 1962 and 18% of those released in 1963 were caught by the trap. The average length of larvae in 1962 was 63 mm; apparently mortality of these small animals was heavy: only 41 were recovered, of which 29 came from section I, immediately above the trap.

Recoveries of the 1963 group by shocking and in the trap were from all four areas of release. The largest numbers came from sections I and III and lesser numbers from II and IV.

All ammocetes marked in 1964-66 and 1968 were released in the three upper sections (III, IV, and V). Total recoveries from these groups ranged from 32% in 1965 and 1966 to 53% in 1968. Captures at the trap ranged from 25 to 52%. These larvae were all large when marked, over 90 mm long, and about half of those captured at the trap had transformed.

Of the total larvae recovered at the trap, marked recoveries increased progressively from a low of 0.8% in 1966 to a high of 5.7% in 1972 (Table 4) and averaged 2.5% for all years combined (1966-72).

Limited information is available on the time and distance of downstream movement for ammocetes. The fastest downstream movement observed was by marked larvae released in section III in October 1963. Some of these larvae traveled the 6.4 km to the trap within 7 months. Larvae of another (smaller) group, released at the upper end of section I in 1962 were first captured at the trap (2.6 km downstream) 31 months later.

Downstream movement of ammocetes was slower and more erratic than that of most fish, for unlike most other fishes, ammocetes are poor swimmers and probably burrow frequently to rest and feed during their downstream migration. The increase in movement of larvae to the trap as the study period progressed has been shown to be due in a large part to the gradual downstream shift of the entire population, and consequently the proximity of large numbers to the trap. However, indications from the movement of marked animals were that large larvae moved downstream faster than did smaller larvae. The exceptionally rapid movement of larvae out of their area of release in section III could have been due to the high density of larvae in that section at that time.

Growth and Size

The mean length of ammocetes collected in the Big Garlic River by electrofishing was 107 mm in 1965. Means in different sections ranged from 97 mm in III, the area of greatest population density, to 130 in IV. Annual growth of the larvae had already slowed substantially; the average annual length increment in 1963-65 was 15 mm, as compared with 24 and 26 mm in the preceding two years.

In 1966, the mean length of larvae (then age VI) was 111 mm (range, 67-179; Table 5) an increase of only 4 mm. Larvae with the largest mean length (133 mm), as well as the longest individual (179 mm), came from section IV. Average lengths in samples from two of the four sections decreased from that of the previous year; perhaps larger larvae migrated

Table 3. Number of marked larvae recaptured by electric shockers (ES) in October and at the downstream trap (DT) in the Big Garlic River, 1963-72. [Lampreys marked as larvae and recaptured after metamorphosis are given in parentheses. See Figure 1 for location of sections.]

Marked and released		Method of capture	Number recaptured										Total 1963-72
Date and section	Number		1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	
October 1962													
I	79	ES	1	1	0		0	0	0	0	0	0	2
		DT	-	0	1	25	0	0	1	0	0	0	27
II	79	ES	0	0	0	0	0	0	0	0	0	0	0
		DT		0	0	0	0	0	0	0	0	0	0
III	80	ES	1	0	1	0	2	0	0	0	0	0	4
		DT	-	0	1	1	0	0	0	0	0	0	2
IV	80	ES	0	1	2	3	0	0	0	0	0	0	6
		DT		0	0	0	0	0	0	0	0	0	0
Subtotal 1962	318	ES	2	2	3	3	2	0	0	0	0	0	12
		DT		0	2	26	0	0	1	0	0	0	29
October 1963													
I	181	ES	-	0	0	0	0	3	0	1	0	0	2
		DT	-	0	3	23	2	(5)	3	(1)	0	1	36
		DT					(1)						(7)
II	149	ES		0	0	0	0	0	0	0	0	0	1
		DT		2	5	4	(2)	(1)	(3)	1	3	1	16
		DT											(6)
III	197	ES	–	7	1	2	0	1	0	0	0	0	11
		DT	–	1	3	3	0	12	1	1	4	6	31
		DT					(1)		(1)	(2)	(5)	(1)	(10)

IV	173	ES	-	6	2	0	1	0	1	0	0	0	10
		DT	-	0	1	1	0	4	1	2	2	3	14
		DT									(5)	(1)	(6)
Subtotal 1963	700	ES	-	13	3	2	2	3	1	0	0	0	24
		DT	-	3	12	31	2	19	5	5	9	11	97
		DT					(4)	(6)	(4)	(3)	(10)	(2)	(29)
May-July 1964													
IV	1,896	ES	-	45	31	59	18	12	8	3	8	0	184
		DT	-	0	0	10	67	77	132	44	30	26	386
		DT				(17)	(89)	(38)	(30)	(40)	(46)	(4)	(264)
May-July 1965													
V	2,060	ES	-	-	106	36	3	10	4	5	15	0	179
		DT	-	-	0	0	9	23	88	42	50	33	245
		DT				(1)	(21)	(27)	(49)	(68)	(69)	(12)	(247)
May-June 1966													
V	4,364	ES	-	-	-	79	82	27	70	24	21	1	304
		DT	-	-	-	0	60	51	113	100	61	93	478
		DT				(6)	(45)	(68)	(99)	(153)	(255)	(44)	(670)
June 1968													
III	551	ES	-	-	-	-	-	2	2	1	0	0	5
		DT	-	-	-	-	-	0	68	28	2	4	102
		DT						(92)	(38)	(40)	(15)	(1)	(186)
Grand Total	9,889	ES	2	60	143	179	107	54	85	33	44	1	708
		DT	-	3	14	67	138	170	407	219	152	167	1,337
		DT				(24)	(159)	(231)	(220)	(304)	(395)	(63)	(1,396)

Table 4. Number of larval and transformed sea lampreys captured at the downstream trap in the Big Garlic River, 1966-72, and the number and percentage that had been marked.

Year	Larvae			Transformed		
	Total catch	Marked		Total catch	Marked	
		Number	Percentage		Number	Percentage
1966	7,925	67	0.8	46	24	52.2
1967	7,872	138	1.8	229	159	69.4
1968	11,168	170	1.5	398	231	58.0
1969	12,884	407	3.2	358	220	61.5
1970	6,015	219	3.6	739	304	41.1
1971	3,546	152	4.3	901	395	43.8
1972	2,957	167	5.1	249	63	25.3
Total	52,361	1,320	2.5	2,920	1,396	47.8

downstream. The smallest mean length (96 mm) was in section II, where the samples indicated a decrease of 11 mm. Before 1966, section II contained several beaver dams, which were washed out in late fall 1965. Evidently, the presence of the beaver dams induced faster growth, probably due to increased water temperatures and deposition of silt and detritus.

In October 1967 the average length of VII-group larvae was 113 mm (range, 72-165) an increase of only 2 mm from October 1966. Again, the largest average length was in section IV and the smallest in section II. Average increments in length continued to decrease even further in 1968: it was 112 mm (range, 72-158) in October 1968, 1 mm less than in 1967.

Mean lengths again increased slightly (2 mm) in 1969 (mean, 114 mm; range, 76-160) and significantly, to a mean of 121 mm (range, 90-177) in 1970. The increase of 7 mm was the first substantial increase since 1965 and was equal to the total growth increment from 1965 to 1969. Judging by trap catches (Table 1) density of the lamprey population in the river decreased about 54% between the 1968-69 catch (13,244) and the 1969-70 (6,095). The increase in growth rates probably was attributable to the reduction in population density.

Coincidental with another large decrease in population between 1969-70 and 1970-71 (when the trap catch dropped to 3,759), mean length increased again in 1971 to 128 mm (range, 85-170), an increase of 7 mm. Growth was negligible in 1972, when the mean increased only 1 mm to 129 mm (range, 98-173). Collections in October 1972 were limited to only 100 specimens because all larvae in section I had been removed by chemical treatment on September 6, 1972, and shocker collections indicated only a sparse population in the other sections.

Extreme variations in growth existed within the study area, and growth fluctuated between sections. From 1966 to 1972, the average increase in mean length was lowest in section I and highest in sections IV and V. Density, based on numbers of lampreys collected per square meter, was corre-

Table 5. Lengths and length increments of sea lamprey ammocetes collected by electric shockers in October from different sections of the Big Garlic River, 1960-72. [Data for 1960-65 from Manion and McLain (1971); see Figure 1 for location of sections.]

Section and year	Number measured	Total length (mm) Mean	Range	Increment
I				
1960	0			
1961	28	45	34-54	
1962	62	75	47-107	30
1963	273	89	63-134	14
1964	197	100	69-134	11
1965	175	108	77-161	8
1966	139	107	67-154	-1
1967	122	105	72-141	-2
1968	200	124	72-149	19
1969	146	105	76-143	-19
1970	127	114	90-141	9
1971	81	115	92-148	
1972	0	-	-	
II				
1960	38	13	11-17	13
1961	33	34	2841	21
1962	118	52	37-72	18
1963	234	69	52-93	17
1964	195	80	58-117	11
1965	203	107	71-155	27
1966	161	96	72-137	-11
1967	100	102	74-129	6
1968	130	103	78-148	1
1969	93	106	80-132	3
1970	124	111	90-148	5
1971	108	117	85-150	6
1972	44	122	98-144	5
III				
1960	33	14	12-19	14
1961	26	38	2549	24
1962	185	65	39-100	27
1963	171	81	52-120	16
1964	163	91	66-126	10
1965	154	97	72-142	6
1966	124	125	88-174	28
1967	146	122	81-165	-3
1968	97	118	85-158	-4
1969	94	120	97-151	2
1970	99	133	92-167	13
1971	108	136	95-166	3
1972	56	134	103-173	-2
IV				
1960	28	13	10-15	13
1961	16	42	3249	29
1962	171	65	41-94	23
1963	102	81	56-131	16
1964	105	100	72-159	19

Table 5. *Continued*

Section and year	Number measured	Total length (mm)		
		Mean	Range	Increment
1965	97	130	81-176	30
1966	80	133	80-179	3
1967	65	126	82-152	-7
1968	41	123	98-147	-3
1969	73	129	108-149	6
1970	20	146	112-164	17
1971	21	151	130-170	5
1972	0	—	-	-
V				
1965	104	101	65-142	
1966	114	107	73-146	-6
1967	37	111	93-144	4
1968	51	119	94-145	8
1969	26	136	110-160	17
1970	9	147	139-161	11
1971	39	143	119-158	-4
1972	0	-	-	-
I-V				
1960	99	13	10-19	13
1961	103	39	25-54	26
1962	536	63	37-107	24
1963	780		52-134	17
1964	660	92	58-159	12
1965	733	107	65-176	15
1966	615	111	67-179	4
1967	470	113	72-165	2
1968	534	112	72-158	-1
1969	432	114	76-160	2
1970	379	121	90-177	7
1971	357	128	85-170	7
1972	100	129	98-173	1

spondingly highest in section I and lowest in sections IV and V, in all years. Density remained highest in section I until the chemical treatment in 1972, as losses through downstream drift were offset by recruitment from upstream areas. The factors that influence growth of ammocetes are complex and interrelated, but the present data strongly indicate that growth of the larvae was highly density dependent.

The maximum length of 179 mm for larval sea lampreys in the Big Garlic River is similar to maximum lengths for larval sea lampreys in other tributaries of Lake Superior (Purvis 1973). Maximum lengths were about the same in 1972 (173 mm) as in 1966 (179 mm). Evidently, sea lampreys in the Big Garlic River reached a maximum length due to environmental (density) or genetical control. Maximum size of larvae also could be regulated by the limitations of filter feeding. Passive filter feeding in streams may impose limits on the maximum lengths ammocetes can reach, as length appears to be somewhat independent of the size of the adults or the species of lampreys. For instance, it has been shown that normally nonparasitic American brook lampreys, *Lampetra lamottei,* that adopted a parasitic existence grew to almost twice normal lengths (Manion and Purvis 1971).

The length-frequency distribution of the ammocetes collected annually in October in 1966-72 are moderately skewed to the right (Fig. 4). Standard deviations decreased from a high of 20.7 in 1966 to 13.6 in 1972, and intervals within the 99% confidence limits increased from ± 2.15 in 1966 to ± 3.49 in 1972 (Table 6).

Estimates of larval growth from length-frequency distribution have been used in the past by many lamprey researchers. Schultz (1930) concluded that earlier workers placed too much confidence in minor modes in length-frequency curves as indications of year classes. His conclusion, based on 2,915

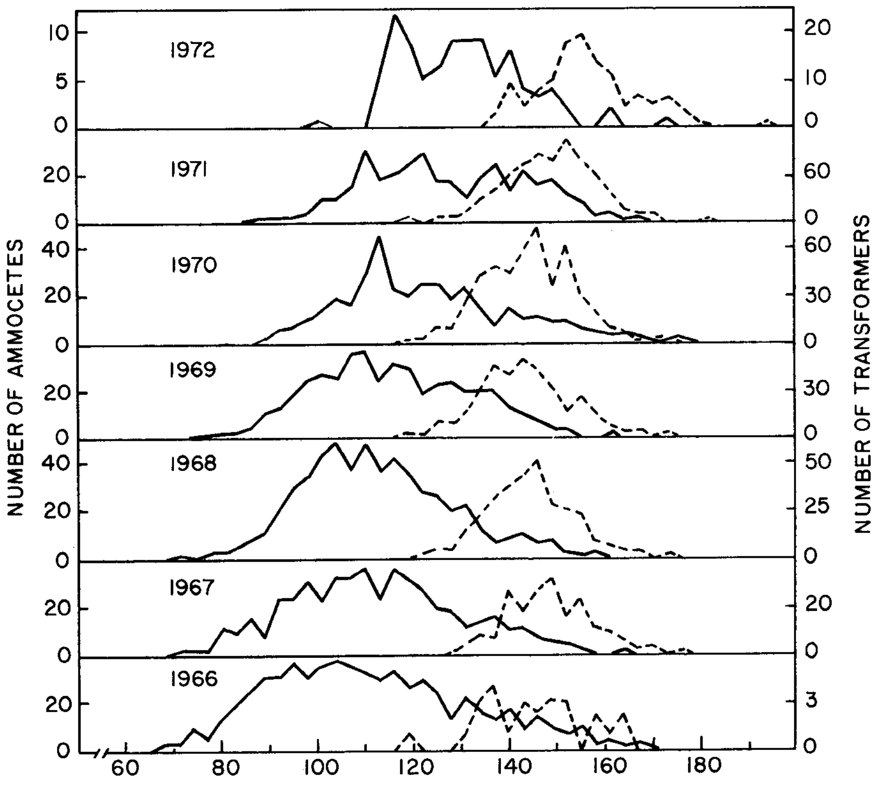

Figure 4. Length-frequency distribution of sea lamprey ammocetes (solid line) and newly transformed lampreys (broken line) collected in the fall from the Big Garlic River, 1966-72.

Table 6. Standard deviation and standard error of the mean within 99% confidence limits for sea lamprey ammocetes taken in the Big Garlic River in October, 1966-72.

Year	Mean length (mm)	Standard deviation	Standard error	99% confidence limits
1966	111	20.7	0.835	±2.15
1967	113	17.4	0.803	±2.06
1968	112	14.9	0.645	Al.66
1969	114	15.7	0.756	±1.95
1970	121	17.4	0.894	±2.30
1971	128	16.9	0.890	±2.30
1972	129	13.6	1.360	±3.49

individuals, was that minor modes were not significant and were attributable to biased sampling. Data from the Big Garlic River demonstrate conclusively that interpretations of modes in length frequencies as year classes are generally unreliable for sea lampreys after age III. Modal lengths after age III probably are not as indicative of a particular age class as they are of yearly differences in growth rates within a stream caused by changes in population density, overlap of year classes due to increase in ranges of length each year, differential growth by sexes, and the migration of smaller or large larvae into a sampling area.

Interpretation of modes can be very misleading; for example, in 1971 the length-frequency distribution of lampreys from the Big Garlic River showed three distinct modes-two for larvae (one each from sections II and III) and one for transformed lampreys (Fig. 4). Normally, they could be interpreted as indicative of three year classes, yet all three modes are known to be from a single year class, and to be caused by differential growth and movement within the stream.

The data from the Big Garlic River also demonstrate that the mode for newly metamorphosed lampreys that corresponds with the mode for large larvae in a length frequency does not necessarily indicate that the transformed lampreys are 1 year older. The study indicated that the mode for larvae directly below that for transforming lampreys could consist of many year classes. Sea lamprey ammocetes in the Big Garlic River generally reached a maximum length over a long period of time, permitting an accumulation of ammocetes at the average maximum lengths for metamorphosis. Some larvae reached these lengths as early as 1963, whereas others had not attained them by the end of the experiment in 1972.

One must therefore question age estimates that indicate metamorphosing individuals are 1 year older than larvae of the same age. Age and growth studies of lampreys based on length frequencies and modal age groups alone have been and are largely subjective estimates and should not be accepted without considerable reservation. The use of moving averages from 7 to 15 mm also appears questionable, because average larval growth after age III or IV is probably often small, as it assuredly was in the Big Garlic River.

A length-weight curve calculated for 1,936 larval sea lampreys collected from the Big Garlic River before 1966 was strengthened by the addition of 877 larvae longer than 120 mm, which were then scarce. The larvae, captured at the trap from 1968 to 1972, were weighed, measured, and fitted into the linear regression. Wet weights were determined to the nearest 0.001 g after the specimens were blotted on paper towels. Parker (1963) demonstrated that this method yielded reproducible results. Except for the largest larvae, empirical weights were in good agreement with weights calculated from the original length-weight equation of Manion and McLain (1971). Weights of larger ammocetes were slightly greater than calculated weights (Fig. 5).

Rest Period

Gage (1928), working with lampreys in the State of New York, believed that all larvae, after they reach full length, live one more year before they metamorphose. Applegate (1950), studying Great Lakes sea lampreys, adopted the term "Rest Period" for this stage in the life history and used it in his estimates of length of larval life, with the stipulation that it was valid unless proved otherwise. The rest period was used to explain why some larvae were as large as or larger than metamorphosed lampreys in the collections. Data from the Big Garlic River study clearly demonstrate that the l-year rest period is not an inherent characteristic of the sea lamprey. Similarly, a rest

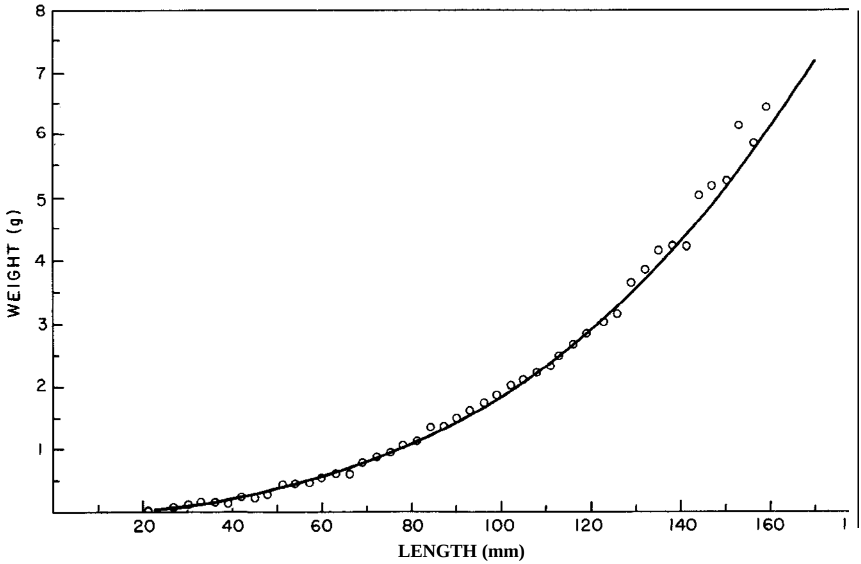

Figure 5. Length-weight relation of sea lamprey ammocetes from the 1960 year class isolated in the Big Garlic River. Points are empirical averages by 3-mm length intervals; the curve is a plot of the length-weight equation calculated by Manion and McLain (1971).

period did not occur in part of a year class of northern brook lampreys, Ichthyomyzon *fossor,* which metamorphosed at age III (Purvis 1970).

To determine whether the life cycle of Big Garlic River lampreys included a l-year rest period, we marked 551 larvae (8 years old) captured at the downstream trap in June 1968, and released them in an area of prime habitat at the upper end of section III. The mean length of the ammocetes was 138 mm (range, 127-164) at the time of release. Although all marked larvae were within the range of length for transformation, only 92 transformed and were captured in the trap in 1968, 38 in 1969, 40 in 1970, 15 in 1971, and 1 in 1972 (total, 186); 107 were captured as larvae from 1968 to 1972, for a total return of 53% of the number released. Mean lengths of the recaptured lampreys increased from 138 mm in 1968 to 149 mm in 1971. Weights similarly increased from about 4.5 g in 1968 to 4.8 g in 1971. Range in length remained about the same from the time of release to recapture.

The concept that growth is arrested only in the year before metamorphosis appears erroneous. Some larvae of transformation size can remain at the same size or possibly fluctuate up and down for at least 5 years, as occurred in the marked individuals. In the Big Garlic River, larvae longer than metamorphosed lampreys in the population existed because larvae of a single year class transformed over several years. Transformation over a period of years has been shown to be typical in the sea lamprey and northern brook lamprey in the Great Lakes, and probably holds true for other species.

NEWLY METAMORPHOSED SEA LAMPREYS

Behavior and Movement

A detailed description of the external metamorphosis of the sea lamprey was presented by Manion and Stauffer (1970). On the basis of their classification, transformation or metamorphosis here refers to lampreys in metamorphic stages I-IV. When the lamprey reaches stage V (October) and has the external appearance of a small adult, it is referred to as a newly transformed adult. At this stage, sea lampreys are capable of emerging from silt beds, migrating downstream, and feeding parasitically.

Transforming sea lampreys in the Big Garlic River were collected for study by shocking and by capture in the inclined-plane trap. We marked and released many at upstream locations to acquire specific information. Electric shockers used for collecting larvae were not particularly effective for collecting transforming lampreys. Like large ammocetes, the transformed lampreys were concentrated in the deeper water. Most metamorphosed lampreys in sections II-V were under leaves and detritus, and others were among tree roots and under stream banks. In section I, where aquatic plants were prevalent, most were near mid-stream-some on the mid-stream side of vegetated areas, and others in silt and gravel. At no time during the fall collecting period were metamorphosed forms observed attached to rocks or free-swimming.

Metamorphosed lampreys from the 1960 year class were recovered with shockers for the first time in October 1968, when three were collected, along with 534 larvae. In section I, the proportion of metamorphosed lampreys remained about 1 for every 200 larvae collected until 1972, when it increased to about 1 for every 100.

Active seasonal migration of transformed lampreys began in September and extended through the following May (Table 7); none were captured in June, July, or August. The earliest movement for all migratory years (1965-72) occurred on September 9, 1968. These migrants were not fully transformed externally, but were in stage IV of Manion and Stauffer (1970). Metamorphosed lampreys were capable of attaching to the sides of holding containers by late September, but usually preferred to hide under detritus or leaves. In the spring, on the other hand, newly transformed lampreys collected usually attached to the sides of the holding containers to rest.

The heaviest downstream movement of metamorphosed lampreys in the Big Garlic River, as indicated by catches at the trap, was from September to December. From 1965 to 1972, an average of 95% (range, 91-98) of the total migration was in these months, and only 5% in the spring. Movement was negligible from January through March, generally increased in April, and ended in May.

Observations of the downstream migration in the Big Garlic River generally agreed with those for two State of Michigan tributaries of Lake Michigan-the Pere Marquette River in Mason County (Hodges 1972) and Carp Lake River in Emmet County (Applegate 1961). During five of six seasons (1962-68) in the Pere Marquette River, an average of 82% of the metamorphosed lampreys migrated downstream during the fall. The data presented by Applegate show that in five of seven seasons, the percentage of downstream migrants in the fall was higher than that in the spring. During the migratory years 1951-57 (1954 and 1955 excepted) the percentage that moved downstream in the fall averaged 61.

Table 7. Number of transformed sea lampreys captured at the downstream trap by month and migration year (September l-August 31) in the Big Garlic River, 1965-72.

	Migration year							
Month[a]	1965-66	1966-67	1967-68	1968-69	1969-70	1970-71	1971-72	1972[b]
Sept.	0	30	0		0	0	4	0
Oct.	1	12	212	241	265	553	42	50
Nov.	3	2	9	98	62	69	725	124
Dec.	0	0	0	12	7	26	59	4
Jan.	0	0	0	5	1	1	11	-
Feb.	0		0	5	7	0	5	-
Mar.	0	0	7	4	1	0	10	-
Apr.	0	2	1	20	15	9	37	-
May	0	0	0	2	0	1	8	-
Total	4	46	229	398	358	659	901	178

[a]Transformed sea lampreys were not captured in June, July, or August.
[b]Study terminated at the end of December 1972.

Numbers of metamorphosed lampreys captured in the trap in the Big Garlic River increased from 4 in 1965-66 to 901 in 1971-72 (Table 7). Collections during the chemical treatment in September 1972 and earlier catches in the trap indicated that the number of transformed migrants would have increased to about 1,200 in 1973. Removal of a large portion of the population in September 1972 prohibited any additional estimates of the numbers metamorphosing.

From 1966 to 1971, an average of 42% (range, 30-68) of the total fall catch (September-December) of transformed lampreys took place in one overnight period (Table 8). Usually movement followed a drop in water temperature below 7.2°C and a rise in water level. From September 1 to October 31, an average of 82% of the total fall migration had reached the trap. Movement in the spring is related to increases in water temperature (above 0°C) and stream flows (Applegate 1950).

The migration of transformed lampreys appears to be more deliberate and rapid than that of ammocetes. To confirm the speed of movement, we marked 198 transformed lampreys (144 in 1968 and 54 in 1969) captured at the trap in October by notching the caudal fin (Hanson 1972) and released them at the 550 Falls (Fig. 1), 2.6 km upstream from the trap. Within 4 days, 48% in 1968 and 42% in 1969 had returned to the trap. Further, newly metamorphosed lampreys from groups of ammocetes that had been marked with insoluble dyes and released in section V (8.8 km above the trap) in May and June in 1966 and 1968 were recaptured at the trap in the fall of the same year, about 6 months later. However, marked individuals from the same release were not captured as larvae at the trap until the following spring (1 year later).

The faster downstream movement of transformed than larval lampreys probably is due in part to their physical development as well as to their instinctive search for prey in the Great Lakes. The transformed lamprey adapts to a free-swimming versus bottom-dwelling existence as fins increase in size and eyes develop during metamorphosis (Manion and Stauffer 1970).

Table 8. Percentage of the September-December catch of transformed sea lampreys taken in a single 12-hour period in the downstream trap in the Big Garlic River in different years, 1966-72.

Year	September-December total catch	Maximum 12-hour catch		Percentage of total 4-month catch
		Date	Number caught	
1966	44	September 30	30	68
1967	221	October 26	66	30
1968	362	October 28	149	41
1969	334	October 14	135	40
1970	648	October 29	303	47
1971	830	November 3	342	41
1972	159	November 4	22	[a]14

[a]Probably not typical because stream section I was treated with lampricide on September 6.

Larvae are more sedentary and probably burrow and rest more frequently during downstream migration.

Sea lampreys marked as larvae and later recaptured at the trap after transformation provided additional information on the process of metamorphosis. Larvae retained a recognizable mark until the end of the study in 1972; however, pigmentation on recently metamorphosed lampreys often obscured the mark and made it necessary to remove the skin to identify the marks.

Of the 9,889 larvae marked from 1962 to 1972, 1,396 were recovered as transformed lampreys at the downstream trap. Proximity to the trap evidently was not a factor in determining the percentage recovered, as only 6% of those captured were from sections I and II, compared with 35% from sections III and IV. However, all marked animals in section I and II were released in 1962 and 1963, when they were small, and recoveries of both larvae and newly transformed adults from those years were considerably fewer than recoveries from later years.

About 50% of the total number of metamorphosed lampreys captured at the trap in 1966-72 had been marked as larvae (Table 4). The highest percentage marked was captured in 1967 (69) and the lowest in 1972 (25). Several factors may have contributed to the high percentage of marked lampreys recovered: (1) Marked larvae were released in areas of low population density where they grew and reached metamorphosis faster. (2) Larvae that migrated to the trap in the spring, and were later marked, may have had an innate stimulus to transform sooner than those remaining in the river. There was some evidence of such a stimulus when an average of 40% of a sample of larvae captured at the trap in the spring and held in live cages metamorphosed in 1967, 1968, and 1970. If this percentage of large ammocetes present in the Big Garlic River had metamorphosed in those 3 years, the numbers of transformed lampreys captured at the trap would have been much higher than observed. (3) Possibly the marking, or the marks themselves, induced faster growth and metamorphosis. However, Hanson (1972) determined that similar marks had no affect on the growth of lampreys.

Growth and Size

Lengths and weights of transforming sea lampreys were determined for each migratory year from 1966 to 1972. A migratory year for transformed lampreys was arbitrarily set from September 1 to August 31 of the following calendar year, to coincide with that for ammocetes. Metamorphosed lampreys were captured by the inclined-plane trap and were also collected during the chemical treatment of section I on September 6, 1972. Lampreys captured during the treatment were in the early stage IV transformation stage of Manion and Stauffer (1970). All specimens were preserved in 10% formalin and later weighed, measured, and sexed. (Numbers in tables may differ among those weighed, measured, and sexed because the poor condition of some of the specimens precluded certain measurements.)

Because mean growth of ammocetes in the Big Garlic River was small, it was suspected that the mean lengths of transformed lampreys also would be small, but this seemed not to be true. The mean length of the first four transformed lampreys collected (in 1965-66) was 162 mm (range, 152-172). Their relatively large size indicated that longer larvae metamorphose first. The average lengths of transformed lampreys were about the same in 1966-67 and 1967-68 (150 mm, Table 9). Mean length decreased to 145 mm in 1968-69 and remained at about that length until 1971-72. In that year it increased slightly to 148 mm, followed by a larger increase of 156 mm in late 1972. The increase in mean length in 1971-72 and 1972 was probably a result of the increased growth of the larvae, reflecting in turn a decrease in population density. The more rapid growth of larvae presumably would permit earlier attainment of a length at which transformation could occur. Although large ammocetes do not necessarily metamorphose, any larvae over 116 mm long in the Big Garlic River had attained a length at which transformation might take place. Although some larvae had reached this length as early as 1963, no transformation was observed until 1965.

The lengths of transformed lampreys in the Big Garlic River were similar to those observed in 12 other Lake Superior tributaries (Table 10). These streams ranged from small (average flow, $< 0.6\ m^3/s$) to large ($> 1.4\ m^3/s$), indicating that length at transformation was not related to size of stream. The average length of newly transformed lampreys in the Big Garlic River was 148 mm (range, 116-193) compared with 145 mm (range, 112-194) for the other streams.

The length-frequency distribution of transforming lampreys collected at the trap from 1966 to 1972 was normal (Fig. 4). Standard deviations varied from 12.5 mm in 1966 to 8.5 mm in 1968 and averaged about 9.8 mm. The intervals within the 99% confidence limits decreased from ± 4.90 in 1966 to ± 0.90 in 1971, but increased again to ± 2.41 in 1972 (Table 11). Females were consistently larger than males in 1966-72, although the average difference was only 3 mm. Since this length difference was small, sex did not noticeably influence the length-frequency curves.

Table 9. Lengths of transforming sea lampreys collected at the downstream trap of the Big Garlic River in different migration years (September 1-August 31) 1965-72.

Migration year	Number measured	Total length (mm)	
		Mean	Range
1965-66	4	162	152-172
1966-67	26	150	121-172
1967-68	192	151	127-180
1968-69	302	145	123-174
1969-70	333	143	122-173
1970-71	485	144	116-179
1971-72	739	148	118-182
1972a	124	156	133-193

[a]Collected in the trap September 1-December 31, after the end of the 1971-72 migratory year.

Table 10. Average length of newly transformed sea lampreys in relation to size of stream for 12 tributaries of Lake Superior.

Size of rivef and name	Number measured	Total length (mm)	
		Range	Average
Small (<0.6 m^3/s)			
Little Garlic River	209	118-162	138
Traverse River	85	135-183	157
Rock River	56	126-162	144
Waiska River	24	148-169	158
Average			149
Medium (0.6-1.4 m^3 /s)			
Amnicon River	**16**	114-136	124
Middle River	**92**	112-152	133
Firesteel River	20	133-170	155
Huron River	79	118-156	138
Chocolay River	214	120-183	147
Average			139
Large (>1.4 m^3/s)			
Ontonagon River	126	120-183	145
Tahquamenon River	48	127-194	160
Sturgeon River	32	132-179	150
Average			152

[a]Water flow values are annual averages.

Table 11. Standard deviation and standard error of the mean within 99% confidence limits for transformed sea lampreys taken in the Big Garlic River, 1966-72.

Year	Mean length (mm)	Standard deviation	Standard error	99% confidence limits
1966	150	12.5	1.903	±4.90
1967	151	9.6	0.648	±1.67
1968	145	8.5	0.490	±1.26
1969	143	8.8	0.484	±1.25
1970	144	9.5	0.433	±1.12
1971	148	9.1	0.348	±0.90
1972	156	10.4	0.937	±2.41

Length-Weight Differences among Downstream Migrants

The lengths and weights of metamorphosed sea lampreys changed during the course of the migratory year (September to August; Table 12). For males and females combined, transformed lampreys were longest near the beginning of the downstream migration (September to mid-October) and shortest near the end (January to May). Average weights of migrants were

Table 12. Average length and weight of transformed sea Lampreys collected in the Big Garlic River during selected migration periods, 1967-70.

Period	Males			Females			Sexes combined		
	Number	Length (mm)	Weight (g)	Number	Length (mm)	Weight (g)	Number	Length (mm)	Weight (g)
Sept. 1-Oct. 15	22	145	4.5	58	145	4.4	80	145	4.4
Oct. 16-Nov. 15	229	143	4.5	730	146	4.9	959	145	4.8
Nov. 16-Dec. 31	79	140	4.5	163	143	4.6	242	142	4.6
Jan. 1-May 31	7	140	4.1	44	144	4.8	51	143	4.7

small (4.4 g) in September, increased in October-November (4.8 g), and then decreased slightly again in January through May (4.7 g).

Changes in length and weight during the migratory year differed between sexes. From the first movement in the fall to the last migration from the river in the spring, the average length and weight of males decreased 5 mm and 0.4 g. The average length of females (144-145 mm), on the other hand, was nearly constant during the migration year; average weight increased from the initial movement through October, declined somewhat in November and December, then increased again by the end of May to an average of 0.4 g more than in the fall. Examination of stomach contents showed that transformed lampreys did not eat during a period of about 10 months (July-May), and it seems logical that they would lose both length and weight, and that such losses would be about the same for each sex. However, the loss in length of males was far greater than that of females, and whereas the males lost about 0.4 g in weight, the females gained a similar amount. A possible reason for the gain in weight of females was the early development of the ovaries. Examination of testes in the fall and spring revealed no discernible development, whereas the size of the cells in ovaries increased during the same period.

The length-weight relation was calculated from a sample of 1,211 newly transformed sea lampreys collected at the downstream trap from 1967 to 1972 (Fig. 6). The specimens were measured to the nearest millimeter and weighed to the nearest 0.01 g. The empirical weights were plotted as averages for 3-mm length intervals. The linear regression fitted to the data by least squares after conversion to logarithms was:

$$\mathrm{Log}_{10}\ W = -2.99 + 2.62\ \mathrm{Log}_{10}\ L$$

where L = total length in millimeters and W = weight in grams.

The weight of transformed lampreys thus increased as the 2.62 power of the length-identical with the rate determined for larvae by Manion and McLain (1971). Empirical weights were in good agreement with weights calculated from the length-weight equation. The length-weight relations for larvae and transformed lampreys were about the same within the ranges where data existed for both.

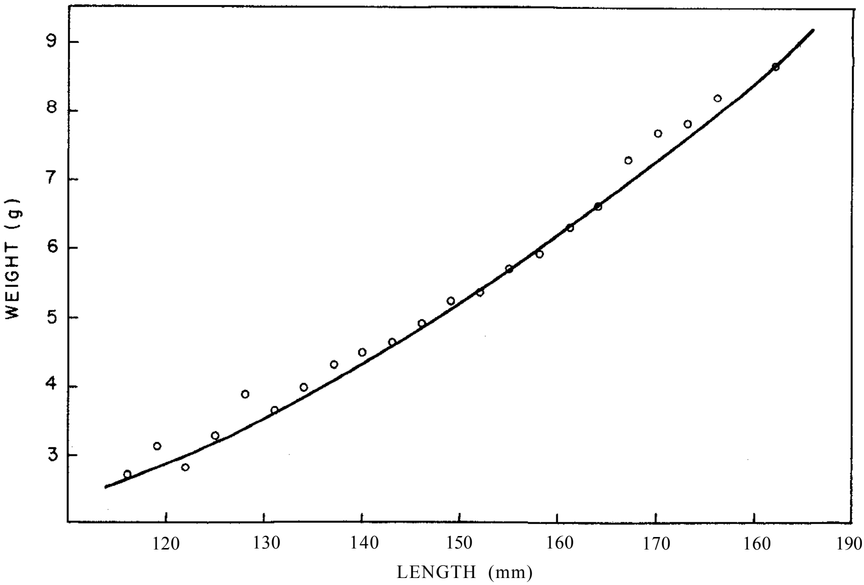

Figure 6. Length-weight relation of transformed sea lampreys from the 1960 year class isolated in the Big Garlic River. Points axe empirical averages by 3-mm length intervals; the curve is a plot of the length-weight equation.

SEX COMPOSITION

Ammocetes

Sex was determined for larvae taken from the downstream trap in the spring from 1966 to 1972 and in the fall in 1968 and 1970. Additional samples for comparison were collected with electric shockers from sections I and II in 1970 and II and III in 1972.

Ammocetes over 100 mm long were sexed by methods described by Hardisty (1965), who reported that a definitive ovary or testis was present in sea lampreys over 90 mm long. Transformed lampreys were sexed by making a longitudinal incision about 25 mm long at the mid-ventral region and identifying the exposed sex organs macroscopically. The ovaries, preserved in formalin, are large, lobed, and gray, whereas the testes appear as slender, creamy-white threads (Fig. 7). A binocular microscope was used to verify the sex of specimens in which sex could not be certainly determined macroscopically.

Although increase in size of ammocetes generally is related directly to increased age, sex differentiation appears to be correlated directly to length. Larvae of the 1960 year class shorter than 90 mm, both as age groups III and XII (9 years apart), could not be sexed reliably, whereas known-age larvae about 120 mm long from the same age groups could be easily sexed. Although

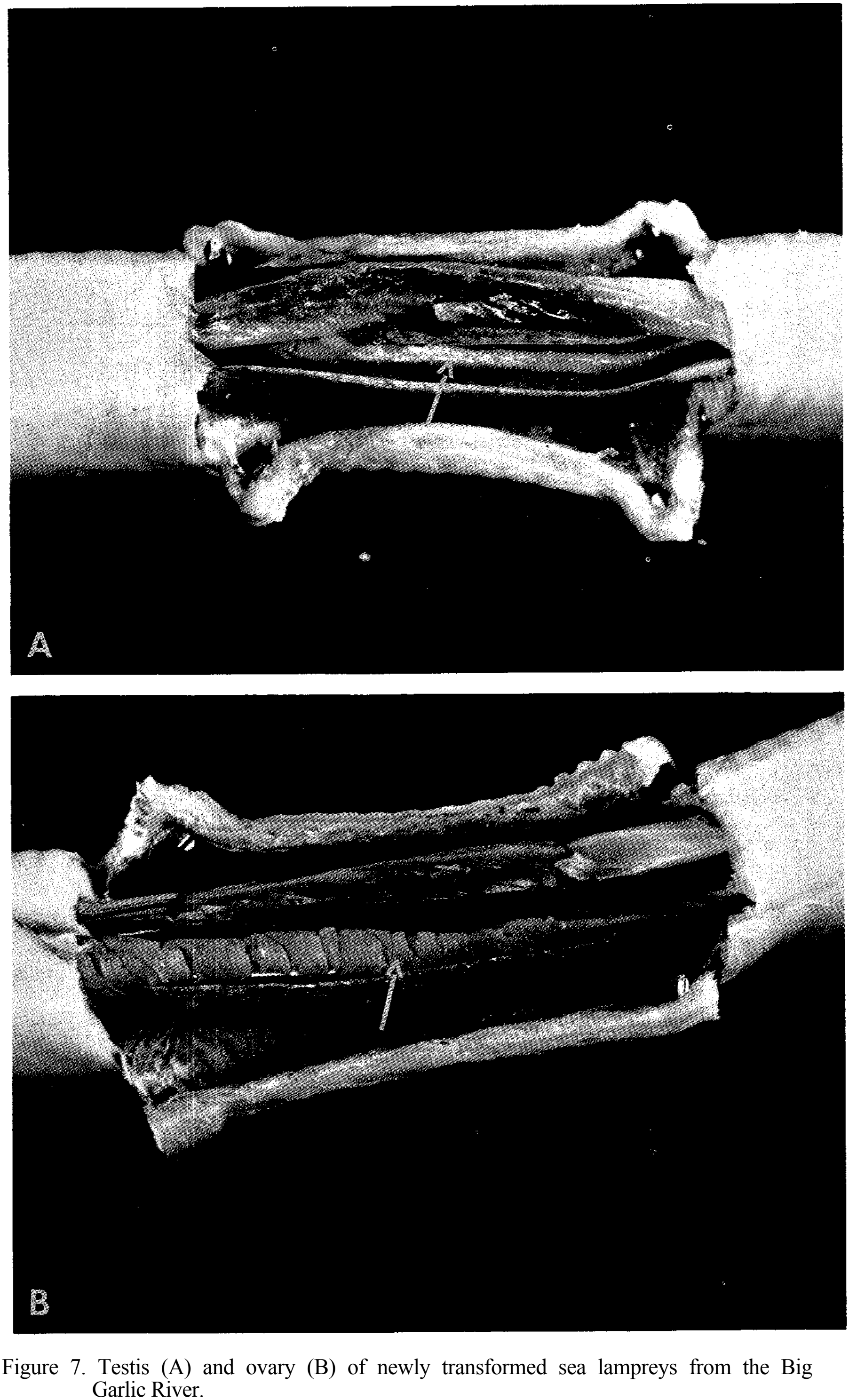

Figure 7. Testis (A) and ovary (B) of newly transformed sea lampreys from the Big Garlic River.

gonad development and size of larvae are directly related, comparisons between gonad development and age of larvae would be valid only if ammocetes generally reached a certain size at a specific age.

Ammocetes in the Big Garlic River were predominantly female in both the original, natural population below the study area and in the introduced, known-age population. In 1959 the section of the river from the downstream trap (at the lower end of the study area) to Lake Superior was first treated with lampricide to remove an original population. A total of 141 large larvae collected during the treatment were 81% females. The average percentage of females in samples from the introduced 1960 year class collected in the study area was 80 from 1966 to 1972, ranging only from a low of 73 in 1967 to a high of 85 in 1969. Evidently, ammocetes from the Big Garlic River always have tended to be predominately female, as the sex ratios in the original and introduced populations were nearly identical.

Newly Transformed Lampreys

The percentage of males in the ammocete population remained near 20 (the percentage varied from a low of 15 in 1969 to a high of 27 in 1967, apparently a reflection of sampling error as there was no trend to this change). However, as the numbers of newly metamorphosed lampreys increased from 46 in 1966-67 to 901 in 1971-72 (Table 7) the percentage of males steadily decreased from 54 to 15 (Table 13). Apparently males metamorphosed at a higher rate than females. The tendency for males to transform earlier than females also was noted among northern brook lampreys by Purvis (1970). The above data tend to indicate that the sex ratios of adult sea lamprey populations evolve in the streams, rather than after downstream migration to the lake.

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.

Table 13. Percentage males among larval and transformed sea lampreys captured in the Big Garlic River, 1966-72.

	Larvae		Transformed	
Year	Total examined	Percentage males	Total examined	Percentage males
1966	289	~~21~~ **27**	46	54
1967	407	19	172	31
1969	672	15	314	23
1970	924	18	541	21
1971	298	22	313	21
1972	357	22	298	15

The percentage of males among adult lampreys captured in Lake Superior began a steady decline in 1963 that continued to 1969, when it was only 26.7 (Smith 1971). Smith suggested that this decrease in percentage of males was a natural population control. However, we believe that the marked decrease in the percentage of males in Lake Superior may have been a result of the removal, by extensive lampricide treatments, of all larvae except the predominantly female residual populations. The populations now in the lake may come primarily from these residuals, either in streams or estuarine environments.

Applegate and Thomas (1965) presented data indicating that female sea lampreys transformed earlier than males in the Ocqueoc River. Although these data conflict with those from the Big Garlic River, sex composition probably differs in the various rivers that contribute to the lake population. Their statement that "populations of recently transformed sea lampreys in the Great Lakes streams are normally characterized by a small but variable preponderance of females," was probably correct for a majority of the rivers before lampricide treatments of streams began. It is obvious that sea lamprey control in Lake Superior is having a profound effect on sex ratios of the animals.

The sex composition of transformed lampreys varied during the migratory year. The percentage males was slightly higher during the initial migration from September to mid-October (28) than it was in collections during the main part of the migration during the last half of October (24). The representation of males increased to 33% during November and December, and then decreased to 14% during January to May. The sex composition varied greatly from year to year, but in all years for which data are available the percentage of males was always lower during the period from January to May than during the rest of the migration period.

Since section I of the river was chemically treated to remove all lampreys before the annual migration of transformed individuals began in 1972, it was possible to compare the lengths, weights, and sexes of transformed lampreys collected during the treatment with those migrating from upstream. In general, the transformed lampreys collected during the treatment were similar to those captured in the trap, except for differences in length and weight. This similarity suggested that the characteristics of the lampreys caught in the trap were indicative of those of the upstream population, throughout the study. Sex composition was nearly identical; males made up 16% of the transformed lampreys collected during treatment and 15% of those taken in the trap. The percentages of marked and unmarked lampreys in both samples were similar; about 31% of the transformed lampreys taken during chemical treatment and 36% of those taken in the trap were marked. The only differences between the treatment sample and trap sample were the lengths and weights. Average lengths and weights (sexes combined) were 144 mm and 5.8 g for the treatment sample and 156 mm and 6.2 g for trap catches. These differences are probably not significant because of the difference in time of collection. Lampreys collected during the chemical treatment (September 7) had only partly metamorphosed. Usually, transforming lampreys increased in length by about 5% from late August to the time they were captured at the trap in late October (Manion and Stauffer 1970).

This increase in length is probably accompanied by a corresponding increase in weight.

NOTES ON MORPHOLOGY AND MORTALITY

Although little effort was made to study morphology of the sea lamprey, myomeres were counted between the last (seventh) gill opening and the anterior tip of the anus in 111 larvae and 59 transformed lampreys. The skin was removed to increase the accuracy of the myomere counts.

In lampreys, the number of trunk myomeres has been shown to vary by genus and species (Sterba 1962). In *Lampetra fluviatilis* the difference in size between adults from the Meuse River in the Netherlands and Italian waters was not correlated with a difference in trunk myomeres (Lanzing 1959).

In the Big Garlic River, the number of myomeres in transformed lampreys differed from the number in larvae, but no difference was found between males and females. The number of myomeres in larvae of a given size decreased progressively as age increased. From 1961 to 1972, average numbers of myomeres decreased from 71.8 to 67.9 - or about 4 myomeres. The range in numbers of myomeres also decreased, from 70 to 73 at first to from 65 to 70 in the later years. Length of larvae did not appear to influence the number of myomeres, as the average in larvae with a mean length of 120 mm decreased in 1966-69. Myomere counts were not significantly different among larvae with mean lengths of 120 and 152 mm sampled in 1972.

Transformed lampreys had about the same number of myomeres (68) in 1967 and 1971. As in ammocetes, length had little influence on myomere numbers; numbers in transformed lampreys 132 to 149 mm long were the same as in those 150 to 161 mm long.

Evidently there is a real loss in the average number of myomeres as larvae increase in age, but there is no change related to size. Perhaps this loss explains some of the wide variations in myomere counts reported by other investigators. For instance, Vladykov (1950) reported the average number of myomeres in sea lampreys to be 69.8 (range, 67-74) whereas Wigley (1959) reported 72.7 myomeres (range, 67-75) in lampreys from Seneca Lake, New York.

About 75,000 larval and transformed sea lampreys collected from the Big Garlic River from 1960 to 1972 were examined for morphological abnormalities. The frequency of occurrence of ammocetes with two tails and deformed bodies and tails was less than 0.05%. The location, description, and cause of morphological abnormalities among larval lampreys were discussed by Manion (1967). Only two deformities were found among the 2,769 transformed lampreys examined.

No true albinos were observed among the 75,000 Big Garlic River lampreys examined; however, Manion (1972a) reported that about 6% of 5,747 larvae had a light body color similar to that of the albino lampreys described by Clay and Carter (1957) and Braem and King (1971). Although the general pigment patterns were identical in the light-colored and the normal (blackish) lampreys, the shape, numbers, and degree of expansion of pigment cells differed greatly. The pale color was caused by the incomplete development of melanophores, which allowed the natural color of fat lipochromes to be visible between cells.

Mortalities of lampreys in the known-age population in the Big Garlic River were impossible to define. Predation by fish and insects were reported by Manion and McLain (1971). Some larvae that had died during the winter were carried by the water into the trap each year from 1964 through 1972. The percentage of dead lampreys among those captured was small, ranging from a high of 1.3 in 1966 to 0.3 in 1969 (average, 0.7). Because these larvae had been dead several months and were in advanced stages of decomposition, the cause of death could not be determined. Anchor ice is a possible contributing cause; it was observed each year in the Big Garlic River in the early winter and early spring. Benson (1955) found that anchor ice killed trout fry, but no insects, in a stream.

We attempted, unsuccessfully, to estimate population size and mortality. We believed marked animals recaptured at the downstream trap to be a reliable sample of the total population in the river, and calculated estimates for each year with the formula $N = \frac{nT}{t}$, where N equals total population, T the total number marked originally, w the number (marked and unmarked) in the sample, and t the number of marked individuals in the sample (Schaefer 1951). Unfortunately, however, it was not possible to determine the mortality of marked individuals each year; this bias, combined with others, made the derived estimates unreliable, and useful only to indicate general trends, For instance, the estimated population was about 950,000 ammocetes in 1964-65, 250,000 in 1966 to 1968, 113,000 in 1970, and 64,000 in 1971. These estimates indicate that mortality was high among younger and smaller ammocetes, and decreased significantly as the lampreys became older and larger.

IMPLICATIONS OF INFORMATION ON SEA LAMPREY LIFE HISTORY IN LAMPREY CONTROL

The Big Garlic River was selected for a definitive study of the early life history of the sea lamprey in 1960 because it contained adequate spawning and larval habitats as well as physical barriers that prevented natural establishment of lampreys in the upper river. Some concern was expressed that, because of the type of stream-cold, turbulent water, and heavily forested watershed-the study area would be atypical for sea lampreys. Later determinations proved this concern to be unjustified. The Big Garlic River had a natural migrating run of adult sea lampreys before 1960 (McLain et al. 1965). The upstream migration of these spawning adults and other fishes was confined to the areas below the dam, where ammocetes of the sea lamprey and American brook lamprey were present in moderate numbers in 1958.

The rate of growth of ammocetes in the study area was as fast as in other streams tributary to Lake Superior, except for some of the largest rivers;

length-frequency distributions also were comparable with those of lampreys in other streams.

Hardisty and Potter (1971) believed that sex ratios of sea lampreys in the Big Garlic River were abnormal, but Smith (1971) showed that sex composition vanes between and within streams and that the population in the Big Garlic River was not atypical in this respect. Evidently the Big Garlic River is one of the streams that normally produce a preponderance of females.

The period of time required to produce the first and last parasitic-phase sea lampreys of a year class in the Big Garlic River may differ from that in other tributaries in the Great Lakes. Larvae in streams in which growth rates are faster or slower may transform earlier or later, and transformation may extend over a different span of years. The Big Garlic River was unique in containing a single year class, and details of its life history were not obscured by larvae of other year classes.

Originally, 76 United States tributaries of Lake Superior contained sea lampreys (Smith 1971). In only 12 were growth rates of larvae believed to be fast enough to yield transforming stages in less than 5 years. Most of the streams in which growth was rapid were large or contained inland lakes within the system-characteristics usually associated with increased growth and early metamorphosis of sea lampreys.

Information obtained from the Big Garlic River study has brought into clear perspective many factors of early life history that are important considerations in sea lamprey control.

The high fecundity (Manion 1972b) and hatching success (Manion 1968) of sea lampreys present serious problems. Destruction of larvae must be highly efficient to be effective. Posttreatment surveys and other observations have demonstrated that some ammocetes survive every lampricide treatment of a stream. Therefore, in even a relatively small stream such as the Big Garlic River, with a potential population of about a million ammocetes, a chemical treatment that was 98% effective in eradicating larvae would leave nearly 20,000. Any control program must necessarily approach the highest possible efficiency and a frequency of chemical treatment must be scheduled to remove not only original populations, but residual and reestablished groups as well.

The Big Garlic River study and others have demonstrated conclusively that population density is one of the most important factors of growth, and that ammocetes grow faster where their density is low than where it is high. Residual lampreys remaining in a stream after chemical treatment increased up to 28% in length before metamorphosis (H. A. Purvis, personal communication). Because residual larvae grow faster and reach the size of metamorphosis sooner, stream treatment schedules must be flexible and revised frequently to neutralize the effects of accelerated growth. An additional consideration is the real possibility that increased growth and survival of ammocetes in a low-density situation results in the production of parasitic lampreys from a 2% survival almost equal to that which would have been produced by a very large original population.

The Big Garlic River study provided additional insight toward many of the characteristics that have enabled the sea lamprey to persevere for so many eons-it has been a member of the biological community at least since the mid-Pennsylvanian era, about 280 million years ago (Bardack and Zangerl 1971) - that make the animal so difficult to eradicate from the Great Lakes. Because of the large egg production and relatively high hatching success, there are probably larger numbers of lampreys in a stream than of any other species of fish. Lampreys burrow and live in a wide range of habitats in both lotic and lentic environments and suffer relatively little predation or natural mortality in the Great Lakes environment. The ability of a single year class to remain in the larval stage for 18 or more years[2] and produce adults each year during all but the first few years of life (5 in the Big Garlic River) protects each year class from total destruction and insures that the lampreys have a continuous niche in the environment.

Metamorphosis in sea lampreys is more closely correlated with size than with age, and as transformation developed in the Big Garlic River, metamorphosed lampreys were more abundant in the lower section of the study area than in the upper sections. Apparently, either the newly transformed adults accumulate or concentrate in the lower reaches of a stream, or larvae in the lower section are larger and transform at a higher rate than do those farther upstream. In addition, there is no longer any doubt that ammocetes-at least large ones-can exist and transform in lentic environments (Smith and Braem 1973), which are comparatively inaccessible to lampricides. Because of the sea lamprey's ability to remain in the larval stage for so many years and to produce adults for 14 or more years (1965-78 in the present study, including the extension referred to in footnote 2), populations in offshore and inland lake waters can contribute to the parasitic stocks in the Great Lakes for many years. Lampreys in inaccessible locations present a difficult control problem because their elimination or drastic reduction requires special applications that are difficult, time-consuming, and expensive, and the chances of transformed lampreys evading lethal doses of chemical by escaping into untreated water is increased.

Inasmuch as major downstream movement of larval sea lampreys occurs during April and May, and that of transformed lampreys from mid-October through November, and chemical treatments of streams usually take place from May to November (the only period during which it can be carried out effectively)-after the migration of ammocetes and before that of transformed lampreys-any metamorphosing lampreys that escape the chemical treatment in October would be expected to escape to the lake. In the Big Garlic River, about 40% of the transformed lampreys migrated from the system in a single 12-hour period each year and 82% were gone by the end of October.

It is obvious that river systems in which larval populations can become established in inland lakes, estuaries, and on extensive delta areas in the main lakes, should be scheduled for treatment at more frequent intervals and that special attention should be given to whatever extraordinary measures are necessary for effective control.

2 Recently transformed sea lampreys were taken at the downstream trap each year in 1973-78, and larval sea lampreys of the 1960 year class were still present in the study area in 1978.

A final consideration for the sea lamprey control program is that the back-pack shockers, which are the primary tool for evaluating lamprey populations in streams, proved to be excellent for assessing larval populations but were relatively ineffective for collecting and evaluating populations of metamorphosing lampreys. Very few metamorphosing lampreys were collected during shocker surveys on the Big Garlic River until 1972, when they were plentiful. Major emphasis of survey crews collecting lampreys by shocking is placed on the sampling of obviously good habitats. Apparently a better overall evaluation could be obtained by collecting in additional, suboptimum habitats similar to those in which ammocetes and transformed lampreys occurred in the Big Garlic River.

The data collected during the Big Garlic River study permit a more detailed interpretation of the life history of the sea lamprey than was previously possible. Some misconceptions of the life history of sea lampreys have survived in the literature through the repetition of erroneous conclusions. Many estimates of the length of larval life and growth were based on small collections and on length-frequencies, which were shown to be inconclusive, first by Schultz (1930) and now by the present study.

As is true for most similar endeavors, the full benefits of the present study to future investigations and to sea lamprey control program cannot now be fully assessed. The general utility of life history studies has been well established, however, and the study will undoubtedly contribute to many future advances that can be expected to occur in the control of the sea lamprey in the Great Lakes.

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