BIOLOGY OF LARVAL SEA LAMPREYS (*PETROMYZON MARINUS*) OF THE 1960 YEAR CLASS, ISOLATED IN THE BIG GARLIC RIVER, MICHIGAN, 1960-65

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BIOLOGY OF LARVAL SEA LAMPREYS (PETROMYZON MARINUS) OF THE 1960 YEAR CLASS, ISOLATED IN THE BIG GARLIC RIVER, MICHIGAN, 1960-65

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Biology of Larval Sea Lampreys (*Petromyzon marinus*) of the 1960 Year Class, Isolated in the Big Garlic River, Michigan, 1960-65 [1]

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ABSTRACT

The early life history of the sea lamprey, from hatching to the first capture of metamorphosed individuals, is described from observations on a known-age population isolated in a tributary of southern Lake Superior. The population had its origin in the spring of 1960, when 722 sea lampreys nearing spawning condition were introduced into the Big Garlic River, Marquette County, Michigan, a stream that had previously been free of lampreys because physical barriers prevented their upstream migration. The adults constructed 206 nests and spawned in 161 of them; an estimated 774,000 larvae were hatched. The average total lengths of larvae collected in October (when yearly growth was nearly complete) in 1960-65 were 13, 39, 63, 80, 92, and 107 mm in the successive years.

A specially designed inclined-plane trap, installed at the lower end of the study area to monitor the downstream movement of larval and newly metamorphosed lampreys, captured 7,562 larvae in 1962-65 (none in 1960-61). The annual catch increased sharply from 9 in 1962 to 370 in 1963, 2,847 in 1964, and 4,336 in 1965. About 90% of each annual catch was taken by June 30. Most movement was at night.

A total of 5,642 larvae were marked in 1962-65 by the subcutaneous injection of an insoluble dye, to study movement and distribution; 222 were recovered as larvae through 1965 (17 in the trap and 205 with an electric shocker). The recoveries of marked lampreys, the increase in density of larvae in the farthest down-

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1 Contribution 437 of the U.S. Fish and Wildlife Service, Great Lakes Fishery Laboratory, Ann Arbor, Michigan 48107. This study, which is part of a program conducted by the Service under contract with the Great Lakes Fishery Commission, was completed while the authors were on the staff of the Laboratory.

stream section of the study area, and the annual catches in the trap demonstrated that a large part of the population gradually shifted downstream. On the other hand, many larvae were still within less than 1 km from the place of hatching, after more than 5 years.

The capture of four recently metamorphosed sea lampreys (two males and two females), 152-172 mm long, in the fall of 1965, established the minimum age at transformation for larvae in the Big Garlic River at 5 years. Age and length (with the exception of a possible minimum length) were determined not to be critical factors in metamorphosis. The presence of larvae 65-176 mm long (mean, 107 mm) in the river in 1965 indicated that metamorphosis of lampreys of a single year class takes place over a period of years.

INTRODUCTION

The applicationof the lamprey larvicide TFM (3-trifluoromethyl-4-nitrophenol) in streams is effective for control of the sea lamprey (Petromyzon marinus) in the Great Lakes (Applegate et al. 1961). Because this method is directed at the larval sea lamprey during its residence in streams, an obvious requirement for control is a thorough knowledge of the larval life history, including distribution, habitat preference, movement, growth, and behavior. Most important, however, is the need for precise information on the age at which the larvae metamorphose to the adult phase and migrate to the lakes. Since larval populations are usually reestablished in a stream after each chemical treatment, periodic retreatments are necessary. Knowledge of the duration of larval life can be used to establish the frequency of treatments and thereby minimize the cost of control.

Various estimates of the duration of the larval stage of sea lampreys have been published:13 or possibly 4 years (Surface 1899); not less than 4, and possibly 5, years (Gage 1928); 41 to 47 months, including the period of transformation and a possible additional 12-month resting period (Applegate 1950); 7 years (Wigley 1959); and an average of 5 years (Hardisty 1961). After a study by Applegate and Stauffer in 1948-61 on the Carp Lake River, Emmet County, Michigan, Applegate (1961) stated that an accurate estimate of the duration of larval life could not be made because of the possibility of undetected recruitment. Stauffer (1962) stated, however, “Thus, for at least some sea lampreys in Carp Lake River, the duration of larval life almost certainly was not less than 7 years.”

Inasmuch as previous investigators did not agree on the duration of larval life for the sea lamprey, we began a study to gather information on this and other aspects of the early life history. In the spring of 1960, spawning sea lampreys were introduced into a tributary of southern Lake Superior that was free of lampreys. This paper describes the introduction and biological characteristics of the adults and presents information on the life history of their progeny from hatching to the first capture of a metamorphosed individual.

BIG GARLIC RIVER

The Big Garlic River, Marquette County, Michigan, was selected for the study because it contained adequate spawning and larval habitats, as well as physical barriers that had prevented the natural establishment of lampreys in the upper river. The main stem is 10 km long, has 66 km of tributary streams, and drains about 80 km^2 (Brown 1944). The river is 3 to 9 m wide and averages 38 cm deep. Water flow fluctuates from 0.3 to more than 3.3 m^3/sec and averages about 0.4 m^3/sec.

The watershed is heavily forested and is characterized by pre-Cambrian granite hills eroded by glaciation. The stream has many natural waterfalls, riffles, and pools; its elevation drops from 305 to 189 m above sea level over a distance of 9 km. The bottom varies from bedrock to boulders, rubble, gravel, and fine sand. Sand, silt, and decaying organic matter are common in pools and areas of low water velocity.

Water quality of the Big Garlic River was determined by the Michigan Department of Health, Lansing, Michigan, and the Great Lakes Fishery Laboratory, Ann Arbor, Michigan, from October 10, 1960, to August 20, 1962. Zimmerman (1968) presented data from chemical analyses of the water for August 1962 through December 1965.

The ranges for values (ppm) of selected measurements from the combined analyses were: aluminum, 0.02-0.2; calcium, 6-29; chloride, 0.5-2.8; copper, 0.01-0.1; iron, 0.04-0.5; magnesium, 0.5-14; nitrate, O-2.9; sodium, 0.49-6.2; sulfate, 3-22; tannin and lignin, O-1.6; potassium, 0.4-1.11; total alkalinity, 14-88; silica, 3-9.5; total hardness, 20-100; and dissolved solids, 30-84. Phosphorus ranged from 0 to 7.8 ppb. Manganese, nitrite, and phenolphthalein alkalinity were not detected. Conductivity ranged from 38.5 to 124 micromhos, and pH from 7.0 to 7.9.

Five species of fish were collected in the section of the river studied: brook trout (Salvelinus *fontinalis),* lake northern chub *(Couesius plumbeus),* brook stickleback *(Culaea inconstans),* northern mottled sculpin *(Cottus bairdi),* and pearl dace *(Semotilus margarita).* Brook trout are abundant throughout the river, but the other species are limited to its lower reaches.

The study area in the Big Garlic River is 8.8 km long and extends from a concrete dam 1 km above the mouth, upstream to Blue Haven Falls. The dam blocks the natural upstream movement of fish and provided the site for a modified inclined-plane trap (McLain and Manion 1967) that was installed to monitor the downstream movement of larval and newly metamorphosed sea lampreys.

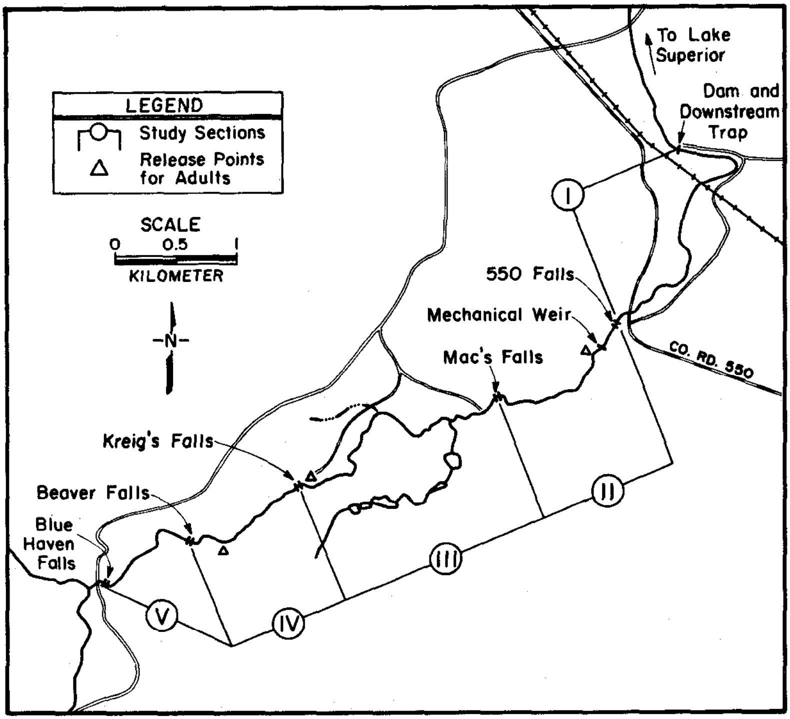

Figure 1. Big Garlic River, Marquette County, Michigan, showing locations of the various sections and the downstream trap.

Table 1. Description of experimental sections of the Big Garlic River.

Section	Limits of section[1] Downstream	Upstream	Length (km)	Gradient (m/km)	Principal bottom types2
I	Dam	550 Falls	2.6	4	s, St
II	550 Falls	Mac's Falls	1.3	36	B, G, R, St
III	Mac's Falls	Kreig's Falls	2.5	19	G, St
Iv	Kreig's Falls	Beaver Falls	1.2	25	B, G, R
v	Beaver Falls	Blue Haven Falls	1.2	19	G, R

1 See Figure 1 for locations.
2 B = boulders; G = gravel; R = rubble; S = sand; St = *silt.*

The study area is divided into five sections by waterfalls, each of which is a barrier to the upstream movement of lampreys and other fish (Fig. 1). The sections were arbitrarily numbered from I (farthest downstream) to V (farthest upstream); the limits, length, gradients, and principal bottom types of each section are shown in Table 1. Larval habitat is good throughout section I and most of III and in the lower reaches of sections II and IV, but is limited in section V. Good spawning habitat is present in sections II, III, and IV.

Water temperatures and discharge measurements were taken throughout the river, Thermographs and permanent staff gauges were installed at the upper and lower ends of section I (county road 550 bridge and the concrete dam) and at the upper end of section III (Kreig's Falls). The thermographs were operated at 550 bridge from April to June 1960, at Kreig's Falls from June 1960 to October 1962, and at the concrete dam from June 1962 to December 1965 (Table 2). Additional water temperatures were taken with maximum-minimum and pocket thermometers in sections II and IV in 1960.

Table 2. Average water temperature (C) by 10- or 11-day periods in the Big Garlic River in April-November, 1960-65.

Period	1960	1961	1962	1963	1964	1965
April						
1-10			1.1			
11-20	1.7		2.8	5.0	3.9	0.6
21-30	3.9	4.4	3.3	5.0	5.6	2.2
May						
1-10	3.3	6.1	7.9	8.9	12.2	8.3
11-20	7.2	9.4	15.0	8.9	11.7	10.6
21-31	12.8	11.1	13.3	10.6	12.2	11.7
June						
1-10	12.2	12.8	12.8	15.6	11.7	12.2
11-20	11.7	13.9	14.4	11.7	13.3	12.8
21-30	13.9	13.9	16.7	17.2	16.7	15.0
July						
1-10	13.9	14.4	18.3	17.2	17.2	14.4
11-20	13.9	16.1	17.2	16.7	17.2	15.0
21-31	16.1	16.1	16.1	18.9	17.8	15.6
August						
1-10	15.0	16.1	16.7	17.8	16.7	14.4
11-20	15.0	15.6	15.6	13.9	17.2	16.7
21-31	15.0	15.6	18.3	14.4	13.3	12.8
September						
1-10	15.6	16.7	15.0	12.8	13.9	12.2
11-20	10.0	12.8	10.6	12.2	10.0	
21-30	10.0	8.3	9.4	9.4	10.0	7.2
October						
1-10	8.3	9.4	11.7	11.1	5.0	7.2
11-20	7.8	8.9	11.7	11.1	6.7	7.8
21-31	4.4	6.1	3.9	10.0	5.0	3.9
November						
1-10	2.8	4.4	3.3	4.4	5.0	2.8
11-20	***1.7***	2.8		3.3	3.3	0.6
21-30	1.7			2.8		0.6

PARENT STOCK OF SEA LAMPREYS

Source and characteristics

Adult sea lampreys were collected in streams near the Big Garlic River from electric barrier traps that were operated as part of the sea lamprey control program (McLain, Smith, and Moore 1965). A total of 722 spawning migrants were collected from May 27 to June 14, 1960: 319 from the Chocolay River and 21 from the Iron River, Marquette County; and 131 from Furnace Creek and 251 from the Rock River, Alger County, Michigan.

The sea lampreys were anesthetized in a solution of M.S. 222 (tricaine-methanesulfonate), measured, weighed, and tagged. Petersen tags, consisting of a white numbered disk, a red disk, and a 45-mm nickel pin were attached through the dorsal musculature anterior to the dorsal fin. The lampreys were held in cages until fully recovered from the anesthesia.

As identified at the time of release, from characteristics described by Vladykov (1949), the adults consisted of 427 (59%) males and 295 (41%) females. Because immaturity of secondary sex characteristics prevented completely reliable sex determination at release, the ratio was revised in accordance with the sex ratio among 268 tagged adults observed during spawning, when the sex characteristics were fully developed. Of these, 163 (61%) were males and 105 (39%) were females.

The average length of the 722 adult sea lampreys was 42.2 cm, and was the same for males and females (based on sex determined at time of collection); the ranges were 34.3-52.1 cm for males and 33.0-53.3 cm for females. The average weight of the lampreys was 149 g; males averaged 147 g (range, 70-265) and females 151 g (range, 80-275).

Distribution in the stream

The sea lampreys were distributed in the study area on June 3-14, 1960; 273 were released in section II, 182 in section III, and 267 in section IV. Planting locations were dictated by access, and no attempt was made to spread the lampreys throughout a section. The exclusion of adults from section I provided the opportunity to monitor downstream drift of larvae into this section. A temporary mechanical barrier was installed at the lower end of section II to prevent any of the spawners from moving downstream and thus to ensure that section I would be initially free of larvae. The barrier, constructed of 1.3-cm-mesh hardware cloth, was similar to the portable weirs described by Applegate and Smith (1950). It was removed in September 1960, well after spawning and ceased.

The adults spread throughout the sections in which they were released and showed little tendency to drift downstream until they had completed spawning. (Upstream migration between sections was prevented by waterfalls.) During the spawning period, 291 of the tagged adults were observed. Of these, 144 were in section II, where they were prevented from moving downstream by the mechanical barrier. Of the remaining 147, which had been released in sections III and IV, 102 (69%) remained in the section where released and 45 (31%) were recovered in a downstream section. Of the 45, however, 29 had spawned and died by the time they were recovered. After spawning, the adults usually remained in or near the nest until near death or until they were too weak to maintain their positions. Downstream drift was greatest in section IV, which has a steep gradient.

Nest building and spawning

The stream was surveyed daily after the adults were released, and each newly constructed nest was marked with an aluminum-painted stone bearing a red number. The construction of nests and spawning by the adults lasted 24 days, from June 27 to July 20, although live adults were seen until July 28 (Table 3). The first nest was started on June 23 by a male in section II, but was abandoned the next day. The first observed spawning was on June 27, when the water temperature reached a high of 17.8 C (mean, 16.1 C; Table 4). Activity subsided on June 30, when the water temperature dropped to a low of 11.7 C (mean, 13.3 C). Water temperatures remained low through July 4, but a slight increase from a mean of 11.7 C on July 4 to 12.8 C on July 5 apparently was sufficient to induce further nest construction and spawning. Spawning reached a peak July 7, under the influence of a continuing warming trend.

The adults constructed 206 nests-86 in section II, 69 in III, and 51 in IV. That 161 were successful was indicated by the observed spawning act or by the presence of eggs or larvae. The 45 unsuccessful nests were either not occupied by females after they were constructed, or were abandoned by a pair of adults before they spawned. Seven nests were used twice, by different pairs.

All nests were constructed on gravel bottoms; 89% were at the upstream edge of a riffle or in the riffle area proper and the rest were in areas with smoothly flowing water. Average water velocity at 100 of the nests constructed in riffle areas was 0.4 m/sec at the upstream edge of the nests and 0.6 m/sec just below the downstream

Table 3. Number of nests and sea lampreys observed daily during the spawning period in the Big Garlic River, 1960.

Day	Nests	Sea lampreys		
		Males	Females	Total
June 27	3	1	1	2
28	2	1	0	1
29	11	5	0	5
30	7	0	0	0
July 3	14	3	1	4
4	10	4	7	11
5	10	3	3	6
6	16	0	2	2
7	22	8	2	10
8	14	10	3	13
9	15	4	8	12
10	8	3	1	4
11	9	18	9	27
12	11	14	4	18
13	0	12	8	20
14	4	14	6	20
15	0	5	4	9
16	0	4	1	5
17	0	3	1	4
18	3	11	3	14
19	0	11	1	12
20	2	9	5	14
21	0	0	0	0
22	0	0	0	0
23	0	0	0	0
24	0	5	1	6
25	0	2	1	3
26	0	1	1	2
27	0	0	0	0
28	0	0	1	1

crest of the nest,

The average nest in the study area was about 45 cm wide (perpendicular to the stream flow), 40 cm long, and had a downstream crest 8 cm high (Table 5). The average dimensions of nests were similar in sections II and IV, but nests in III had larger diameters, lower downstream crests, and shallower pockets. The difference in size of nests is attributed to a difference in the gravel, which is smaller and in less dense patches in section III than in the other sections.

"Community" nests-nests constructed side by side, so close together that individual nests lost their identity-completely spanned the stream at 11 locations; the largest, 3 m wide, was on the upstream lip of a riffle.

Of the 161 spawning acts observed, 144 were monogamous, 15 were polygamous, and 2 were polyandrous. One male and two

Table 4. Daily water temperatures (C) in the Big Garlic River, 1960, during spawning by sea lampreys (June 27 to July 20) and embryological development of larvae (June 27 to about August 4).

	Day	Maximum	Minimum	Mean
	June 20	13.3	10.0	11.7
	21	13.3	10.6	11.7
	22	13.9	11.7	12.8
	23	13.3	11.1	12.2
	24	13.3	10.0	11.7
	25	15.0	11.1	12.8
	26	16.1	12.8	14.4
Embryological development; Spawning	27	17.8	14.4	16.1
	28	17.8	14.4	16.1
	29	17.8	14.4	16.1
	30	15.6	11.7	13.3
	July 1	13.3	10.0	11.7
	2	13.9	12.8	13.3
	3	12.8	11.7	12.2
	4	13.3	10.6	11.7
	5	14.4	11.1	12.8
	6	15.0	11.1	13.3
	7	15.0	11.7	13.3
	8	17.8	13.3	15.6
	9	18.3	15.0	16.7
	10	18.3	15.6	16.7
	11	16.7	15.6	16.1
	12	17.8	14.4	16.1
	13	15.0	12.2	13.3
	14	13.9	10.6	12.2
	15	15.6	11.7	13.3
	16	14.4	13.3	13.9
	17	15.0	11.7	13.3
	18	15.6	12.8	13.9
	19	14.4	12.8	13.3
	20	13.9	11.1	12.2
	21	15.0	12.8	13.9
	22	16.1	14.4	15.0
	23	16.7	13.3	15.0
	24	16.7	13.9	15.0
	25	18.3	14.4	16.1
	26	18.3	15.0	16.7
	27	18.3	15.0	16.7
	28	17.8	13.9	15.6
	29	16.1	15.0	15.6
	30	16.1	13.9	15.0
	31	16.1	13.3	15.0
	Aug. *1*	15.0	14.4	14.4
	2	18.3	14.4	16.1
	3	17.2	13.9	15.6
	4	15.6	12.2	13.9
	5	15.6	12.2	13.9
	6	17.8	13.9	15.6
	7	17.2	15.6	16.1
	8	15.6	13.3	14.4

Table 5. Dimensions, water depth, and gravel size for sea lamprey nests in the Big Garlic River, 1960.
[Ranges of measurements are shown in parentheses.]

Section[1]	Number of nests		Dimensions (cm)				Water depth (cm)	Gravel size (cm)
	Total	Sampled	Length	Width	Crest height	Depth below stream bottom		
II	86	64	(15-91)	41 (23-91)	9	4	28 (13-43)	2.8 (0.6-12.7)
III	69	53	38 (18-91)	51 (25-91)	7	3	(8-31)	3.3 (0.6-12.7)
Iv	51	30	41 (20-76)	43 (18-76)	9	5	25 (13-58)	4.1 (0.6-7.6)
Total or average	206	147	40 (15-91)	45 (18-91)	8	4	24 (8-58)	3.4 (0.6-12.7)

1 See Figure 1 for location of sections.

females spawned in 11 nests, one male and three females in 3 nests, and one male and five females in 1 nest; one female spawned with three males and another with two.

Observations of the spawning act on the Big Garlic River agreed closely with those of Gage (1928) and Applegate (1950), except that these authors reported vibration of both sexes during extrusion of the eggs and milt, whereas we detected active vibration only by the females.

All of 36 males and 28 females that were measured and weighed after they had spawned had decreased in length and weight. The extent of the decrease was directly related to time spent in the river before spawning. After 30, 35, and 40 days in the river, the average length of males decreased 10, 11, and 11%, respectively, and the weight decreased 20, 21, and 29%; for females the respective values were 13, 17, and 18% for length and 40, 42, and 46% for weight.

The difference between the average loss of weight in males (23%) and females (42%) can be attributed mostly to the difference in the weight of sex products. The loss in length, however, was due to shrinkage caused by the gradual deterioration of the animal during the spawning season.

Estimated production of eggs and larvae

Of the 282 females released in the study area, 182 are known to have spawned. Applegate (1950) estimated that a 42.4-cm female (near the average length of lampreys released in the present study) from Lake Huron produced 57,000 eggs. Unpublished fecundity estimates by the senior author for 29 specimens ranging from 34.0 to 51.0 cm, however, show that a 42.4-cm female sea lamprey from Lake Superior contains about 69,000 eggs. On the basis of fecundity estimates for Lake Superior sea lampreys and the average number of retained eggs (see below), the 182 females in the study area could have deposited 12,282,000 eggs.

The number of eggs retained after spawning was determined for 28 females (Table 6). Unspawned eggs averaged 2.2% (range, 0.3 to 6.7%) of the total number produced (as estimated from the length of females at the time of release). Longer females retained relatively more eggs than shorter ones; retention of eggs averaged 2.9% for females above 41.7 cm and 1.5% for those less than 41.7 cm. Applegate (1950) reported an average residual egg count of 5% (range, 0.0-19.4%), estimated on the basis of postspawning length of the females; percentages based on prespawning length undoubtedly would have been lower.

Samples of eggs were removed from 11 nests to determine the ratio of live to dead eggs. Nests sampled for the first time after

Table 6. Percentage egg retention in 28 spent females from the Big Garlic River, 1960.

Prespawning length (cm)	Unspawned eggs	
	Number	Percentage[1]
36.8	2,987	4.8
38.6	764	1.2
39.1	447	0.7
39.4	376	0.6
39.6	338	0.5
40.1	407	0.6
40.6	712	1.1
40.9	3,563	5.3
41.1	922	1.4
41.1	383	0.6
41.4	1,051	1.6
41.6	355	0.5
41.6	580	0.9
41.6	762	1.1
41.9	4,047	5.9
42.4	4,641	6.7
42.4	1,951	2.8
42.7	232	0.3
43.4	3,863	5.5
43.7	262	0.4
43.9	1,807	2.6
44.7	2,066	2.9
44.7	1,687	2.4
45.2	1,290	2.5
45.2	431	0.6
46.0	205	0.3
47.2	5,186	6.7
48.5	489	0.6

1 Calculated from fecundity estimates of 29 sea lampreys (length range, 34-51 cm) from Lake Superior (Manion, unpublished data); based on prespawning lengths.

7 or 8 days had higher proportions of live eggs than nests sampled 2 or 3 days after spawning-which suggests high initial mortality and disintegration of dead eggs or their loss from the nest within a short time. Unfortunately, the number of samples obtained within 3 days after spawning was too small to permit a reliable estimate of egg survival.

The hatching success of sea lamprey eggs in the Little Garlic and Traverse Rivers, tributaries of Lake Superior, ranged from 5.3 to 7.8% and averaged 6.3% (Manion 1968). Similar success in the Big Garlic River could have produced 651,000 to 958,000 larvae (average estimate, 774,000).

LARVAL POPULATION OF SEA LAMPREYS

Behavior

Development of the embryos in 48 nests kept under close observation in the Big Garlic River was closely similar to that described by Piavis (1961). The eggs hatched 11 to 14 days after fertilization, and most of the newly hatched larvae left the nests within 22 days, although one group remained in the nest 34 days. Piavis (1961) stated that development to the burrowing stage is complete after 17 to 33 days, and Applegate (1950) reported that larvae leave the nest 18 to 21 days after spawning.

During the first 2 years of life the larvae were concentrated in sand-silt habitats in shallow water. During 1962 and 1963, at ages II and III, the larger ammocetes (more than 80 mm long) showed a distinct tendency to move into deeper water and to seek sand-silt bottoms that were covered with detritus. Wagner and Stauffer (1962a) also noted a direct relation between larval length and water depth for sea lampreys in East Bay, Alger County, Michigan.

Particle size in addition to depth may be a factor in the selection of habitat by sea lamprey larvae. Particle size in three sand-silt bottom types in the Big Garlic River (Table 7) was mechanically

Table 7. Percentage of particles of different sizes present in three sand-silt bottom types used by sea lamprey ammocetes in the Big Garlic River1

Particle size of sand (mm)	Bottom type		
	Fine	Medium	Coarse
<0.05	5	4	1
0.05-0.09	12	7	2
0.10-0.24	47	33	15
0.25-0.50	27	24	15
>0.50	9	32	67

1 Use by sea lampreys was heaviest for the fine bottom type, intermediate for the medium bottom type, and lightest for the coarse bottom type.

analyzed by procedures described by Kelmer and Alexander (1949). The most common bottom type in the Big Garlic River averaged about 68% fine sand. Although the larvae occupied nearly every type of bottom into which they could burrow, they were most plentiful in habitats where about 90% of the sand particles were fine (<0.5 mm) and sparsest in habitats where only about 30% of the sand particles were fine.

Downstream movement by ammocetes was studied in the several sections of the river. This movement is important to sea lamprey control because the larvae drift into Inland lakes and into estuaries and bays off the mouths of rivers (Wagner and Stauffer 1962b), and control in such environments is difficult and costly (Gaylord and Smith 1966; Manion 1969). Since spawning had been confined to sections II, III, and IV, the rate at which ammocetes moved into section I could be measured.

Larvae remained concentrated near the spawning sites in 1960, but then gradually scattered. By the spring of 1961 a few had drifted into the upper 200 m of section I. By late 1962 they were spread throughout the study area, including all of section I-although they were still scarce at the lower end. The progressive increase in density in this section was indicated by annual collections with an electric shocker in October. The average number per square meter was 0.3 in 1961, 2.2 in 1962, 2.9 in 1963, 3.6 in 1964, and 4.7 in 1965.

The extent of downstream drift was also indicated by the catches of larvae in the trap at the lower end of the study area. These catches increased sharply, from 9 in 1962 to 370 in 1963, 2,847 in 1964, and 4,336 in 1965 (Table 8). Since larvae less than 40 mm long could pass through the 3-mm-mesh screens on the trap, some may have escaped in 1961 and 1962 - although only a few larvae had drifted into the lower part of section I by the spring of 1962, and by October 95% of those collected in this section by electrofishing were longer than 40 mm.

The heaviest seasonal downstream drifts, as indicated by the trap catches, were in April 1963 (95% of the annual total taken), May and June 1964 (75%), and April and May 1965 (87%). In each year about 90% of the annual catch was taken by June 30. Downstream drift was directly related to high water, and was influenced by water temperature. In 1963, 324 larvae (88% of the annual total) were taken on April 1-2, during an early spring breakup. Although the relation was not as obvious in the next 2 years (Fig. 2), the correlation between water level and the daily number of larvae taken at the trap for the period April 26-June 12 was significant in 1964 (r = 0.411) and highly significant in 1965 (r = 0.737). Applegate (1961) also reported that most larval lampreys move downstream during floods; in Carp Lake River the greatest activity was in late March, April, and May, during the spring breakup.

The ammocetes typically were inactive at water temperatures below 4.4 C. The heavy catch on April 1-2, 1963, was taken when maximum daily temperatures ranged from 4.4 to 5.6 C; no larvae were taken, however, at equally high water levels on April 12-14,

Table 8. Number of sea lamprey ammocetes captured at the downstream trap in the Big Garlic River, 1962-65.

Month	1962	1963	1964	1965
January	2	0	1	0
February	1	0	0	2
March	1	1	0	2
April	1	351	376	1,249
May	1	7	1,389	2,510
June	0	3	713	286
July	2	0	282	71
August	0	2	55	96
September	1	1	13	40
October	0	2	10	29
November	0	2	4	14
December	0	1	4	37
Total	9	370	2,847	4,336

1964, when the daily temperature remained below 4 C. An exception occurred in 1965: the largest daily catch (350 larvae) was taken on April 27, when the temperature reached a maximum of only 2.2

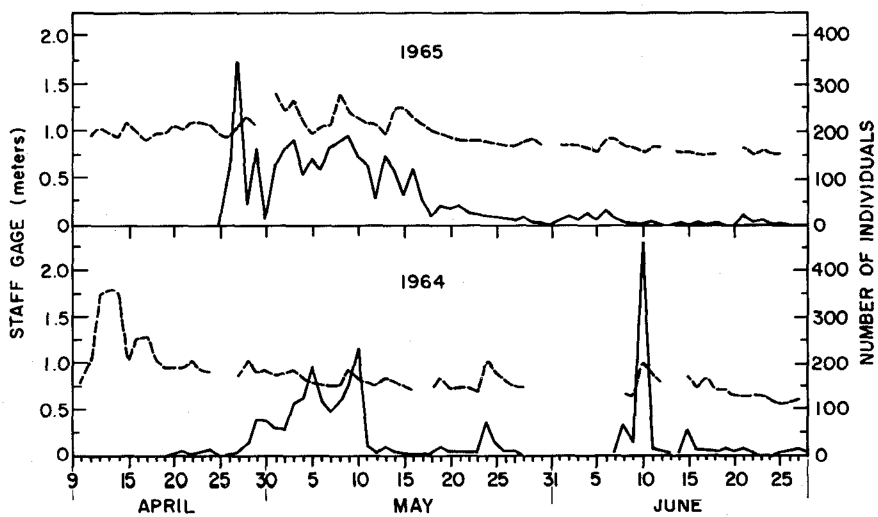

Figure 2. Daily water levels (broken line) and numbers of larval sea lampreys captured at the downstream trap (solid line) during the spring of 1964 and 1965 (see Table 8).

C. (The temperature had reached 5.6 C, however, during the preceding day.) At water temperatures of 4.4 C or more, the number of larvae taken by the trap appeared to be unrelated to temperature.

Most ammocetes were taken in the trap at night, principally after midnight. Daytime movement to the trap during maximum flood stage was sufficient, however, to account for 15 and 22% of the April catch in 1964 and 1965, respectively. After peak floods had subsided, less than 0.5% of the movement was by day.

To provide further information on downstream drift, the movement of marked ammocetes was observed. Ammocetes for marking were collected with an electric shocker each October in 1962-65 in sections I-IV and released near the point of capture, or collected at the downstream trap in May-July 1964 and 1965, and transported upstream. Marking was by the subcutaneous injection of an insoluble dye (Wigley 1952). The color of the dye and the location of the mark on the body of the ammocete identified the date and location of release.

A total of 5,642 larvae were marked and released from 1962 to 1965 (Table 9). The total includes October releases of 318 in 1962, 700 in 1963, 400 in 1964, and 268 in 1965; and May-July releases of 1,896 in 1964, and 2,060 in 1965. Of these, 222 were recovered as larvae through 1965-17 at the downstream trap and 205 with electric shockers. Three marked in October 1963 (two in section II and one in III) were the first ones recaptured in the trap (in the spring of 1964). Of the 14 recovered in the trap in 1965, 2 had been marked and released in October 1962 (in sections I and III) and 12 in October 1963 (3 in section I, 5 in II, 3 in III, and 1 in IV). Proximity to the trap was a factor in the time to recovery: 11 (65%) of the 17 ammocetes recovered had been released in sections I and II. The ammocete released in section IV had moved about 8 km to reach the trap.

Of the 205 recoveries in 1963-65 by electrofishing (Table 9), only 2 had moved from the section of release-l from section III to I and 1 from section V to IV. Recoveries in the section of release were 1 in section 1, 10 in III, 87 in IV, and 105 in V (none in II). The high density of larvae in sections I and II greatly limited the coverage necessary to collect an adequate sample to meet other objectives of the study, and thus reduced the probability of recovering a marked animal. In contrast, the relatively large number of recoveries in section IV reflects the high ratio of marked to unmarked larvae in the section (as well as the relative shortness of the period during which they could have moved downstream). The recoveries in section V have little significance, since all larvae in the section were marked.

The increasing density of larvae in section I, the annual increase in the trap catch, and the recoveries of marked larvae all show that the movement involved a gradual downstream shift of

Table 9. Number of ammocetes marked and recaptured in the Big Garlic River, 1962-65.[1] [All shocker collections were in October; recaptures at the downstream trap were in May-July. Marked ammocetes recaptured by shocker were in the section of release exceptwhere indicated.]

Marked and released			Recaptured				
			Electric shocker			Downstream trap	
Date	Section[2]	Number	1963	1964	1965	1964	1965
October 1962	I	79	1	31	0	0	1
October 1962	II	79	0	0	0	0	0
October 1962	III	80	1	0	1	0	1
October 1962	IV	80	0	1	2	0	0
Subtotal, 1962		318	2	2	3	0	2
October 1963	I	181	-	0	0	0	3
October 1963	II	149	-	0	0	2	5
October 1963	III	197	-	7	1	1	3
October 1963	IV	173	-	6	2	0	1
Subtotal, 1963		700	-	13	3	3	12
May-July 1964	IV	1,896	-	45	31	0	0
October 1964	I	200	-	-	0	0	0
October 1964	III	200	-	-	0	0	0
Subtotal, 1964		2,296	-	45	31		0
May-July 1965	V	2,060	-	-	[4]106	-	0
October 1965	II	116	-	-	-	-	0
October 1965	V	152	-	-	-	-	0
Subtotal, 1965		2,328	-	-	106	-	0
Grand total		5,642	2	60	143	3	14

1 Does not include two recently metamorphosed individuals captured at the trap in 1965.

2 See Figure 1 for location of sections.

3 Released in section III.

4 0ne recaptured in section IV.

the population. The recovery data also indicate, however, that a large part of the population tended to remain static. Not only did some marked larvae stay near the point of release for at least 3 years, but a considerable number of unmarked larvae in section IV (the uppermost section in which spawning occurred) had not moved out of the section after more than 5 years.

Table 10. Annual growth of sea lamprey ammocetes collected by electric shockers in October from different sections of the Big Garlic River, 1960-65.

Stream section[1] and year	Number measured	Total length (mm) Mean	Range	Mean 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
II				
1960	38	13	11-17	13
1961	33	34	28-41	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
III				
1960	33	14	12-19	14
1961	26	38	25-49	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
Iv				
1960	28	13	10-15	13
1961	16	42	32-49	29
1962	171	65	41-94	23
1963	102	81	56-131	17
1964	105	100	72-159	19
1965	97	130	81-176	30
v				
1965	104	101	65-142	
I-V				
1960	99	13	10-19	13
1961	103	39	25-54	26
1962	536	63	37-107	24
1963	780	80	52-134	17
1964	660	92	58-159	12
1965	733	107	65-176	15

1 See Figure 1 for location of sections.

Growth and size

Collections to determine growth of the larval sea lampreys in 1960-65 were taken each October, when the year's growth was almost complete. Additional samples were collected in May in 1961, 1962, and 1963 for information on seasonal growth. Larvae were collected randomly within each section of the study area with an electric shocker, anesthetized with M.S. 222, measured, and returned to the stream.

The mean length of young-of-the-year larvae was 13 mm (range, 10-19 mm; Table 10), or considerably less than the means of 16

Table 11. Average length (mm) of sea lamprey ammocetes collected in October in relation to size of stream and average water temperature (June-August) for 13 tributaries of Lake Superior.

[Number of ammocetes measured shown in parentheses.]

Size of stream[1] and name	Temperature (C)	Age 0		I		112	
Small (< 0.6 m³/sec)							
Seven Mile Creek		16	(18)	42	(31)	63	(17)
Little Garlic River		16	(73)	45	(68)	63	(164)
Big Gratiot River	15.0	18	(94)	39	(76)	60	(57)
Traverse River	16.1	18	(96)	40	(114)	62	(163)
Sullivans Creek		16	(38)	33	(60)	62	(143)
Average	15.6	17		40		62	
Medium (0.6-1.4 m³/sec)							
Two Hearted River	15.6	18	(54)	44	(44)	65	(20)
Sucker River	15.6	21	(28)	42	(67)	-	(0)
Huron River	17.2	21	(9)	46	(29)	63	(18)
Silver River	17.2	18	(22)	46	(29)	69	(16)
Average	16.7	20		45		66	
Large (> 1.4 m³/sec)							
Sturgeon River	20.0	34	(63)	63	(16)	so	(112)
Salmon-Trout River		23	(238)	75	(49)	100	(57)
Bad River		28	(83)	63	(7)	84	(74)
Brule River	**18.9**	26	(16)	63	(199)	-	(0)
Average	19.4	28		66		91	

1 Water flow values are annual averages.
2 Modal lengths.

to 34 mm for O-group larvae collected in October from 13 other tributaries of Lake Superior (Table 11). Because the slow growth of larvae in the Big Garlic River caused apprehension that survival might be low, collections in October 1960 and 1961 were limited to about 100 individuals.

In October 1961, the average length of I-group larvae was 39 mm (range, 25-54 mm), an increase of 26 mm from October 1960. Growth of ammocetes differed among sections. The largest larvae (mean length, 45 mm) were collected in section I, where density was low and the sample consisted entirely of animals that had drifted downstream into the formerly unoccupied area. Section IV produced the next best growth-mean length, 42 mm; range, 32-49. This section was the farthest upstream area in which spawning adults were introduced, and downstream drift had reduced the density of larvae. Growth was least in section II-mean length, 34 mm; range, 28-41 mm.

In October 1962 the length of ammocetes averaged63 mm (range, 37-107 mm). The largest animals (average length, 75 mm) again were collected in section I and the smallest (52 mm) in section II.

Growth of age-1 larvae in the Big Garlic River was similar to that of larvae of the same age in other small streams, but less than that of larvae in medium and large streams (Table 11). The range in length for age-II larvae from other streams could not be determined because of the overlap in growth between year classes; modal lengths, however, indicate that growth in the Big Garlic River was similar to that in other small streams and approached that in medium-sized rivers, but was considerably below that in large rivers.

Annual growth of the larvae in the Big Garlic River slowed substantially in 1963, 1964, and 1965, when mean lengths were 80, 92, and 107 mm, respectively, The average annual increase in 1963-65 was 15 mm, as compared with 26 mm in 1961 and 24 mm in 1962. Mean length of larvae was identical in sections I and IV in 1964, but was much the larger in section IV by 1965.

The May collections yielded some data on seasonal growth. The percentage of annual growth gained from May to October varied among sections and with age of the larvae;

Year	Stream section			
	I	II	III	Iv
1961	-	72	87	90
1962	80	72	67	-
1963	-	76	-	-

The average for 1961-63 for all areas was 78%.

Factors that affect the growth rate of ammocetes are many, and they have complex interrelationships. Although we did not attempt to isolate the various factors, it seemed obvious that the density of the ammocetes and temperature of the water are very important.

Growth of ammocetes changed in different sections as the density changed. It gradually slowed in section I as the concentration of ammocetes increased through downstream drift (see Table 10). Growth was slowest in sections II and III, where the abundance of ammocetes was high and losses through downstream drift were offset by recruitment from the sections upstream.

The growth of ammocetes is obviously related to size of stream (Table 11). The mean lengths (in October) of O-group ammocetes in five small streams (<0.6 m^3/sec), four medium streams (0.6-1.4 m^3/sec), and four large streams (>1.4 m^3/sec) were 17, 20, and 28 mm, respectively. The dominating feature, however, broadly related to the physical size of streams, was the temperature of the water. The average temperature was highest in the large streams (Smith 1962). High water temperatures probably increase the metabolic rate of the ammocetes and affect other factors that determine growth rate. Furthermore, water in the large streams tends to warm more rapidly in the spring and cool more slowly in the fall than it does in small streams; consequently, the growing season is longer in the large streams. Additionally, since upstream movement of spawning sea lampreys in tributaries of Lake Superior is directly related to a rise in water temperature (McLain et al. 1965), lampreys presumably spawn earlier in the large streams, and thus give their progeny the advantage of an earlier beginning of first-year development.

The length-frequency distributions of the ammocetes collected annually in October in 1960-65 (all stream sections combined) are moderately skewed to the right (Fig. 3). Standard deviations increased from 1.8 to 19.2 from 1960 to 1965 and the intervals within the 99% confidence limits increased from $\pm$ 0.48 to $\pm$ 1.83 (Table 12).

The length-frequency distribution curves for ammocetes in sections I and IV changed shape between 1962 and 1965 (Fig. 4). The distribution in section I approximated a normal curve in 1962, but became nearly rectangular by 1963, probably because of the large recruitment of smaller larvae from section II. The length-frequency curve for section IV gradually flattened between 1963 and 1965 (the number of individuals in the samples remained about the same). This change was due to increased growth, after downstream drift had reduced the density of the animals.

A total of 1,936 sea lamprey ammocetes collected from the downstream trap 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. A linear regression fitted

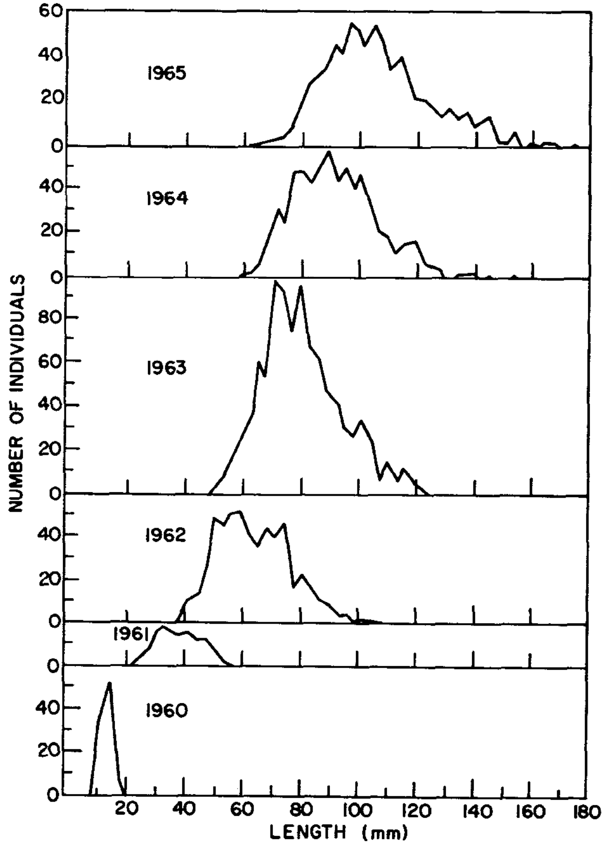

Figure 3. Length-frequency distributions of sea lamprey ammocetes collected in October, 1960-65.

Table 12. Standard deviation and standard error of the mean within 99% confidence limits for sea lamprey ammocetes taken in the Big Garlic River in October, 1960-65.

Year	Mean length (mm)	Standard deviation	Standard error	99% confidence limits
1960	13	1.8	0.181	± 0.48
1961	39	6.2	0.611	± 1.61
1962	63	12.4	0.536	± 1.38
1963	80	14.3	0.512	± 1.32
1964	92	15.0	0.584	± 1.51
1965	107	19.2	0.709	± 1.83

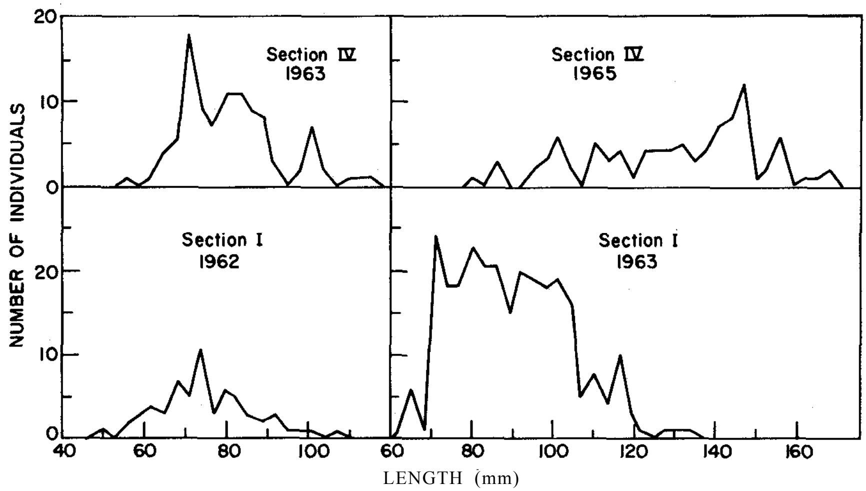

Figure 4. Comparison of length-frequency curves for sea lamprey larvae in a section where density decreased and growth increased (section IV; 1963-65) with curves for larvae in a section where density increased and growth decreased (section I; 1962-63).

to the length-weight data by least squares after transformation to logarithms was :

$$\mathrm{Log}_{10}\ W - -4.99 + 2.62\ \mathrm{Log}_{10}\ L$$

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

The weight of the ammocetes thus increased as the 2.62 power of the length. Empirical weights were in good agreement with weights calculated from the length-weight equation, except for the largest ammocetes, whose weights were slightly greater than the calculated weights (Fig. 5).

Sex ratio

Sex ratios in spawning populations of sea lampreys have been reported by several authors (Applegate 1950; Wigley 1959; McLain et al. 1965), but little information has been published on sex ratios among larval or recently metamorphosed individuals. Applegate and Thomas (1965), who discussed the sex composition of recently metamorphosed sea lampreys from four streams tributary to Lakes Michigan and Huron, concluded that populations of recently transformed sea lampreys in the Great Lakes are normally characterized by a slight but variable preponderance of females.

Determination of sex was restricted to collections of ammocetes

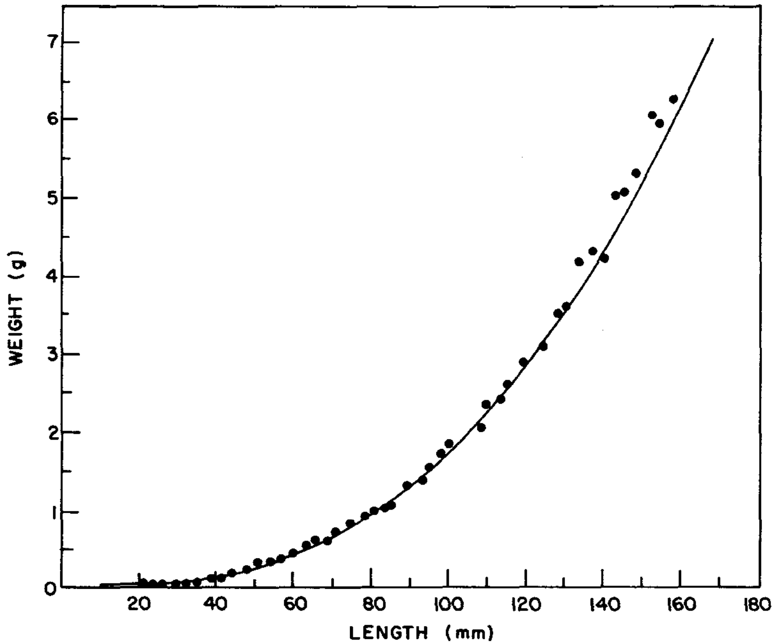

Figure 5. Length-weight relation of sea lamprey ammocetes from the 1960 year class isolated in the Big Garlic River. Points are empirical averages by 3-mm length intervals; the curve is a plot of the length-weight equation.

over 100 mm long taken from the downstream trap in the spring; Hardisty (1965) reported that a definitive ovary or testis is present in sea lamprey larvae over 90 mm long. Fifteen of 128 (12%) larvae examined in 1964 were males and 31 of 160 (19%) in 1965. The females were slightly longer than the males in both years; the respective lengths were 112 and 107 mm in 1964 and 120 and 118 mm in 1965. Since minimum length and transformation appear to be directly related, more rapid growth by females would bring them to this minimum sooner than males. Continued transformation could well change this high preponderance of females among the larvae.

Population estimates and mortality

We attempted to estimate population size and survival of the ammocetes from the mark-and-recovery data. The data were examined by a variety of procedures, including analysis by individual section, sections combined; by years, years combined; and from both shocker collections and trap catches (separately and combined).

The relative scantiness of the data, sampling bias in the lower sections, and drift by the ammocetes, however, caused such great variation in the results obtained by different methods that all the estimates were deemed questionable. (All mark-and-recovery data pertinent to population and survival estimates are presented in Tables 8, 9, and 10.)

No data collected nor observations made during the study indicated possible causes of natural mortality of ammocetes. In April 1964 and 1965, a few ammocetes which apparently had died during the winter were carried by the water into the trap. Decomposition of the remains was so far advanced, however, that the cause of death could not be determined.

Several ammocetes were observed with cysts similar to those described by McLain (1952).

Although some newly hatched larvae may have been eaten by brook trout, no ammocetes were found in the stomachs of about 50 brook trout, over 100 mm long, that were examined each year in 1961-65. Most of the brook trout were collected when the ammocetes were active and moving into the trap.

The other species of fish in the study area were restricted to section I; only two-mottled sculpins and brook sticklebacks-were plentiful (634 mottled sculpins and 1,213 brook sticklebacks were caught in the trap in 1962-65). Neither of the two species appears to be an important predator on small fish. Aquatic insects are the principal food of sculpins (Koster 1937; Zarbock 1952), and sticklebacks feed mainly on insects and other invertebrates (Markley 1940; Carl 1953; Greenbank and Nelson 1959). Although it seems likely that the small larvae drifting into section I in early 1961 were vulnerable to predation by these two species, they grew rapidly in this section, and vulnerability no doubt decreased with increasing size.

The only observed predation by insects was by the predacious diving beetle (Dytiscus sp.). It occasionally fed on larval sea lampreys confined in the catch baskets of the downstream trap. (Insects caught in the trap included representatives of 19 families and 8 orders.)

Food

Sea lamprey larvae begin to ingest diatoms shortly after hatching; the species composition of diatoms taken by larval sea lampreys up to 24 mm long was determined by the methods described by Manion (1967a). Any broken frustule was counted as a fragment. To provide information on changes in selection of diatoms with a change in size, 20 larvae each were sampled from three length groups, 7-8, 12-15, and 20-24 mm.

Table 13. Percentage of total diatoms contributed by different genera to the food of sea lamprey ammocetes from the Big Garlic River, 1960-61.

[Analyses were based on 20 ammocetes from each of the three length ranges shown; number of diatoms in parentheses.]

Genus	Length range of ammocetes (mm)		
	7-8	12-15	20-24
Navicula	31.3 (5)	25.0 (8)	58.9 (86)
Cyclotella	31.3 (5)	- (0)	(0)
Eunotia	18.8 (3)	6.3 (2)	(0)
Synedra	6.2 (1)	6.3 (2)	13.7 (20)
Cocconeis	6.2 (1)	12.5 (4)	1.4 (2)
Fragilaria	6.2 (1)	3.1 (1)	(0)
Pinnularia	- (0)	21.8 (7)	6.8 (10)
Cymbella	- (0)	6.3 (2)	8.2 (12)
Diploneis	- (0)	6.3 (2)	1.4 (2)
Stauroneis	- (0)	3.1 (1)	8.2 (12)
Diatoma	- (0)	3.1 (1)	(0)
Gomphonema	- (0)	3.1 (1)	(0)
Nitzschia	- (0)	3.1 (1)	(0)
Amphora	- (0)	- (0)	1.4 (2)
Total number of diatoms	16	32	146
Fragments	5	15	32
Average size of diatoms and fragments (microns)	10	41	66

Diatoms of the genera *Navicula, Cyclotella,* and *Eunotia were* most common in the intestines of larvae 7 to 8 mm long (Table 13). Other genera represented in newly hatched larvae were *Synedra,* Cocconeis, and *Fragilaria.*

Ammocetes 12 to 15 and 20 to 24 mm long ate a greater variety of diatoms, but *Navicula* remained the dominant genus. *Cyclotella* was absent in the two larger groups of ammocetes. Schroll (1959) has demonstrated that the use of diatoms by larval lampreys is influenced by availability, by preference of the ammocetes, or by the selectivity of their feeding apparatus. *Navicula* also was the preferred diatom in Snyder-Deadhorse Creek, Schoolcraft County, Michigan; it was not the most abundant diatom in the stream, however, and appeared 2 to 4 times more frequently in the food of large larvae than in the water (Manion 1967a).

The average size of the diatoms and fragments increased from 10 microns for larvae 7-8 mm long to 66 microns for the 20-24 mm group. Sterba (1962) stated that the fineness (a purely mechanical property) of the oral filter may decrease with age and that the particles may be presorted by size.

Teratology

Ammocetes captured in the trap and by electric shocker were examined for morphological abnormalities. Of the 10,476 ammocetes examined in 1960-65, 5 had two tails and 12 had deformed tails or bodies. The frequency of occurrence of abnormalities was thus less than 0.05%. The location, description, and cause of morphological abnormalities among larval lampreys were discussed by Manion (196713).

About 6% of the larval sea lampreys examined from the Big Garlic River were yellowish. Vladykov (1960) referred to these ammocetes as "light color phase" lampreys. In those from the Big Garlic River the melanocytes were small and had poorly developed processes.

FIRST METAMORPHOSIS

The major objective of the study in the Big Garlic River was realized in the fall of 1965 when four recently metamorphosed sea lampreys were captured at the downstream trap:

Date of capture	Total	Sex
October 18	152	Male
November 1	162	Fe male
November 9	161	Male
November 9	172	Female

The minimum age at transformation for the sea lampreys in the Big Garlic River was thus established as 5 years (from the average time of hatch in July 1960 to the start of transformation in July 1965). External evidence of the initial stages of metamorphosis first appeared in July in the Big Garlic River (Manion and Stauffer 1970).

The captures of transformed lampreys also established that age is not the dominant or critical factor that triggers metamorphosis. The range in length of the remaining ammocetes in the Big Garlic River (65-176 mm; mean, 107 mm), the length of recently transformed adults in other streams (smallest reported is 95 mm, by Applegate 1961), and the variation in growth of the ammocetes clearly reveal that metamorphosis by members of a single year class takes place over a period of several years.[2]

Length, except for a possible minimum, also is not a critical factor of metamorphosis, The largest transformed sea lamprey was smaller than the largest ammocete (176 mm) taken during the annual collections in October 1965. The lengths of recently metamorphosed sea lampreys vary widely; Applegate (1961) reported a range in length of 95 to 243 mm among 15,110 recently transformed lampreys collected in the Carp Lake River, Emmet County, Michigan, in 1948-58. Recently transformed sea lampreys shorter than 100 mm are uncommon.

Although the mechanism that triggers metamorphosis in sea lampreys is unknown, it probably is a function of the animal's endocrine system. Age is obviously not the sole determinant of the rate of development. Growth rate is a factor to the extent that it is apparently necessary for the animal to reach a certain minimum length before transformation. Consequently, the period of time required to produce the first parasitic-phase sea lampreys from the known-age population of larvae in the Big Garlic River may not be the same as that in other tributaries of the Great Lakes. The more rapid growth of larvae in larger rivers presumably would permit them to reach a length at which transformation could occur earlier than in the Big Garlic River. On the other hand, the minimum time to transformation by an ammocete of a given year class in certain other rivers could be longer than 5 years; the ammocetes in the Big Garlic River had no competition from earlier or later year classes, which could have slowed growth and thereby increased the time to transformation.

IMPLICATIONS OF LARVAL BIOLOGY IN SEA LAMPREY CONTROL

The study of the known-age population of sea lampreys in the Big Garlic River provided the first positive information on the minimum duration of larval life. Since the time to metamorphosis obviously varied widely among larvae of the same age, a fixed schedule for the chemical treatments of all streams producing sea lampreys clearly is not possible. Effective control requires a knowledge of each stream and, in particular, a knowledge of the growth rate of the ammocetes in each stream.

Density of the larvae and temperature of the water are important factors in growth. Downstream drift by larvae alters population density; growth probably is fastest in areas of the stream

2 Recently transformed sea lampreys were taken at the downstream trap each year in 1966-71, and larval sea lampreys were still present throughout the study area in 1971.

where the population density is lowest. Surveillance of streams that produce sea lampreys should thus include the monitoring of areas of low ammocete density.

Data from collections of ammocetes in 13 other Lake Superior tributaries revealed that growth of larvae is faster in large streams than in small ones, probably because average water temperatures are usually higher in the large streams. Since the time to metamorphosis is variable and appears to be somewhat size-dependent, transformation to the adult phase could occur in rivers with rapid growth earlier than in the Big Garlic River. Such rivers require close monitoring and probably more frequent treatments.

Problems in the eradication of sea lamprey larvae inhabiting lentic environments are well known. Downstream drift of larvae is the apparent source of ammocetes in inland lakes, estuaries, and bays. Data of the present study suggest that temperature and water levels influence the extent of that drift. The role of water temperature is limited, inasmuch as ammocetes are active at all temperatures above about 4.4 C. Most movement is at night and, during periods of activity, an increase in water level commonly increases the extent of downstream drift. The manner in which the ammocetes move downstream produces a "heading and tailing out" pattern, as indicated by the trap catch and by the increasing density of ammocetes in the lower part of the experimental section and the decreasing density in the upper part.

Because of downstream drift, tributary systems in which larval populations become established above inland lakes or near estuaries and bays require special consideration. Frequent chemical treatments may be necessary to eradicate newly established populations in streams where drift into lentic environments can produce populations that are large enough to threaten the control program.

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