DISTRIBUTION AND ECOLOGY OF LAMPREYS IN THE LOWER PENINSULA OF MICHIGAN, 1957-75

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ABSTRACT

In 1957-7.5, more than one-half million lampreys representing five species were collected from tributaries of Lakes Michigan, Huron, and Erie in the Lower Peninsula of Michigan during execution of the sea lamprey *(Petromyzon marinus)* control program. The distributions of the five species-chestnut lamprey *(Ichthyomyzon castaneus),* northern brook lamprey (I. fossor), silver lamprey *(I. unicuspis),* American brook lamprey *(Lampetra lamottei),* and sea lamprey-are described by stream and within streams. The species were geographically sympatric and widely distributed except that I. *castaneus* was restricted to the western drainage, *I. unicuspis* was mainly limited to the eastern drainage, and *P. marinus* was absent from most of the interior drainage. Larval populations were more dense and extensively distributed in streams draining the northern half of the Peninsula.

Comparisons of the distributional patterns of larval lampreys in streams occupied by two or more species disclosed partial ecologic allopatry among populations. The distribution and species composition of populations changed longitudinally along an environmental gradient from the mouth to the headwaters in most streams.

The *Ichthyomyzon* congeners were chiefly associated with warmwater habitat and exhibited a greater tolerance of unstable environments in terms of discharge, water temperature, and bottom than the other species. *Ichthyomyzon castaneus* and *I. unicuspis* occurred principally in the main branches of large streams, avoiding headwaters and small tributaries. *Ichthyomyzon fossor* was allied with watersheds of poor natural drainage, mainly inhabiting warmwater reaches that were appreciably influenced by outflow from lakes, swamps, marshes, and ponds. *Lampetra lamottei* was affiliated mainly with stable, high quality, coldwater habitat and was the predominant species in tributaries and headwaters. *Petromyzon marinus* demonstrated great adaptability, occupying the widest range of streams and habitats.

The species composition of populations differed among streams. Streams manifesting diverse habitats contained more species than environmentally homogeneous streams, except where dams stopped spawning runs. *Lampetra lamottei* was the most sympatric and most allopatric species. This lamprey and *P. marinus* demonstrated the greatest mutual affiliation of any two species, whereas *L. lamottei* and *I. unicuspis* displayed the weakest mutual association among any two overlapping species.

Data were also collected on the reproductive behavior of 1,359 lampreys representing five species. Spawning seasons of the species overlapped, although *L. lamottei* spawned the earliest (April 20) and *P. marinus* spawned the latest (September 2).

Key words: lampreys, streams, distribution, ecology, habitats, sympatry, allopatry, associations., lentic, spawning.

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

INTRODUCTION

The invasion of the upper Great Lakes by the sea lamprey (Petromyzon *marinus)* in the late 1930's and the later devastating impact of this parasite on the lake trout *(Salvelinus namaycush)* and other valuable commercial and sport fishes led to an extensive program of research and control. The invasion and the resulting control efforts have been fully reviewed by Shetter (1949), Applegate (1950, 1951), Applegate and Moffett (1955), Baldwin (1964, 1968), Howell (1966), Lawrie (1970), Smith (1971), Smith et al. (1974), and Crowe (1975).

The sea lamprey research and control program, directed by the Great Lakes Fishery Commission, collected an enormous amount of material on the sea lamprey and, coincidentally, on the native lampreys inhabiting the upper Great Lakes drainage. Data collected in the Lower Peninsula of Michigan during the period 1957-75 provide the basis for the present study.

Five lamprey species inhabit the Lower Peninsula of Michigan drainage: chestnut lamprey (Ichthyomyzon castaneus), northern brook lamprey (I. fossor), silver lamprey (I. *unicuspis),* American brook lamprey *(Lampetra lamottei),* and sea lamprey *(P. marinus). Ichthyomyzon castaneus, I. unicuspis,* and *P. marinus are* parasitic; I. *fossor* and *L. lamottei* are nonparasitic and largely nonmigratory.

The distribution of lampreys in the Lower Peninsula of Michigan has not previously been treated in detail. The purpose of this study was to delineate the distributions of each of the five species, to suggest reasons for those distributions, and to explore the species interrelationships.

DESCRIPTION OF THE STUDY AREA

Michigan's Lower Peninsula, and a small contiguous region in northern Indiana that encompasses major segments of the St. Joseph River and headwaters of the Galien River and State Creek, constitute the study area (Fig. 1). This land mass, covering about 112,000 km^2, is bordered by all three of the upper Great Lakes: Lake Michigan on the west and northwest, Lake Huron on the east and northeast, and Lake Erie on the southeast. The area is roughly divided along a north-south axis into two almost equal drainages; streams on the western slope enter Lake Michigan and those on the eastern slope enter Lakes Huron and Erie.

The surface drainage consists of 237 streams that enter the Great Lakes (Table 1), and which in turn are fed by 1,500 tributaries. Drainage systems vary from small single-lobed peripheral basins of less than 3 km^2 to multi-lobed interior basins as large as 16,848 km2 (Saginaw River). Minimum stream discharges in summer or fall range from less than 0.03 to 31 m^3/s. The St. Clair River, an inter-lake channel that carries the discharge from Lake Huron into Lake St. Clair, has a low summer flow of about 4,415 m^3/s (Velz and Gannon 1960). The Lower Peninsula has

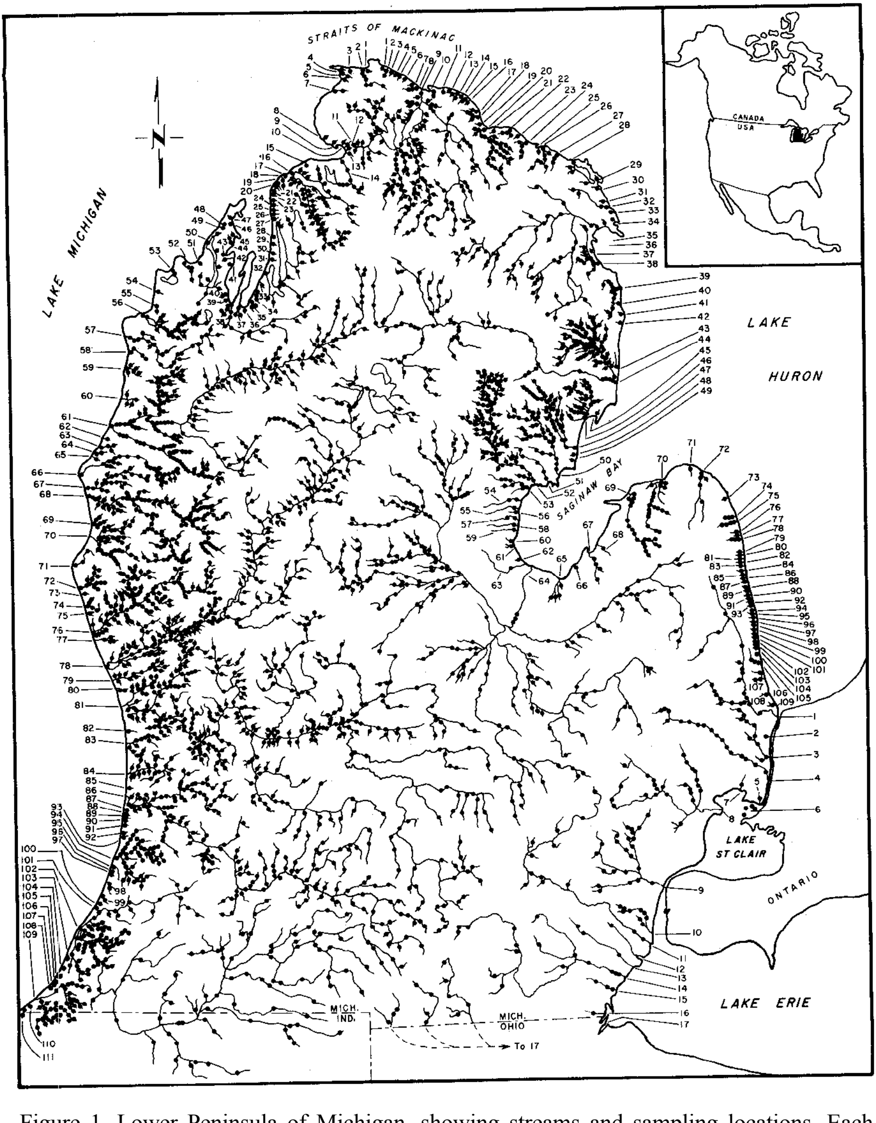

Figure 1. Lower Peninsula of Michigan, showing streams and sampling locations. Each symbol represents one to three collection sites. The numbers shown correspond to stream numbers and names in Table 1.

developed few major river systems because of its geologically youthful land surface, insularity, and comparatively narrow breadth (248 km). McNamee (1930) listed 21 primary Lower Peninsula streams with drainage areas of 647 km2 or larger. The length of the Grand River, the longest, is 422 km. The main channel of the Detroit River, connecting Lake St. Clair and Lake Erie, was not surveyed for lampreys; therefore, it was not included among the streams in this paper.

Table 1. Distribution of lampreys in the streams of Michigan's Lower Peninsula, 1957-75. Stream number corresponds to location in Figures l-7. Stream names and numbers are listed separately for each lake and run sequentially from north to south. *[I = Ichthyomyzon* spp., *Ic = I. castaneus, If = I. fossor, Iu = I. unicuspis, Ll = Lampetra lamottei,* and *Pm = Petromyzon marinus.]*

Drainage basin, number and stream	Species	Drainage basin, number and stream	Species
Lake Michigan Drainage		46 Ennis Cr.	
1 French Farm Cr.	*Ll*	47 Northport Cr.	
2 Carp Lake R.	***I, If, Iu, Ll,*** *Pm*	48 Roaring Brook Cr.	
3 Big Stone Cr.	***Ll,*** *Pm*	49 Gills Cr.	
4 Little Sucker Cr.		50 Leland R.	*Ll*
5 Big Sucker Cr.	*Ll, Pm*	51 Good Harbor Cr.	
6 Cool Cr.[a]		(L. Good Harbor Cr.)	
7 Wycamp Cr.	***Ll,*** *Pm*	52 Shalda Cr.	*Z, Ll, Pm*
8 Five Mile Cr.		(Good Harbor Cr.)	
9 MacArthur Cr.[a]		53 Crystal R.	***I, If,*** Pm
10 Ramona Cr.[a]		54 Bar Lake Cr.[a]	
11 Lake Cr.[a]		55 Otter Cr.	
12 Menonaqua Cr.[a]		56 Platte R.	***I,*** *Ic,* ***If, Ll,*** *Pm*
13 Tannery Cr.		57 Betsie R.	*I, Zc,* ***If, Ll,*** *Pm*
14 Bear R.	*I,* ***If,*** *Pm*	58 Herring Cr.	
15 Susan Cr.		59 Bowen Cr.	*Ll, Pm*
16 Pine R.	*I, Zc,* ***Ll,*** *Pm*	60 Portage Lake Cr.[a]	
(Lake Charlevoix)		61 Manistee R.	***I,*** *Zc,* ***If,*** *Ll, Pm*
17 Medusa Cr.[a]		62 Magoon Cr. (Cedar Cr.)	
18 McGeach Cr.	*Ll, Pm*	63 Gumee Cr.	*Ll, Pm*
19 Inwood Cr.		64 Cooper Cr.	*Ll*
20 Outwood Cr.[a]		65 Porter Cr.	
21 Clipperview Cr.[a]		66 Big Sable R.	*I, zc,* ***If,*** *Ll*
22 Whiskey Cr.		67 Lincoln R.	*I,* ***Ic, If,*** *Ll, Pm*
23 Top Cr.[a]		68 Pere Marquette R.	*Z, Ic,* ***If,*** *Ll, Pm*
24 Antrim Cr.		69 Bass Lake Cr.[a]	*Ll, Pm*
25 Fourteen Cr.[a]		70 Pentwater R.	*Z, Zc, Ll, Pm*
26 Dennis Cr.		71 Silver Cr.	*Ll*
27 Guyer Cr.		72 Stony Cr.	***I, Ll,*** *Pm*
28 Powell Cr.[a]		73 Whiskey Cr.	
29 Levi Cr.[a]		74 Flower Cr.	*Ll, Pm*
30 Erickson Cr.[a]		75 Meinert Cr.[a]	
31 Paradine Cr.		76 White R.	*I, Zc,* ***If,*** *Ll, Pm*
32 Elk R. (Intermediate R.	***I,*** *Ll, Pm*	77 Duck Cr.	*Ll, Pm*
system)		78 Muskegon R.	*I, Zc,* ***If,*** *Ll, Pm*
33 Tobeco Cr.		79 Black Cr.	*I, Ll, Pm*
34 Yuba Cr.	*Ll, Pm*	80 Little Black Cr.	
35 Acme Cr.	***Ll,*** *Pm*	81 Grand R.	*I, Zc,* ***If, Ll,*** *Pm*
36 Joint Cr.0	*Ll*	82 Little Pigeon Cr.	
37 Mitchell Cr.	*Ll, Pm*	83 Pigeon R.	***I,*** *Ll, Pm*
38 Boardman R.	***I,*** *Ll, Pm*	84 Black R.	*Ll, Pm*
39 Brewery Cr.[a]		85 Gibson Cr.[a]	*Ll, Pm*
40 Cedar Cr.	*Z*	86 Kalamazoo R.	***I,*** *Zc,* ***If,*** *Ll, Pm*
41 Lee Cr.		87 Allegan 1 Cr.[a]	
42 Leo Cr.		88 Allegan 2 Cr.[a]	
43 633 Cr.[a]		89 Allegan 3 Cr.[a]	*Ll, Pm*
44 Belanger Cr.		90 Allegan 4 Cr.[a]	*Ll, Pm*
(Belonga Cr.)		91 Allegan 5 Cr.[a]	*Ll, Pm*
45 Weaver Cr.		92 Allegan 6 Cr.[a]	

Table 1 (continued)

Drainage basin, number and stream	Species	Drainage basin, number and stream	Species
Lake Michigan Drainage (continued)			
93 Allegan 7 Cr.[a]	*Ll*	29 Bell R.	
94 Black R.	*I, If, Ll, Pm*	30 Ferron Cr.[a]	
95 Deerlick Cr.		31 Middle Lake Cr.[a]	*Pm*
96 Wildwood Cr.[a]		32 Long Lake Cr.	
97 Na Wa Kwa Cr.[a]	*Ll*	33 Grass Cr.	
98 Brandywine Cr.	*Ll, Pm*	34 Potter Cr.[a]	
99 Rogers Cr.	*Ll. Pm*	35 Norwegian Cr.	
100 Berrien 1 Cr.[a]		36 Thunder Bay R.	*I, If*
101 Berrien 2 Cr.[a]	*Ll*	37 Squaw Cr.[a]	*I, Pm*
102 St. Joseph R.	*I, Ic, If, Ll, Pm*	38 Devils R.	*I, If, Iu, Pm*
103 Grand Marais Lake		39 Black R.	*I, If, Iu, Pm*
Cr.[a]		40 Alcona Cr.	
104 Bridgeman Cr.[a]		41 Bluejay Cr.[a]	
105 Pointerville Cr.		42 Mill Cr.	
106 Berrien 3 Cr.[a]		43 Cedar Cr.	
107 Berrien 4 Cr.[a]	*Ll*	44 Au Sable R.	*I, If, Iu, Pm*
108 Berrien 5 Cr.[a]	*Ll*	45 Solitude Cr.[a]	
109 Galien R.	*I. Ll. Pm*	46 Tawas R.	*I, Iu, Ll, Pm*
110 New Buffalo Cr.[a]		47 East Au Gres R.	*I, If, Iu, Ll, Pm*
111 State Cr. (White Ditch)	*Ll, Pm*	48 Dime Drain	
		(Cranberry Dr.)	
		49 Hammel Cr.	
		50 Au Gres R.	*I, If, Iu, Ll, Pm*
Lake: Huron Drainage		51 Big: Cr. Drain	
1 Twenty One Cr.[a]		52 Rifle R.	*I, If, Iu, Ll, Pm*
2 Mill Cr.		53 Pine R.	*I, If, Iu*
3 Cheboygan 266-20 Cr.[a]	*Pm*	54 Saganing R.	
4 Cheboygan 344-23 Cr.[a]		55 White Feather Cr.	
5 Le Dues Cr.[a]		56 Selleck Drain	
6 Nipigon Cr.[a]		57 Pinconning R.	
7 Be&grand Cr.	*Pm*	58 Johnson Dram	
8 Little Black R.	*Ll, Pm*	59 Tebo Drain	
9 Cheboygan R.	*I, If, Iu, Ll, Pm*	60 Gregory Drain	
10 Elliot Cr.	*Ll, Pm*	61 Railroad Dram	
11 Grass Cr.[a]	*Ll. Pm*	62 Tobico Drain	
12 Banks Cr.[a]		63 Kawkawlin R.	
13 'Greene Cr.	*Ll, Pm*	64 Saginaw R.	*I, If, Iu, Ll, Pm*
14 Lone Pine Cr.[a]		65 Quanicassee R.	
15 Mulligan Cr.	*Ll, Pm*	66 Bay Drain[a]	
16 Three Cr.[a]		67 Wiscogin Cr.	
17 Grace Cr.	*Ll, Pm*	68 Sebewaing R.	
18 Carp Cr.	*Ll, Pm*	69 Pigeon R.	*I, If*
(Black Mallard Cr.)		70 Pinnebog R.	*I*
19 Seventeen Cr.[a]	*Ll, Pm*	71 Eagle Cr.0	
20 Ocqueoc R.	*I, If, Iu, Ll, Pm*	72 Willow R.	
21 Johnnv Cr.[a]	*Pm*	73 Ocka Cr.	
22 Schmidt Cr.	*Pm*	74 Spring Cr.	*Ll*
23 Nagels Cr.		75 Rock Falls Cr.	*I, Pm*
24 Trout R.	*Pm*	76 Buckley Cr.	
25 Calcite Cr.[a]		77 Purdy Cr.[a]	
26 Swan R.	*I, Pm*	78 Elm Cr. (Sucker Cr.)	*I, Pm*
27 Little Trout R.		79 County Line Cr.	
28 Grand Lake Cr.		(Sanilac 1 Cr.)	

Table 1 (continued)

Drainage basin, number and stream	Species	Drainage basin, number and stream	Species
Lake Huron Drainage (continued)			
80 Sanilac 2 Cr.a		104 Sanilac 65 Cr.a	
81 Mill Cr.		105 Sanilac 72 Cr.a	
82 Benake Cr.		106 Mill Cr.	*I, Iu, Ll, Pm*
(Sanilac 9 Cr.)[a]		107 Birch Cr.	*I, Iu*
83 Mat-tell Cr.		108 Metcalf Cr.a	
(Sanilac 11 Cr.)[a]		109 Garden Cr.a	
84 Elk Cr.		Lake Erie Drainage[b]	
85 Indian Cr.			
86 Sanilac 19 Cr.a		1 Black R.	*I, If, Iu, Pm*
87 Sanilac 20 Cr.a		2 Chrysler Drain[a]	
88 Big Cr.		3 Pine R.	*I, If, Iu*
89 Cherry Cr.		4 Belle R.	*I*
90 Bridgehampton Cr.		5 Marsh Drain	
91 Sherman Cr.		6 St. Clair R.	*I, Ll, Pm*
92 Miller Cr.	*Ll*	7 Swan Cr.	
93 Sanilac 32 Cr.a		8 Clinton R.	*I*
94 Liens Cr.		9 Rouge R.[c]	*I*
(Sanilac 37 Cr.)[a]		10 Brownstown Cr.[c]	
95 Sanilac 40 Cr.”		11 Huron R.	*I, If, Ll*
% McKenzie Cr.		12 Swan Cr.	
97 Sanilac 46 Cr.a		13 Stony Cr.	
98 Sanilac 48 Cr.a		14 Raisin R.	*I, If*
99 Sanilac 52 Cr.0		15 Otter Cr.	
100 Sanilac 57 Cr.a		16 Halfway Cr.	
101 Sanilac 59 Cr.a		17 Maumee R.	*I, Ll*
102 Sanilac 61 Cr.a		(Headwaters	
103 Sanilac 64 Cr.a		in Michigan)	
Total			

Species	*Ichthyomyzon* SPP.	*I. castaneus*	*I. fossor*	*I. unicuspis*	*Lampetra lamottei*	*Petromyzon marinus*
Number of streams						
Lake Michigan	25	13	15	1	52	43
Lake Huron	20	0	12	13	18	29
Lake Erie	9	0	4	2	3	2
Total all lakes	54	13	31	16	13	74

a Unofficial name.
b Streams numbered 1 through 8 are tributary to the Lake St. Clair system.
c Tributary to the Detroit River.

The topography of the region is constructed on thick glacial drift of Wisconsin age and remains in an immature stage of development (Wayne and Zumberge 1965). Reflecting this youthfulness, the drainage network is poorly developed, and inland lakes and swamps are numerous (Dorr and Eschman 1970). McNamee (1930) classified the surface into pervious formations (sand 25%, sandy till 22.5%, and gravelly loam 8.2%) and impervious formations (clayey till 32.7% and lakes and swamps 11.6%). Gross physiographical features divide the land surface into the Northern and Southern Uplands, which cover most of the interior of the Peninsula, and four peripheral but prominent lakeshore lowlands (Veatch 1953). Basins in the Northern Upland are developed largely on porous outwash plains, and to a lesser extent on moraines and till plains (Martin 1955). Consequently they have a low surface runoff, a high groundwater discharge, and a correspondingly stable streamflow. In the Southern Upland, impermeable till plains are more predominant, particularly in the large Grand River basin where they compose about 47% of the surface (McNamee 1930; Martin 1955). Hence, flows are more variable there. The lakeshore lowlands, bordering most of the Lower Peninsula, are mainly flat and featureless and consist of sandy or clayey lake bed plains deposited during the high-water stages of the glacial Great Lakes (Veatch 1953; Martin 1955; Dorr and Eschman 1970). Many of the smaller basins were developed entirely on the coastal lowlands. Lowland plains streams whose basins are underlain mainly by impervious clays have highly unstable flows, or may be seasonally intermittent.

The gradients of the Lower Peninsula streams range generally from low to moderate, except for scattered short segments in which they are at least as steep as 5 m/km. There are only two major waterfalls, on the Ocqueoc and Rainy Rivers, and over 550 man-made dams that are probably high enough to influence lamprey distribution by preventing upstream movement (Michigan Department of Natural Resources unpublished records).

Although the natural water quality of the streams affords a highly suitable environment for lampreys throughout most of the region, this condition is offset in many areas in varying degrees by the deleterious influences of agriculture, industry, and urban centers-primarily in the southern half of the Peninsula, and especially in the Saginaw Valley and the Lake Erie drainages.

MATERIALS AND METHODS

Lampreys were collected during stream surveys and lampricide treatments of streams (Baldwin 1964, 1968; Smith 1971; Smith et al. 1974), and at electromechanical barriers (Applegate et al. 1952b; Erkkila et al. 1956; McLain et al. 1965; Smith 1971). A total of 4,353 stations were sampled on the 237 streams (Fig. 1). Some distributional data for I. *castaneus* and I. *fossor* in the upper Manistee River, collected by the Michigan Department of Natural Resources in 1958 and 1966, were supplied by Gary T. Schnicke, District Fisheries Biologist, Michigan Department of Natural Resources.

Stream surveys, carried out mainly from May to October, provided most of the distributional information and were the sole source of spawning data. Small portable electrofishing units, and sometimes the lampritide, granular Bayer 73[2] (2' ,5-dichloro-4'-nitrosalicylanilide, containing 5% active ingredient), were used to drive larval lampreys from the stream bottom for collection. Sampling for burrowed lampreys was confined largely to the soft-bottom portions of the stream, and gravelly portions were examined for nests and spawning adults. At most stations, all lampreys were taken, irrespective of species, size, or stage of development. Water temperatures were recorded, and the stream width, depth, discharge, current velocity, bottom composition, water color, and turbidity were described at each station. All permanent streams, most permanent tributaries, and most intermittent streams were surveyed periodically. The number of stations established on a stream was determined principally by its size (length and number of tributaries), its apparent suitability for lampreys, accessibility, and the presence of dams. Usually more stations were established in large streams than in smaller ones; in streams suitable for lampreys than in marginal streams; in streams with many access points than in streams with fewer access points (although this was partly offset by hiking or boating to remote sections); and in open streams (no dams) than in obstructed ones. The distance between stations usually ranged from 0.8 to 8 km, but was as great as 145 km. Samples taken at most stations that were less than 0.4 km apart (on the same branch) were combined, Often additional points on streams were visually examined but not sampled or counted as stations because of the poor quality of the habitat (such as hard bottom or stagnant water), or because the reaches were dry. Such adverse conditions account for some of the long distances between sampling points and the occurrence of only one station on some streams or tributaries.

Before 1972, observations for spawning adults were largely incidental to sampling for larvae. In 1972-75, systematic surveys were conducted from late May to early July on 10 streams-5 entering Lake Michigan (Carp Lake, Pine, Platte, Betsie, and Muskegon Rivers) and 5 entering Lake Huron (Cheboygan, Trout, East Au Gres, and Rifle Rivers and Carp Creek). The primary purpose was to assess the extent of *P. marinus* spawning, although information on native species was also gathered. Streams were examined by boat or on foot, depending on the distance covered. Lengths of the reaches examined on each stream ranged from about 0.4 to 65 km. Although species could usually be identified on nests, most spawning lampreys were collected and examined.

Stream treatments with lampricides (Applegate et al. 1961) provided an additional source of larval and adult specimens. Treatments, however, were limited to a comparatively small portion of the Lower Peninsula drainage network. Sections of 60 of the 237 streams were treated during 1957-75; and all treatments, except one, were conducted during April-November. The number of treatments per stream ranged from one to five, usually spaced at 1- to 4-year intervals. Chemicals used to treat streams were 3-trifluoromethyl-4-nitrophenol (TFM) and a mixture of TFM and

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2 Registered trade mark of Farbenfabriken Bayer AG, Leverkusen, West Germany. Reference to trade names does not imply Government endorsement of commercial products.

powdered Bayer 73 (2',5-dichloro-4'-nitrosalicylanilide, containing 70% active ingredient). Lampreys were collected with modified fyke nets, dip nets, and by hand at stations along the streams being treated.

During 1969-75, surveys for populations of larval lampreys in inland lakes, embayments, and along Great Lakes shores were conducted with granular Bayer 73 spread at an average rate of 112 kg/ha on plots ranging in size from 0.2 to 0.4 ha. Smith et al. (1974) briefly described a similar use of this lampricide in the Lake Superior watershed. The distance of the plot from the stream mouth was measured or estimated, and the physical characteristics of each plot were described in terms of depth, bottom composition, bottom water temperatures, and the nature of the surrounding area.

Electromechanical barriers were operated on Lakes Michigan and Huron (Great Lakes Fishery Commission 1957-74) and provided data on species of adult lampreys migrating upstream to spawn. Seventeen of these barriers were run for 2 to 4 years, mostly during 1957 and 1958, on 12 streams entering Lake Michigan: (1) Wycamp Creek, (2) McGeach Creek, (3) three Pine River tributaries (Boyne River, Jordan River, and Monroe Creek), (4) Yuba Creek, (5) Mitchell Creek, (6) Betsie River, (7) Little Manistee River, tributary of the Manistee River, (8) Lincoln River, (9) Pere Marquette River, (10) two Pentwater River tributaries (North and South Branches), (11) three St. Joseph River tributaries (Paw Paw River, Blue Creek, and Pipestone Creek), and (12) Galien River. Another barrier, on the Ocqueoc River, a Lake Huron stream, was operated each year during 1957-75, except 1958. The use of similar trapping devices on Lower Peninsula streams before 1957, and the catches, were reported by Shetter (1949), Applegate (1950), Applegate and Smith (1950), Applegate et al. (1952a), and Smith (1971). Electromechanical structures were largely ineffectual in capturing brook lampreys, mainly because of the large mesh (about 12 mm, bar measure) of the screen in the traps.

Characteristics described by Vladykov (1950) were used to identify all larval lampreys. Characteristics given by Hubbs and Trautman (1937) were used in the identification of adult *Ichthyomyzon*. In addition, examinations of the gut, gonad, teeth, and oral disc were applied in separating metamorphosing stages of I. *fossor* from those of *I. castaneus* and I. *unicuspis*. The identification of *L. lamottei* and *P. marinus* adults was based on physical characters reported by Trautman (1957).

Larvae of the genus *Ichthyomyzon* are indistinguishable as species. Consequently the classification of larval populations was inferred on the basis of spatially associated adult forms. *Ichthyomyzon* adults were not found in association with every larval population. Accordingly, in distribution records, populations of *Ichthyomyzon* larvae were designated by species (adults present) or by genus (no adults collected).

Water temperatures were recorded during all surveys and were also obtained from U.S. Geological Survey published reports (U.S. Geological Survey 1965-74b). To detail the thermal regimes of specific habitats, and to obtain temperature data during the spawning season, field personnel recorded water temperatures continuously with Peabody Ryan recording thermometers (models D-15 and F-15) at nine stations in four streams during April-August 1973: upper Pere Marquette River (one station); Little South Branch of the Pere Marquette River (two stations); McDuffee Creek, a tributary of the Pere Marquette River system (one station); lower Rifle River (one station); Platte River (two stations); Brundage Creek, a tributary of the Platte River (one station); and South Branch of the Pine River, a tributary of the Au Sable River system (one station). Dale Pettengill, of the U.S. Geological Survey, Grayling, Michigan, provided recording thermometer charts from two additional stations for the same period-one each for the lower Pere Marquette River and the upper Rifle River.

Some stream lengths were obtained from Brown (1944) while others were measured on U.S. Geological Survey topographic maps, county road maps, or aerial photos supplied by the Agricultural Stabilization and Conservation Service, U.S. Department of Agriculture. The gradient was computed by dividing stream kilometers into the number of meters of fall (elevation difference) obtained from contour lines on U.S. Geological Survey topographic maps.

Flow data were obtained from stream survey records (estimated flow), stream treatment records (measured flow), and published records of the U.S. Geological Survey (1965-74a) for the period 1965-74.

Stream basin areas were obtained principally from McNamee (1930), Brown (1944), and the U.S. Geological Survey (1965-74a,b).

ECOLOGY

Distribution and Stream Habitat

Ichthyomyzon spp. larvae

Collectively, larval *Ichthyomyzon* were broadly distributed, inhabiting streams entering all three lakes-Michigan, Huron, and Erie. Over 60,000 specimens were captured from a total of 54 streams (Tables 1 and 2, Fig. 2). These lampreys inhabited fewer streams than either *L. lamottei* or *P. marinus,* and fewer tributaries and kilometers of stream than *L. lamottei,* but occupied a greater number of tributaries and kilometers of stream than P. marinus (Table 2). *Ichthyomyzon* larvae were present in 23% of 237 streams, 17% of 1,529 stream tributaries, about 3 1% of 19,600 km of stream, and in collections at 23% of 4,353 stations. Furthermore, *Ichthyomyzon* occurred in 54% of the 100 streams and 31% of the 840 tributaries that contained larval lampreys of any species. They were collected from all major stream systems; small, isolated populations were noted even in the Black, Belle, Clinton, Rouge, Huron, and Raisin Rivers-all of which, owing mainly to their location on the flat and clayey Huron-Erie Lowlands, featured generally unfavorable habitats for lampreys, with low and unstable flows, sedimentation, hard clay-gravel bottoms, and high temperatures.

Table 2. Summary of the distribution of lampreys in Michigan's Lower Peninsula, 1957-75.

Species	Number of streams (N=237)				Number of tributaries (N= 1,529)				Kilometers of stream[a] (N= 19,600)				Number of stations (N=4,353)			
	Drainage basin				Drainage basin				Drainage basin				Drainage basin			
	Michigan	Huron	Erie	Total	Michigan	Huron	Erie	Total	Michigan	Huron	Erie	Total	Michigan	Huron	Erie	Total
Ichthyomyzon spp. (larvae)	25	20	9	54	146	102	13	261	3,500	2,200	200	5,900	587	397	36	1,020
I. castaneus	13	0	0	13	28	0	0	28	1,700	0	0	1,700	80	0	0	80
I. fossor	15	12	4	31	72	74	3	149	2,300	1,800	<100	4,200	142	140	5	287
I. unicuspis	1[b]	13	2	16	0	12	1	13	<100	700	<100	900	1	42	3	46
Lampetra lamottei	52	18	3	73	577	141	8	726	6,700	1,700	<100	8,500	1,570	477	14	2.061
Petromyzon marinus	43	29	2	74	120	106	1	227	1,600	1,100	<100	2,800	562	456	4	1,022
No lampreys	56	73	8	137	380	267	42	689	4,500	3,000	1,200	8,700	869	707	156	1,732

[a]Linear distance, rounded to nearest hundred.
[b]Carp Lake River, at the Straits of Mackinac.

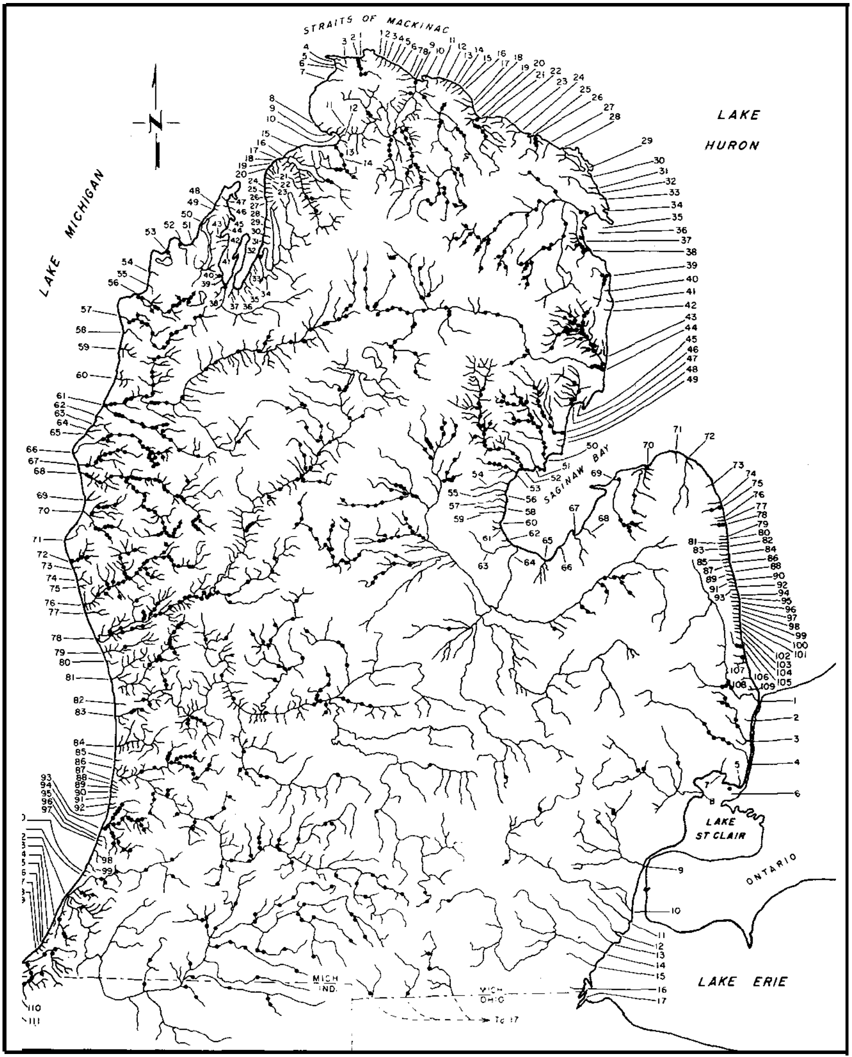

Figure 2. Distribution of *Ichthyomyzon* spp. larvae by localities of capture. Each symbol represents one to three collection sites. The numbers shown correspond to stream numbers and names in Table 1.

Ichthyomyzon castaneus, chestnut lamprey

This species was collected from only 13 streams, all tributary to Lake Michigan (Table 1, Fig. 3). It ranged from the Pine River (Lake Charlevoix system) in northwestern Michigan southward into northern Indiana, where it was found in the White Pigeon River, an upper branch of the St. Joseph River near La Grange. Its furthest inland occurrence was ob-

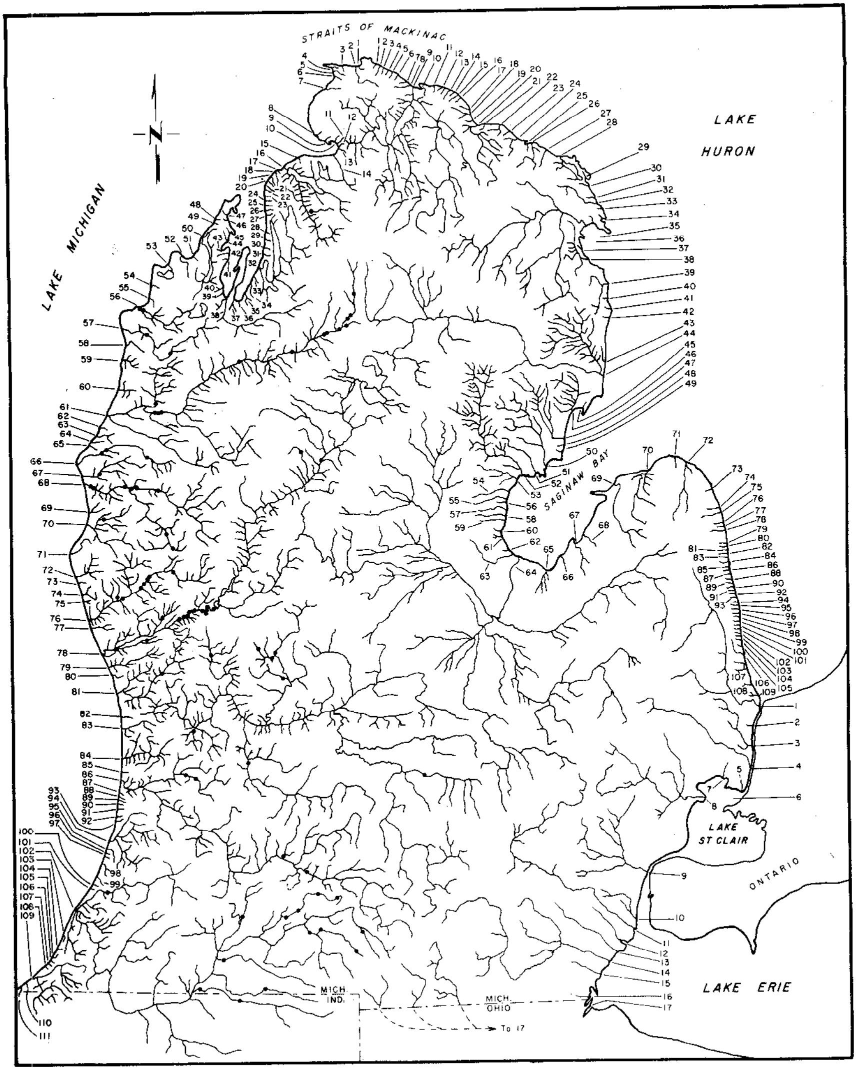

Figure 3. Distribution of metamorphosing, recently metamorphosed, or adult *Ichthyomyzon castaneus,* by localities of capture. Each symbol represents one collection site. The numbers shown correspond to stream numbers and names in Table 1.

served in the Manistee, Muskegon, Grand, Kalamazoo, and St. Joseph Rivers. Fourteen metamorphosing specimens were collected on October 7, 1974, in Sand Creek, a headwater tributary of the St. Joseph River near Litchfield, Michigan, about 453 km upstream from the river mouth at Lake Michigan, above a series of barrier dams. Isolated remnant populations were present upstream from long-established, permanent, man-made dams in eight streams: (1) Betsie River above Homestead dam, (2) Manistee River above Tippy dam, (3) Big Sable River above Hamlin dam, (4) White River above Hesperia dam, (5) Muskegon River above Croton dam, (6) Grand River above dams on the Rogue, Thornapple, and Flat Rivers, (7) Kalamazoo River above Allegan dam, and (8) St. Joseph River above Berrien Springs dam. Its presence has been documented previously in six of the streams from which it was collected during the present investigation, and also in the Black River (Table 3). Likewise, Hubbs and

Table 3. Published descriptions of the geographical distribution of lampreys (that include the Lower Peninsula of Michigan drainage) or documentations of their presence in streams.

Species	Geographic distribution	Lower Peninsula streams
Ichthyomyzon castaneus	Jordan and Evermann 18%; Michael 1906; Greene 1935; Hubbs and Trautman 1937; Hubbs and Lagler 1967; Hubbs and Potter 1971; Scott and Crossman 1973.	Lake Michigan - Manistee River[a] (Hubbs and Trautman 1937; Hall 1963); Pere Marquette River[a] (Hubbs and Trautman 1937; Hodges 1972); Kalamazoo River[a] (Bollman 1891; Hubbs and Trautman 1937); Muskegon[a], Grand[a], Black, and St. Joseph[a] Rivers (Hubbs and Trautman 1937). Lakes Huron and Erie-none.
I. fossor	Creaser and Hubbs 1922; Hubbs 1925; Hubbs and Greene 1928; Berg 1931; Greene 1935: Hubbs and Trautman 1937; Radforth 1944; Vladykov 1949; Trautman 1957; Hubbs and Lagler 1967; Van Meter and Trautman 1970; Hubbs and Potter 1971; Scott and Crossman 1973.	Lake Michigan-Carp Lake Rive@ (Stauffer 1962); Pere Marquette River[a] (Hubbs and Trautman 1937; Hodges 1972); Grand River[a] (Creaser 1925; Hubbs and Trautman 1937); Kalamazoo River[a] (Hubbs and Trautman 1937); Galien River[b] (Hankinson 1920; Creaser 1925). Lake Huron-Cheboygan River[a] (Hubbs and Trautman 1937); Ocqueoc River[a] (Shetter 1949); Thunder Bay River[a] (Okkelberg 1922; Hubbs and Trautman 1937); Devils River[a] (Hubbs and Trautman 1937); Au Sable River[a] (Creaser 1925; Hubbs and Trautman 1937); Rifle River[a] (Hubbs 1925; Saginaw River[a] (Hubbs and Trautman 1937). Lake Erie-Huron Rive@ (Reighard and Cummins 1916; Okkelberg 1922; Creaser 1925; Hubbs and Trautman 1937); Raisin Rive@ (Hankinson 1920, 1932; Hubbs and Trautman 1937).
I. unicuspis	Hubbs and Trautman 1937; Radforth 1944; Vladykov 1949; Hubbs and Lagler 1967; Van Meter and Trautman 1970; Hubbs and Potter 1971; Scott and Crossman 1973.	Lake Michigan - Carp Lake River[a] (Applegate and Smith 1950; Applegate and Brynildson 1952; Applegate et al. 1952a; Applegate 1961). Lake Huron-Little Black River (Applegate and Smith 1950; Applegate et al. 1952a); Cheboygan River[a] (Hubbs and Trautman 1937); Greene Creek (Applegate and Smith 1950; Applegate et al. 1952a); Ocqueoc River[a] (Shetter 1949; Applegate 1950); Trout River (Applegate et al. 1952a); Au Sable[a] and Saginaw[a] Rivers (Hubbs and Trautman 1937).

Table 3 (continued)

Species	Geographic distribution	Lower Peninsula streams
I. unicuspis		Lake Erie - Clinton[b], **Maumee**[b], and St. **Clair**[b] Rivers (Hubbs and Trautman 1937).
Lampetra lamottei	Jordan and Evermann 18%; Surface 1899; Evermann 1902; Huntsman 1917; Creaser and Hubbs 1922; Hubbs 1925, 1926; Gage 1928; Hubbs and Greene 1928; Hubbs and Brown 1929; Berg 1931; Greene 1935; Hubbs and Trautman 1937; Radforth 1944; Vladykov 1949; Trautman 1957; Hubbs and Lagler 1967; Van Meter and Trautman 1970; Hubbs and Potter 1971; Scott and Crossman 1973.	Lake Michigan - Carp Lake **River**[a] (Applegate 1950, **1961;** Applegate and Brynildson 1952; **Stauffer 1962;** Manion and Purvis 1971); Pere Marquette **River**[a] (Hodges 1972); Grand **River**[a] (Michael 1906). Lake Huron--Ocqueoc River[a] (Shetter 1949; Manion and Purvis 1971). Lake Erie-Huron **River**[a] (Young and Cole 1900; Schaffner 1902; Michael 1906; Okkelberg 1921).
Petromyzon marinus	Hubbs and Brown 1929; Berg 193 1; Hubbs and Pope 1937; Radforth 1944; Shetter 1949; Trautman 1949, 1957; Vladykov 1949; Applegate 1950, 1951; Applegate and Smith 1950; Applegate and Moffett 1955; Great Lakes Fishery Commission 1960-74; Baldwin 1964, 1968; Howell 1966; Moffett 1966; Hubbs and Lagler **1967;** Lawrie 1970; Van Meter and Trautman 1970; Smith 1971; Scott and Crossman 1973; Crowe 1975.	Lake Michigan - Carp Lake River[a] (Applegate 1950, **1961;** Applegate and Brynildson 1952; Stauffer **1962;** Applegate and Thomas **1965;** Manion and Stauffer 1970); Pere Marquette **River**[a] (Applegate and Thomas **1965;** Hodges 1972). Lake **Huron**[c,d]**—Ocqueoc River**[a] (Applegate 1950; Applegate and Thomas **1965).** Lake **Erie**[d]**—none**

a Species also represented in collections from the stream for the present study.
b Our collections from the stream contained *Ichthyomyzon* spp. larvae but no identifiable adults.
c References limited to those mentioning larvae or newly metamorphosed lampreys, not exclusively adults.
d Most *P. marinus* streams reported in the present study have been reported by the Great Lakes Fishery Commission (1960-74), but were usually identified according to details of their treatment with lampricides. Moreover, certain stream tributaries were handled as Great Lakes tributaries. Thus discrepancies occur between the reports and this paper in numbers and names of streams.

Trautman (1937) reported that its distribution in the Lower Peninsula was restricted to the Lake Michigan drainage. But its range was described by Hubbs and Lagler (1967) as extending into upper Lake Huron to the Cheboygan River system.

A total of 1,358 adult or newly metamorphosed specimens were collected, of which 133 were measured. The average length of the 23 adults was 207 mm (range, 178-250) and that of the 110 metamorphosing individuals was 122 mm (range, 94-165).

Except for I. unicuspis, I. *castaneus* was more weakly represented in collections than the other lampreys, occurring in 5% of 237 streams, 2% of 1,529 stream tributaries, about 9% of 19,600 km of stream, and in collections at 2% of 4,353 stations (Table 2). Its occurrence was limited to 13% of 100 streams and 3% of 840 tributaries that contained larval lampreys of any species. Judging by its known distribution and habitat preference, however, it probably inhabited an additional 6 streams and 28 tributaries (about 600 km of stream) from which *Ichthyomyzon* larvae, but no identiliable adults, were taken.

The five largest populations, estimated according to densities and linear distribution of larvae, occurred in the St. Joseph, Muskegon, Pere Marquette, White, and Grand Rivers. But Hall (1963) reported "almost certainly the population of the chestnut lamprey in the Manistee River is the most dense of this species anywhere in its range." His estimate was based on the marking and recapture of parasitic-phase specimens.

The species inhabited chiefly medium-sized to large streams. Its occurrence was restricted to 13 of the 19 largest streams in the Lake Michigan drainage. These streams have low summer flows, ranging from 0.8 to 31 m^3/s, and basin areas ranging from 289 to 14,370 km^2. Of the remaining six largest Lake Michigan streams, five contained Ichthyo-*myzon* larvae, but no adults were collected. It apparently prefers main river channels largely avoiding stream tributaries. It was found in only 3% of the 324 lamprey-inhabited Lake Michigan stream tributaries that occurred below dams and thus were open to all species. Likewise, its occurrence was limited to only 6% of the 278 lamprey-inhabited tributaries above dams. Eleven of the streams populated by ***I.*** castaneus were characterized by embayments, or base-level lakes, at or near their mouths which provided accessory habitat for host fishes. Hubbs and Trautman (1937) reported that I. *castaneus* was predominant in base-level lakes along the eastern shore of Lake Michigan.

Larvae of I. *castaneus,* as well as the larvae of its two congeners, seemed to burrow more commonly in firm, relatively stable, sand-silt substrate in areas with higher current velocities, rather than in the softer, silt-detritus materials in quiet or slow current areas adjacent to the stream banks, which are usually preferred by *L. lamottei* and *P. marinus.* Scott and Crossman (1973) described a similar habitat for I. *castaneus* larvae, although Hardisty and Potter (1971), who discussed larval lamprey habitats based on the observations reported by other investigators, concluded that there were no marked species differences in the stream areas occupied by larvae.

In previously published literature, the habitat of I. *castaneus* has been variously described as rivers and large creeks (Hubbs and Trautman 1937); medium-sized clear rivers and their chief tributaries (Hall and Moore 1954); unglaciated watersheds in Illinois where tributary streams have higher gradients and more riffles than in unglaciated areas, and have clean gravel bottoms (Starrett et al. 1960); and the main courses of moderate-sized rivers, but not the smaller tributaries (Scott and Crossman 1973).

Ichthyomyzon fossor, northern brook lamprey

This lamprey was the most abundant and widely distributed member of the genus. Nonetheless, it occurred principally as relict populations. It was collected from 31 streams tributary to Lakes Michigan, Huron, and Erie (Table 1, Fig. 4). The distribution of I. fossor in the Lake Michigan watershed extended from Carp Lake River at the Straits of Mackinac southward into Christiann Creek and the Little Elkhart and White Pigeon Rivers, which are tributaries of the upper St. Joseph River in northern Indiana. Its distribution in Lake Huron streams extended from the Cheboygan River system near the northern tip of the Peninsula, southward to the Pigeon River, a tributary to southeastern Saginaw Bay. In the Lake Erie drainage, it was represented by small, discrete populations in four streams: the Black and Pine Rivers (tributaries of the St. Clair River), and the Huron and Raisin Rivers. Its occurrence in 13 of these streams was previously reported (Table 3). In addition, Hankinson (1920) and Creaser (1925) reported its presence in the Galien River, where collections during the present study produced only larval forms of Ichthyomyzon.

A total of 1,386 adult specimens were captured, of which 1,114 were measured. The average length of 156 adults was 115 mm (range, 86-166) and that of the 958 animals in metamorphosis was 126 mm (range, 84-182).

The species occurred in 13% of 237 streams, 10% of 1,529 stream tributaries, about 21% of 19,600 km of stream, and in collections at 6% of 4,353 stations (Table 2). It probably also occurred in another 9 streams and 79 tributaries (about 970 km of stream) that yielded only larvae. It was collected in 31% of 100 streams and 18% of 840 tributaries inhabited by larval lampreys of any species.

Unlike L. lamottei and P. marinus, I. fossor rarely occurred in small stream systems, but was found most frequently in small, isolated segments of moderate-sized to large streams. Two of the smallest streams inhabited by it, the Pine and Pigeon Rivers (tributaries of Saginaw Bay), are characterized by summer low flows of 0.2 and 0.03 m3/s, and basin areas of 258 and 402 km2, respectively. In main river channels, its range overlapped more with the ranges of its two congeners than with the ranges of L. lamottei and P. marinus-typically it lived in the warmer, less rapid, lower reaches. It was present in the 10 largest river systems, which have summer flows of 0.2 to 31 m3/s, and drainage basins of 2,760 to 16,848 km^2: the Saginaw, Grand, St. Joseph, Kalamazoo, Muskegon, and Manistee Rivers (Lake Michigan): the Cheboygan, Thunder Bay, and Au Sable Rivers (Lake Huron); and the Raisin River (Lake Erie). Ichthyomyzon fossor was found less frequently in stream tributaries than L. lamottei and P. marinus, but more frequently than its two congeners. Of the 490 lam-

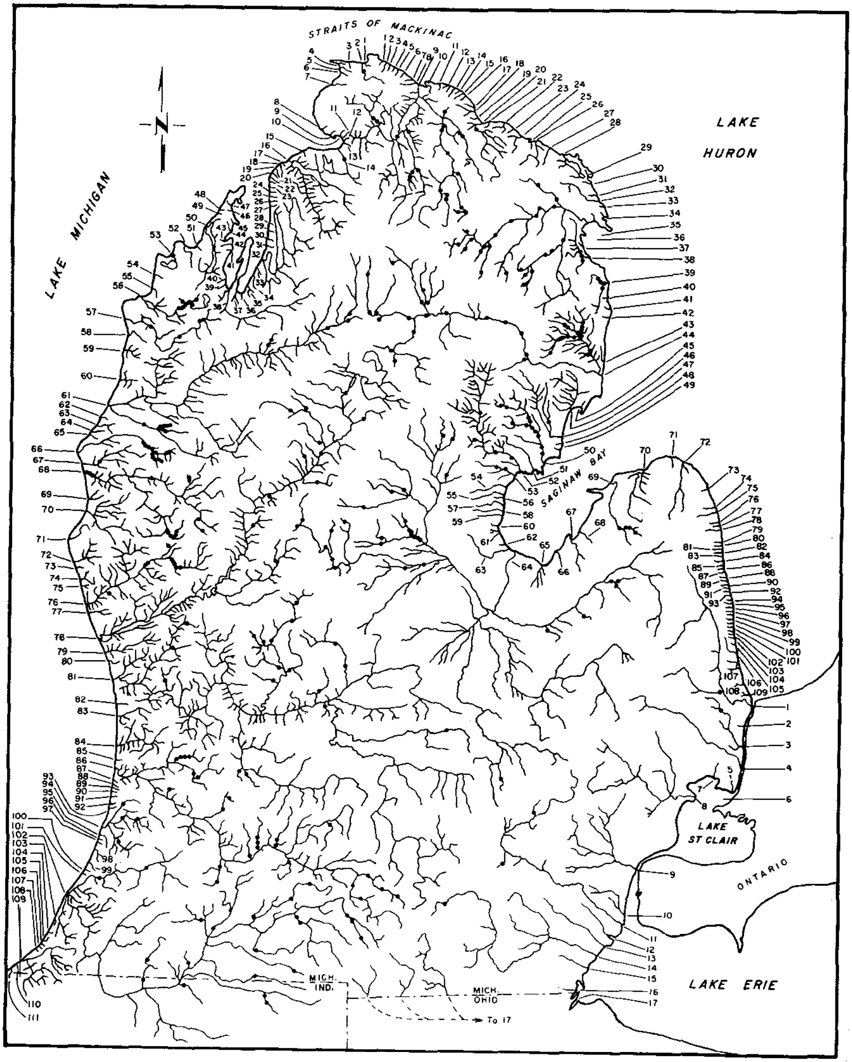

Figure 4. Distribution of metamorphosing, recently metamorphosed, or adult Ichthyomyzon fossor, by localities of capture. Each symbol represents one collection site. The numbers shown correspond to stream numbers and names in Table 1.

prey-populated tributaries that occurred downstream from dams, 10% were occupied by I. *fossor, 2%* by I. *castaneus,* and 2% by I. *unicuspis,* as compared with 89% inhabited by *L. lamottei* and 46% by *P. marinus.* Many of the stream tributaries in which I. *fossor* lived were small and had low flows. A somewhat divergent view was presented by Hubbs and Trautman (1937), who noted that I. *fossor* largely avoided both small brooks and large rivers.

Ichthyomyzon fossor was more tolerant of warm water than the other lampreys, and was preeminent in streams and tributaries that received a proportionately large surface flow of warm water from lakes, swamps, marshes, and ponds. The Thunder Bay River, which contains probably the largest population of I. fossor, and no other lampreys, is integrated with large tracts of swampland and ponded water that apparently enhance its suitability for this species. Water temperatures recorded by hand thermometers at 20 locations on all major branches from July 17 to August 9, 1.974, ranged from 14° to 25.6° C (mean 19.4°). The highest densities of larvae were usually found in the warmer sections. Similarly, the headwaters of the Au Sable River, warmed by lake surface runoff (Shetter 1968; Richards 1976), supported what was probably the second largest population. Richards (1976) also found the frequency of occurrence of Ichthyomyzon larvae higher in the warm headwaters than in the coldwater habitats of the Au Sable River, and demonstrated a reduction in numbers of these lampreys and other warmwater fishes concurrent with the trend toward an increase in the relative abundance of coldwater species between the 1920's and 1972; he hypothesized that these changes were caused by a decrease in average water temperatures after the basin was reforested and low-head impoundments were removed.

Ichthyomyzon fossor also lived in coldwater environments, though less commonly. In the upper South Branch of the Pine River, a tributary of the lower Au Sable River system inhabited exclusively by I. fossor, water temperatures were relatively low. Mean daily water temperatures during mid-June to August ranged from 14° to 20° C, with daily maxima up to 21.5° C. However, the numerous small kettle lakes and extensive swampland in the watershed indicate the possibility that higher water temperatures sometimes occur, or existed during an earlier post-glacial period. This possibility is supported by the absence of the coldwater *L. lamottei* from this large river system.

The habitat of I. *fossor* was described previously as "creeks and small rivers" (Hubbs and Trautman 1937); and "small rivers, with rather warm water, unsuitable for speckled trout *(Salvelinus fontinalis)"* (Vladykov 1949).

Ichthyomyzon unicuspis, silver lamprey

This species was collected from 16 streams and, except for the Carp Lake River which enters Lake Michigan at the Straits of Mackinac, all are in the Huron-Erie watershed (Table 1, Fig. 5). It was scattered throughout the Lake Huron drainage, ranging from the Cheboygan River in the north southward to Birch Creek, near the Lake Huron outlet. Its occurrence in the Lake Erie drainage was restricted to two tributaries of the St. Clair River, the Black and Pine Rivers. In these streams, in both of which the habitat was poor (unstable or low flows, hard clay-rubble bottoms, sedimentation, and high temperatures), larval populations were small and discrete, and confined to the most habitable sections. Remnant populations of *I. unicuspis* were present in reaches upstream from long-

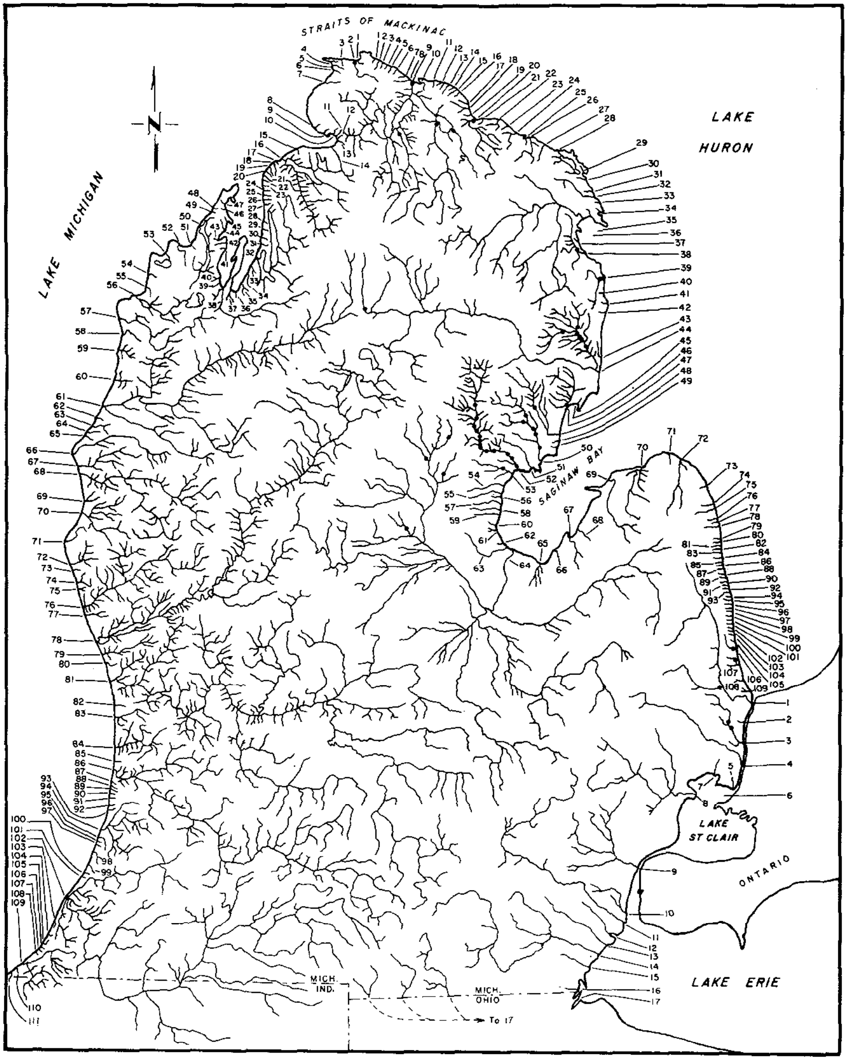

Figure 5. Distribution of metamorphosing, recently metamorphosed, or adult Ichthyomyzon unicuspis by localities of capture. Each symbol represents one collection site. The numbers shown correspond to stream numbers and names in Table 1.

established (early 1900's), permanent dams on three streams: (1) Black and Rainy Rivers (Cheboygan River system) above Alverno dam; (2) Au Sable River above Foote dam; and (3) Tittabawassee River (Saginaw River system) above Sanford and Edenville dams on the Molasses River, above Smallwood dam on the Sugar River, and above Secord dam on the East Branch of the Tittabawassee River. Each of these isolated reaches is associated with impoundments or inland lakes; although some are small, they provide habitat for host fishes. In fact, I. ***unicuspis*** was found attached to lake sturgeon *(Acipenser fulvescens)* in Black Lake (Cheboygan River system) above Alverno dam in May 1970. Trautman (1957) emphasized the erection of dams on streams after 1875 as an important causal factor in the decline of *Z. unicuspis* in Lake Erie waters of Ohio, and listed "large waters containing an abundant fish supply" as an essential ecological requirement. However, he did not mention the persistence of populations in reaches upstream from barriers. The furthest inland distribution of I. *unicuspis* observed was in the main stream of the Au Sable River. One burrowed, metamorphosing larva (126 mm long) was captured on November 8, 1974, near Grayling, 240 km upstream from the river mouth, above a series of seven dams. The four largest populations of I. *unicuspis* were in the Cheboygan, Au Sable, Rifle, and Saginaw Rivers.

The general distribution delineated in the present study agrees with that reported by Hubbs and Trautman (1937), who defined this lamprey's range in the Lower Peninsula as the northern and eastern drainage. Other workers have collected *I. unicuspis* in five streams from which it was collected during the present study, and in six other streams in the eastern drainage (Table 3). The present samples from three of these other streams-the Clinton, Maumee, and St. Clair Rivers--did, however, include larval *Ichthyomyzon.*

Of 414 adults collected, 246 were measured. The average length of the 41 spawning lampreys was 248 mm (range, 157-308) and that of the 205 metamorphosing individuals was 114 mm (range, 91-155), considerably smaller than the spawning adults.

Ichthyomyzon unicuspis was uncommon, and probably the least abundant of the five species. It occurred in 7% of 237 streams, 1% of 1,529 stream tributaries, about 3% of 19,600 km of stream, and in collections at 1% of 4,353 stations (Table 2). In addition, it probably occupied 7 streams and 20 tributaries (about 340 km of stream) from which *Ichthyomyzon* larvae were taken. Adults were observed spawning in southern Lake Huron near the narrows at the origin of one of these streams, the St. Clair River, in 1971 and 1972 (J. J. Tibbles personal communication). Of the 100 streams and 840 tributaries inhabited by larval lampreys of any species, 16% and 1%, respectively, contained I. *unicuspis*.

Ichthyomyzon unicuspis was collected in streams varying widely in size. They ranged from 0.06 to 34 m^3/s in low-water discharge, and from 21 to 16,848 km^2 in drainage area. This species, like I. *castaneus,* was most common in main river channels, and inhabited only 5% of the 238 stream tributaries in the Huron-Erie watershed that harbored larval lampreys of any species.

The habitat of *I. unicuspis* has been described by other investigators as large streams, and smaller streams for spawning (Hubbs and Trautman 1937); large rivers (St. Lawrence) and large lakes (Vladykov 1949); in Ohio, chiefly in the Ohio River and the lower portions of its larger tributaries (Trautman 1957); in Illinois, in unglaciated watersheds where tributary streams have relatively steep gradients and clean gravel bottoms (Starrett et al. 1960); generally in large lakes and rivers (Hubbs and Lagler 1967); and large rivers and lakes (Scott and Crossman 1973). Scott and

Crossman noted further that this species migrates farther upstream than I. *castaneus* in areas where the ranges of the two species overlap, but does not use the smaller streams inhabited by the nonparasitic lampreys.

Lampetra lamottei, American brook lamprey

This species was by far the most abundant and widely distributed lamprey. Almost 256,000 larvae and 1,872 adults were collected. It was present in collections from 73 streams tributary to Lakes Michigan, Huron, and Erie (Table 1, Fig. 6). This lamprey ranged along the western slope of the Lower Peninsula from French Farm Creek at the Straits of Mackinac southward to the headwaters of State Creek and Galien and St. Joseph Rivers in northern Indiana, and along the eastern slope from the Little Black River in the north southward to the headwaters of the Maumee River at the Michigan-Ohio border. It was most abundant in the Lake Michigan drainage, where 71% of the streams and 7% of the tributaries in the Lower Peninsula that it inhabited, were located. Moreover, of the 55 Lake Michigan tributaries that supported larval lampreys of any species, 94% contained *L. lamottei.* It was virtually nonexistent in the main channels of the three largest Southern Upland rivers (Grand, Kalamazoo, and St. Joseph), probably due to pollution, sedimentation, and unstable flows. It was more weakly represented in the Huron-Erie drainage, where its distribution was marked by broad gaps. In the Lake Huron drainage, large concentrations were confined to three regions, all located principally on the Northern Upland: (1) the Cheboygan-Ocqueoc drainage, (2) the Tawas-Au Gres-Rifle drainage, and (3) the upper Tittabawassee River, a subbasin of the Saginaw River. It was not collected in the large portion of the northeastern drainage that includes the large Thunder Bay and Au Sable Rivers, and the smaller yet seemingly suitable Devils and Black Rivers. In the southeastern drainage, the distribution of *L. lamottei* was limited to a few, small, widely scattered populations. It was collected in three tributaries of the Shiawassee River (Saginaw River system), Spring Creek, Miller Creek, Mill Creek, St. Clair River and delta, and Honey Creek (Huron River system), and the headwaters of the Maumee River in Michigan. The six largest populations were in the Manistee, Muskegon, Pere Marquette, Grand, and White Rivers (Lake Michigan), and the Cheboygan River (Lake Huron). The occurrence of this species in five of these streams was reported in previous studies (Table 3).

Lampetra lamottei occurred in 3 1% of 237 streams, 47% of 1,529 stream tributaries, about 43% of 19,600 km of stream, and in collections at 47% of 4,353 stations (Table 2). This species was clearly the most common lamprey in stream tributaries. Of the 100 streams and 840 tributaries occupied by larval lampreys of any species, 73% and 86%, respectively, supported populations of *L. lamottei.*

Lampetra lamottei inhabited a variety of stream types, as indicated by its widespread distribution. But it was most abundant in clear, permanent, unpolluted, pool-riffle streams that were characterized by a large proportion of groundwater inflow (with accompanying high base flow and

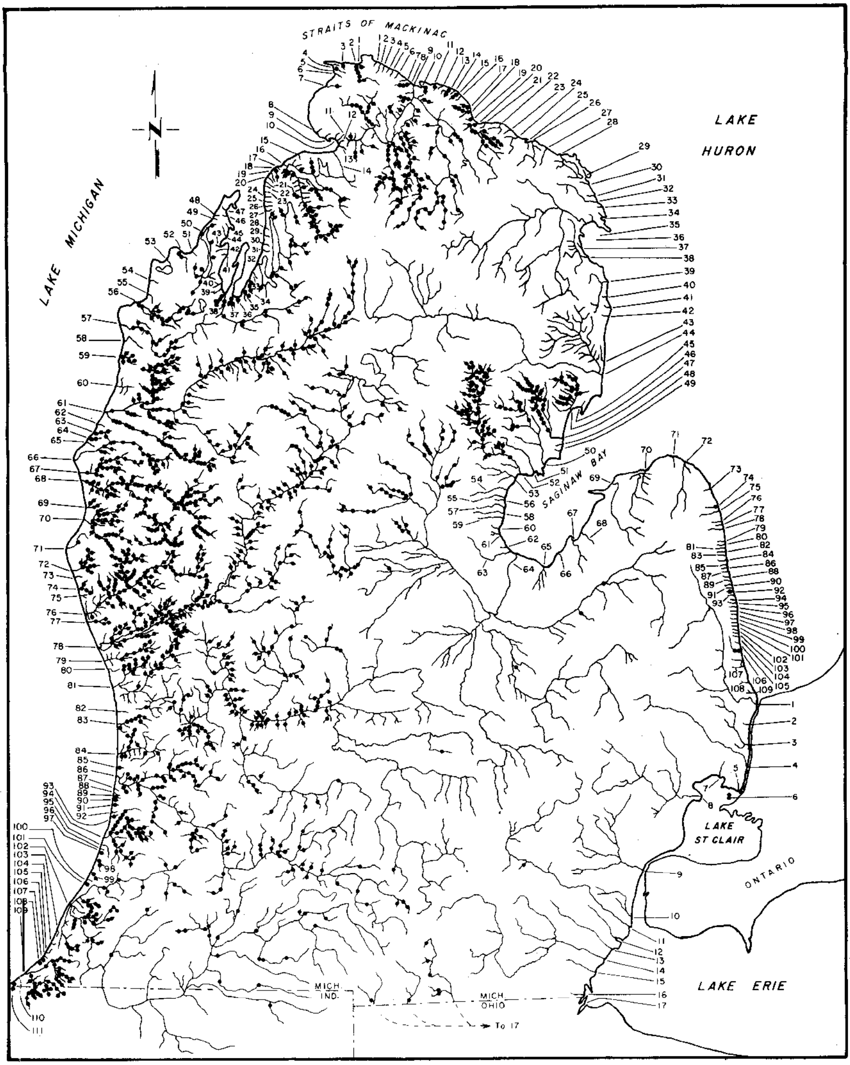

Figure 6. Distribution of larval *Lampetra lamottei* by localities of capture. Each symbol represents one to three collection sites. The numbers shown correspond to stream numbers and names in Table 1.

uniform discharge), comparatively low temperatures, and stable bottom. This stream type was common on the Northern Upland and in areas relatively undisturbed by man on both uplands and lowlands in the southern Lake Michigan drainage. It was in streams ranging from 0.03 to about 4,400 m3/s in low flows, and from 2.6 to 16,848 km* in basin area. It largely avoided warmwater habitat. The three lamprey-inhabited Lake Michigan streams that did not contain *L. lamottei* (Bear and Crystal Rivers and Cedar Creek) originate in inland lakes. Bear and Crystal

Rivers, which receive a proportionately large surface flow, have summer temperatures as high as 26.7° and 27.2° C, respectively. Possibly the upper tolerable temperatures for the species are exceeded in these two streams. In spite of its relatively high tolerance for low water temperatures, *L. lamottei* was not collected in many extremely cold, spring-fed streams and tributaries in which the environment seemed otherwise suitable for it. For example, *L. lamottei* was generally a common inhabitant in the Platte River, but one tributary, Brundage Creek, contained no lampreys. Presumably the low water temperature in Brundage Creek was the major, or only limiting factor. Mean daily water temperatures during mid-June to August 1973 ranged from 11° to 14.5° C, compared with the main channel where temperatures ranged from 16° to 26° C. The daily maximum rose above 15° C, to 16° C, only once.

The habitat of *L. lamottei* was described by other authors as small, gravelly, moderately swift creeks (Young and Cole 1900); small creeks and streams (Schaffner 1902; Radforth 1944; Hubbs and Lagler 1967); cold brooks and small rivers, usually in association with slimy sculpins *(Cottus cognatus)* and brook trout *(Salvelinus fontinalis)* (Vladykov 1949); same habitat as I. fossor and other brook lampreys, mostly in headwater streams with an average width greater than 4.5 m, composed of high-gradient areas for spawning and low-gradient reaches for larvae (Trautman 1942, 1957); and streams cooler than those preferred by I. fossor (Scott and Crossman 1973).

Petromyzon marinus, sea lamprey

The occurrence of this species in the Lower Peninsula of Michigan watershed was first documented in 1930, when an adult specimen was captured from the St. Clair River in southeastern Michigan (Hubbs and Pope 1937). Its presence ‘was later reported in Lake Michigan in 1936 (Hubbs and Pope 1937) and in Lake Huron in 1937 (Shetter 1949). Notwithstanding this lamprey’s recent invasion into the area, its larvae have become abundant and widely distributed in streams (Great Lakes Fishery Commission 1960-74). Well over 200,000 larvae were collected from 74 streams tributary to Lakes Michigan, Huron, and Erie (Table 1, Fig. 7). Their presence in most of these streams has been reported (Table 3). In addition, about 43,000 adults were captured, mainly in weirs operated on 13 streams, 12 tributaries of Lake Michigan and the Ocqueoc River, Lake Huron.

The distribution of *P. marinus* in the Lower Peninsula was conspicuously peripheral, mainly because numerous dams blocked its inland dispersal and excluded it from about 60% of the entire drainage network: major segments of the Elk, Boardman, Manistee, Big Sable, White, Muskegon, Grand, Kalamazoo, and St. Joseph Rivers of the Lake Michigan drainage; almost the entire Thunder Bay River and large portions of the Cheboygan, Au Sable, and Saginaw Rivers of the Lake Huron drainage; and the limited but more favorable headwater habitat on the interior uplands of the Lake Erie drainage. In other respects its distribution was similar to that of *L. lamottei*.

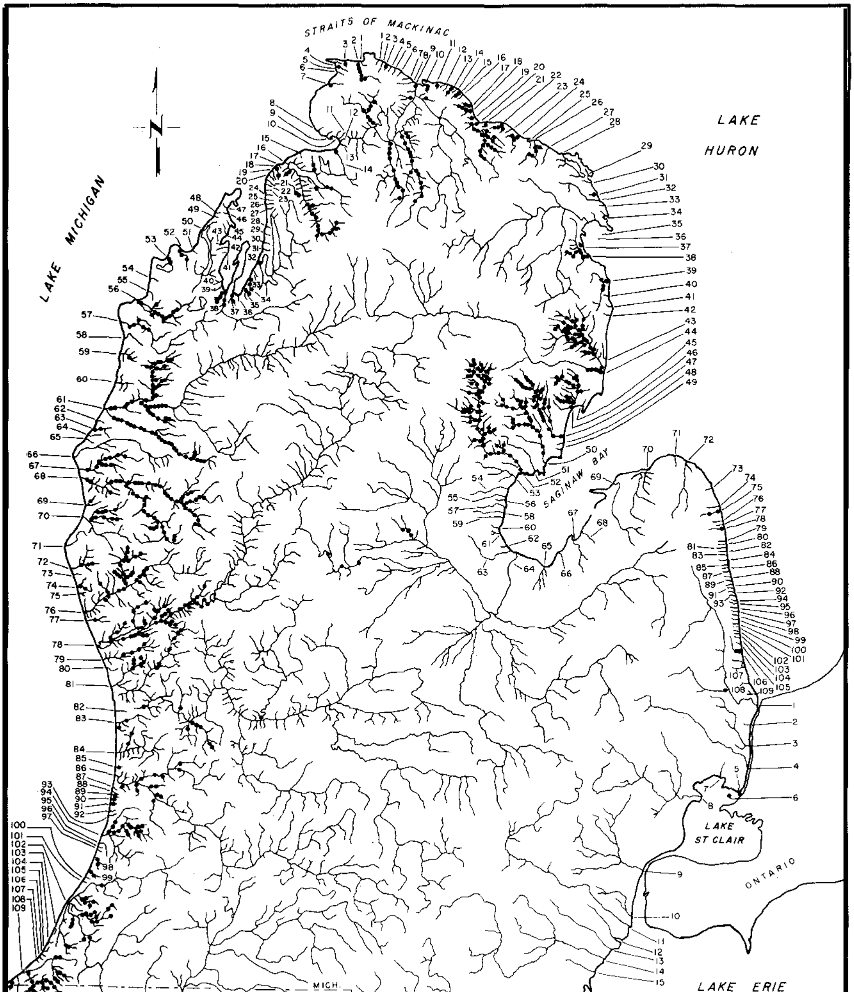

Figure 7. Distribution of *larval Petromyzon marinus* by localities of capture. Each symbol represents one to three collection sites. The numbers shown correspond to stream numbers and names in Table 1.

Petromyzon marinus was generally more abundant and widespread in the Lake Michigan watershed than in the Lakes Huron and Erie watersheds. It ranged from Carp Lake River at the northern tip of the Peninsula southward into the headwaters of the Galien River in northern Indiana. Larvae were present in 39% of 111 Lake Michigan tributaries, in comparison with 25% of 126 tributaries of Lakes Huron and Erie. Within the Lake Michigan drainage, *P. marinus* larvae were more strongly represented in streams in the northern region, being abundant and extensively distributed in sections of eight streams: Carp Lake, Pine, Platte, Betsie, Manistee, Pere Marquette, White, and Muskegon Rivers. In the other 20 northern streams inhabited by *P. marinus,* populations were small to moderate. In southern Lake Michigan streams, south of the Muskegon River, larval populations were small, occasional, and discretely distributed.

In streams of the Huron-Erie watershed, *P. marinus* larvae ranged from Cheboygan 266-20 Creek near the Straits of Mackinac southward to the St. Clair River. Nevertheless, as in the Lake Michigan drainage, year classes were produced more frequently and the larvae reached much higher densities in the northern than in the southern half of this range. In the Saginaw River basin, the largest in the Lower Peninsula, dams and ecologically marginal conditions (e.g., low and unstable flows, pollution, sedimentation, and firm substrate) limited the distribution of *P. marinus* larvae to small segments in two tributaries (Bluff Creek and Chippewa River). South of the Saginaw River, in the southern Lake Huron and Lake Erie drainages, *P. marinus* larvae were found in only five streams. They occurred rarely in Rock Falls Creek, Elm Creek, Black River, and St. Clair River, and sporadically in Mill Creek.

The five largest populations of larvae occurred in the Rifle, Au Sable, Pere Marquette, East Au Gres, and Cheboygan Rivers. The population in the Ocqueoc River may once have been as large as the ones in these streams, but the almost continuous operation of experimental control devices that blocked spawning runs since 1949 had undoubtedly reduced the population density by the time the present study was begun (V. C. Applegate personal communication).

Petromyzon marinus larvae occupied more streams but fewer stream tributaries and fewer kilometers of stream than the larvae of either *Ichthyomyzon* or *L. lamottei* (Table 2). They occurred in 31% of 237 streams, 15% of 1,529 stream tributaries, about 14% of 19,600 km of stream, and in collections at 23% of 4,353 stations. They were collected from 74% of 100 streams and 27% of 840 tributaries containing larval lampreys of any species.

Petromyzon marinus exhibited more adaptability than the other species, using a wide variety of stream types and habitats for spawning and larval nurseries. Its larvae inhabited streams with low flows ranging from 0.03 to about 4,400 m^3/s, and with basins of 2.6 to 16,848 km^2. The median summer-low flow of 74 streams supporting larvae was 0.4 m^3/s. In the State of Michigan streams in the Lake Superior drainage. Stauffer and Hansen (1958) found larvae more frequently in streams with volumes over 0.8 m^3/s than in those with volumes less than 0.3 m^3/s, although Thomas (1962) noted their presence in Great Lakes tributaries with volumes less than 0.03 m^3/s. Except where limited by dams and unsuitable habitat, larvae in the Lower Peninsula were widely distributed in streams, occurring in both main streams and tributaries, from their mouths to their headwaters. In the Lake Superior drainage, Stauffer and Hansen (1958) found them mostly in main streams.

Although *P. marinus* adults are poor swimmers, with a low endurance in comparison to most teleosts (Beamish 1974), they ascended streams for fairly long distances during spawning migrations. The larvae farthest upstream were found in the Chippewa River (a Saginaw River tributary) near Weidman, 181 km upstream from the main river mouth. Larvae were also found at considerable distances upstream from river mouths in 11 other river systems: Manistee (106 km), Pere Marquette (141 km), White (75 km), Muskegon (80 km), Grand (168 km), Kalamazoo (78 km), Cheboygan (79 km), Au Sable (70 km), East Au Gres (69 km), Au Gres (90 km), and Rifle (118 km). The low gradients in these rivers probably facilitated the long migrations of adult lampreys.

The habitat preference of *P. marinus* was similar to that of *L. lamottei.* Both species were relatively abundant in cool, pool-riffle streams with high water quality, stable and high base flows, and low sediment discharge as typified by most streams on the Northern Upland, but *P. marinus* seemed to be more restricted by low water temperatures, and occurred less frequently in stream tributaries than *L. lamottei.* Thomas (1962) also reported that the habitat and distribution of these two species were similar. Stauffer and Hansen (1958) reported that *P. marinus* larvae in Michigan streams of the Lake Superior drainage were most numerous in streams with summer water temperatures of 10° to 26.1° C and rarely occurred in cool spring-fed streams where brook trout and slimy sculpins were abundant. The restriction of *P. marinus* larvae to habitats where water temperatures during the season of spawning and embryonic development are in the "intermediate" range is undoubtedly due in part to the failure of embryos to develop successfully at temperatures outside this range. Laboratory experiments demonstrated that *P. marinus* embryos developed successfully only within a narrow water temperature range-at constant temperatures of 15.5° to 21.1°C (Piavis 1961) and 15° to 25° C (McCauley 1963), and fluctuating temperature ranges of 18.4° to 23.9° C and 15.5° to 21.1° C (Piavis 1971). *P. marinus* exhibited a greater tolerance than *L. lamottei* to unstable stream flows. In the Manistee and Muskegon Rivers, in courses below hydroelectric dams where daily flows fluctuated severely, *P. marinus* was abundant, whereas *L. lamottei* larvae, though numerous in the upper areas, were sparse. Moreover, of the 18 small streams on the Cheboygan Lowland that had seasonally unstable flows and supported larval populations, all were inhabited by *P. marinus* but only 11 by *L. lamottei;* furthermore, *P. marinus* was abundant in 10 of these streams, but *L. lamottei* in only 4.

The habitat of *P. marinus* in Great Lakes tributary streams has been described by previous investigators chiefly in terms of spawning (Coventry 1922; Gage 1928; Shetter 1949; Loeb and Hall 1952; Loeb 1953), spawning and larval populations (Applegate 1950; Wigley 1959; Manion and McLain 1971), and larval populations (Stauffer and Hansen 1958; Hansen and Hayne 1962; Smith and McLain 1962).

The highly adaptable character of *P. marinus* was demonstrable in its parasitic phase as well. Although regarded as an inhabitant of large lakes during its adult feeding stage (Applegate 1950), it was found parasitizing host fishes in three small (< 1 ha) artificial ponds. These privately owned impoundments, used for holding rainbow trout *(Salmo gairdneri),* were interconnected with small tributaries of the Manistee, East Au Gres, and Tawas Rivers. Since the ponds adjoined segments of the stream inhabited by larvae, the lampreys presumably entered the ponds naturally as larvae or as recently metamorphosed adults through inlets and remained in the ponds as feeding adults. Of three specimens captured and measured, one 480 mm long was taken from the pond on Big Beaver Creek (Manistee River) on August 3 1, 1971, and two from a pond on upper Cold Creek (Tawas River&one 441 mm long on July 3, 1974, and one (metamorphosis incomplete), 167 mm long, on August 27, 1974. The predation on trout by *P.* marinus in a pond on Sand Creek (East Au Gres River) during the early 1960's was reported by Arthur Leitz (personal communication).

Longitudinal Distribution in Four Streams

Patterns of intrastream distribution of species varied among streams and were broadly correlated with the diversity and availability of habitats. The distribution and relative abundance of different species changed longitudinally from mouth to source in most streams that contained more than one species. Typically, *I. castaneus* and I. *unicuspis* were more common in the lower sections of main streams and comparatively large tributaries, and diminished progressively upstream, where they were replaced by *L. lamottei* and *P. marinus. Ichthyomyzon fossor* occurred in main streams but more typically as relict populations in small, warmwater tributaries and warm headwaters. Larval lampreys lent themselves well to distributional studies because of their basically sedentary habits and lack of gross changes in seasonal abundance.

Linear succession of species was abrupt in some streams but gradual, with extensive overlapping, in others. To demonstrate species succession, I explored the distribution of lampreys in detail in the main streams of three rivers (Pere Marquette, Platte, and Rifle) and in one tributary (Little South Branch of the Pere Marquette River). To compare species zonation within each of these streams, I divided all larval lampreys captured into two groups, representing species collected in the lower river and those collected in the upper river. The boundary between the lower and upper courses was selected as the point where the greatest change occurred in species composition and the physical environment.

The differential distribution of larval lamprey populations throughout the linear extent of a stream has not been previously detailed. Hall (1963), in addition to reporting an upstream distributional limit for *I. castaneus,* also suggested a downstream attenuation of this species in the upper Manistee River, though he found it difficult to establish with certainty. Stauffer and Hansen (1958) reported a close association (no noticeable segregation) of larval lampreys *(Ichthyomyzon, L. lamottei,* and *P. marinus)* in Michigan tributaries of Lake Superior. However, the spatial or ecological segregation of lampreys within river systems has been reported by many others (Enequist 1937; Hubbs and Trautman 1937; Vladykov 1950; Hall and Moore 1954; Trautman 1957; Bailey 1959;

Zanandrea 1961; Zhukov 1965; Rembiszewski 1968; Hardisty and Potter 1971; Scott and Crossman 1973). It was typically noted that nonparasitic lampreys occupied the upper reaches and parasitic lampreys the lower reaches of streams in which both occurred.

Pere Marquette River

The Pere Marquette River is a large, principally coldwater stream (Hendrickson and Doonan 1971, 1972b) which lies largely on interior uplands in the west-central region of the Lower Peninsula and enters Lake Michigan at Ludington. It has a summer flow of 6 m^3/s and a basin area of 1,971 km^2. The lower main river crosses mostly flat topography--first till plains and then ancient lake bed (Martin 1955) - whereas the upper main river courses through rolling land, chiefly outwash and moraines. Gross physical differences between the lower and upper river are gradient, bottom composition, and thermal characteristics (Table 4). Water temperatures in the lower and upper rivers were similar, although maximum daily temperatures during April to August 1973, which includes the season of spawning and embryonic development for all lamprey species, ranged from 0.4 to 2.9 Celsius degrees (mean difference 1 Celsius degree) higher in the lower river than in the upper river.

Ichthyomyzon castaneus, I. fossor, L. lamottei, and *P. marinus* inhabited the main stream. The percentage composition of *Ichthyomyzon* larvae was highest in the lower river and attenuated upstream, whereas that of both *L. lamottei* and *P. marinus* was highest in the upper river (Fig. 8). In the lower 34 km, represented by six collecting sites, *Ichthyomyzon* was dominant in all samples; the combined collections of 1,115 larvae (taken by electrofishing and application of lampricide) consisted of *89% Ichthyomyzon, 8% L. lamottei,* and *3% P. marinus.* In the upper 61 km of the main stream, conversely, lampreys at 9 of the 12 collecting stations were dominated by *L. lamottei* and *3* by *P. marinus:* the combined collection of 6,091 larvae consisted of *21% Ichthyomyzon, 54% L, lamottei,* and 25% *P. marinus.* There was a highly significant correlation between the distance above the stream mouth and the percentage composition of *Ichthyomyzon* and *P. marinus,* whereas there was no such correlation for *L. lamottei.*

Most of the *Ichthyomyzon* larvae in the main stream were undoubtedly *castaneus:* of the total of *924 Ichthyomyzon* adults taken from the main stream in 1962-72,99% were *castaneus* and only 1% were *fossor.*

The spatial segregation of larval lampreys was also apparent in tributaries of the Pere Marquette River, as it was in most other stream systems. Its 37 lamprey-inhabited tributaries were occupied exclusively as follows: *I. castaneus, I. fossor, L. lamottei,* and *P. marinus* (1); I. *fossor* (II); *I. fossor, L. lamottei,* and *P. marinus (2); Ichthyomyzon* and *L. lamottei* (1); *Ichthyomyzon, L. lamottei,* and *P. marinus* (1); *L. lamottei* **(25);** and *L. lamottei* and *P. marinus (6). Two of these tributaries were* above man-made barriers which blocked the upstream migration of lampreys. Generally, in streams and tributaries inhabited by larvae of more than one species, the overlapping of species was greatest in the middle to

Table 4. Comparison of species dominance and some physical characteristics of the lower and upper sections of four streams in the Lower Peninsula of Michigan.

Stream	Predominant species	Topography and predominant surface formation of basin[a]	Major habitat[b]	Predominant bottom materials[c]	Average gradient (m/km)	Water temperature (°C)[d]	
						Mean daily range	Daily maximum
Pere Marquette River							
Lower	*Ichthyomyzon* spp. (mostly *I. castaneus)*	flat; till plains and ancient lake bed	LC,P	S	0.3	15.5-22	22.5
Upper	*Lampetra lamottei* and *Petromyzon marinus*	rolling; outwash and moraine	P,R	S,G	0.7	14-20	21.5
Little South Branch Pere Marquette River							
Lower	*L. lamottei*	rolling; outwash and moraine	P,R	S,G	1.6	14.5-20	21.5
Upper	I. *fossor*	rolling; swamp/marsh	P	S	0.8	17.5-27	31
Platte River							
Lower	*P. marinus* and *L. lamottei*	rolling; outwash and moraine	P,R	S,G	2.5	16.5-22.5[e]	25[e]
Upper	*I. fossor*	rolling; outwash plain pocked with numerous ice block lakes and swamps	P,R	S,G	2.0	20.5-25.5	26
Rifle River							
Lower	*Ichthyomyzon* spp. (mostly *I. unicuspis)*	flat; clayey lowland plains	LC,P,R	S,G	0.6	16.5-23.5	26
Upper	*P. marinus*	rolling and hilly; outwash, moraines and lake bed	P,R	S,G	1.0	14-20.5	22

a Source: McNamee (1930) Martin (1955), Hendrickson and Doonan (1971, 1972a).
b LC = large channel, P = pools, R = riffles.
c G = gravel, S = sand.
d Based on temperatures recorded with thermographs during the high water-termperature season of 1973, mid-June to August.
e Stream temperatures 1 km downstream from thermograph, as influenced by discharge from coldwater Brundage Creek, were 2-6 Celsius degrees lower during the recording period, based on occasional readings with a pocket thermometer.

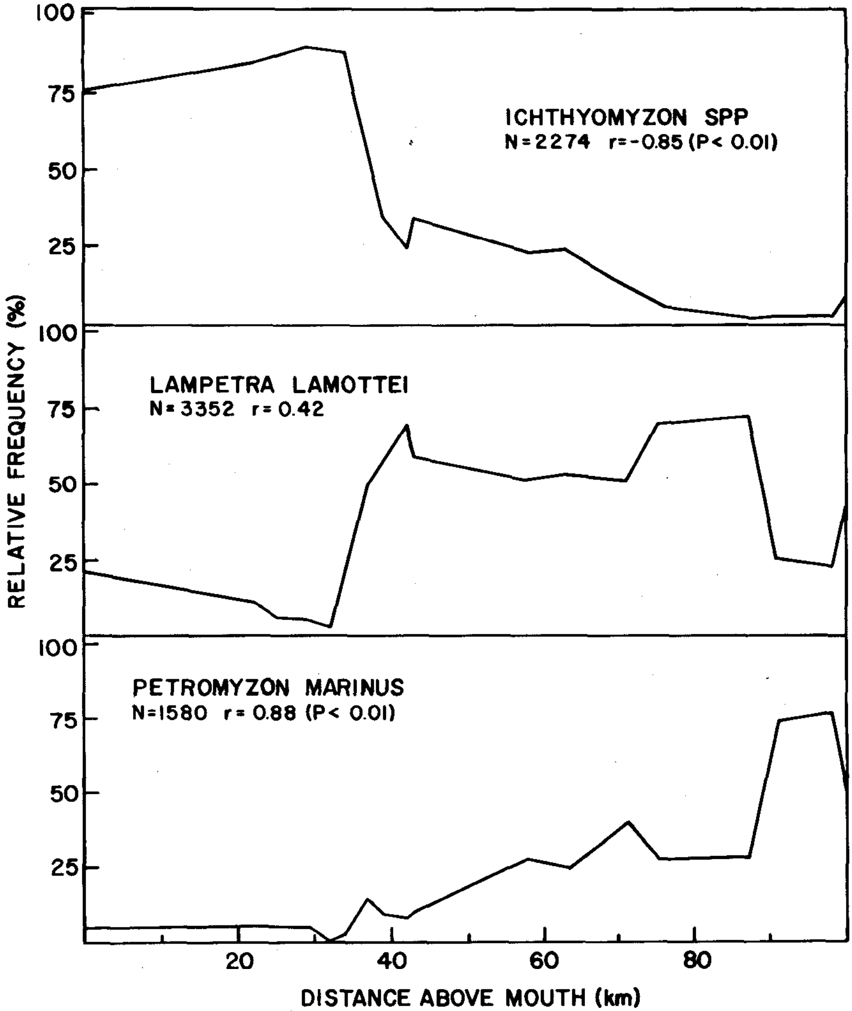

Figure 8. Longitudinal distribution of larval lampreys (percentage collected at different stations) in the main stream of the Pere Marquette River, 1968.

lower reaches and least in the upper reaches. From the mouth to the headwaters in 10 tributaries of the Pere Marquette River, populations graded from two species to one in 7 tributaries, from three species to two in 2, and from three species to one in 1 tributary. As in the main stream of the: Pere Marquette River, these longitudinal differences in species distribution were correlated with changes along an environmental gradient from the lower to the upper sections of the tributaries.

Little South Branch of the Pere Marquette River

The Little South Branch has a summer low flow of 2 m^3/s and a basin area of 272 km^2. There are major physical differences between its upper and lower reaches (Table 4). The upper river runs largely through an upland swamp-marsh (Oxford Swamp): and is characterized generally by moderate currents, pools but no riffles, and principally sand-silt bottom with sparse and widely scattered gravel. Stream temperatures were high and unstable, with wide daily fluctuations. In contrast, the lower river traverses comparatively high ground of flat and undulating outwash and moraines (Martin 1955), and is distinguished by generally swift currents and pool-riffle habitat throughout. It was materially cooled by discharge from groundwater and spring-fed tributaries, consequently water temperatures were lower and more stable. Maximum daily temperatures in April-August 1973 in the lower river ranged from 0.3 to 10.3 Celsius degrees (mean difference 5.2 Celsius degrees) lower than in the upper river.

This tributary was inhabited by *I. fossor, L. lamottei,* and *P. marinus.* Since the upper river was considerably warmer than the lower river, distribution of the lampreys was generally inverted in comparison with their distribution in the main stream (Fig. 9). Species composition of the total catch of 511 specimens taken at the four stations in the lower river was 5% *Ichthyomyzon,* 81% *L. lamottei,* and 14% *P. marinus,* whereas in the total catch of 767 specimens collected at the three stations in the upper river, 7170 were *Ichthyomyzon,* 27% *L. lamottei,* and 2% *P. marinus.* There was no significant correlation between percentage composition of each species and distance above the stream mouth.

Platte River

The Platte River is largely a coldwater stream with a summer flow of 3.5 m^3/s and a basin area of 482 km^2; it lies chiefly on outwash and morainal deposits (Martin 1955) on the Northern Upland in the northwestern region of the Peninsula, and enters Lake Michigan near Frankfort. Major physical differences were apparent between the upper, or I. *fossor* zone and the lower, or *L. lamottei-p. marinus* zone (Table 4). The most prominent difference between these two reaches was water temperature which, because it was high in the upper course presumably limited the upstream extension of *L. lamottei* and *P. marinus,* and, conversely, because it was low in the lower course, it presumably restricted the downstream extension of I. *fossor.* Maximum daily temperatures in April-August 1973 were from 0.1 to 4.1 Celsius degrees (mean difference 0.7 Celsius degree) higher in the upper river than in the lower river.

In this stream, I. *fossor* was restricted largely to the warmer, upper main stream below the Lake Ann outlet, and the warmwater tributaries that drain Woodcock, Ransom, Bellew, and Big Mud Lakes. In the lower main stream, which is cooled substantially by springs and spring-fed tributaries, and in the coldwater tributaries, it was replaced by *L. lamottei* and *P. marinus.* The distributional pattern (Fig. 10) was similar to that in

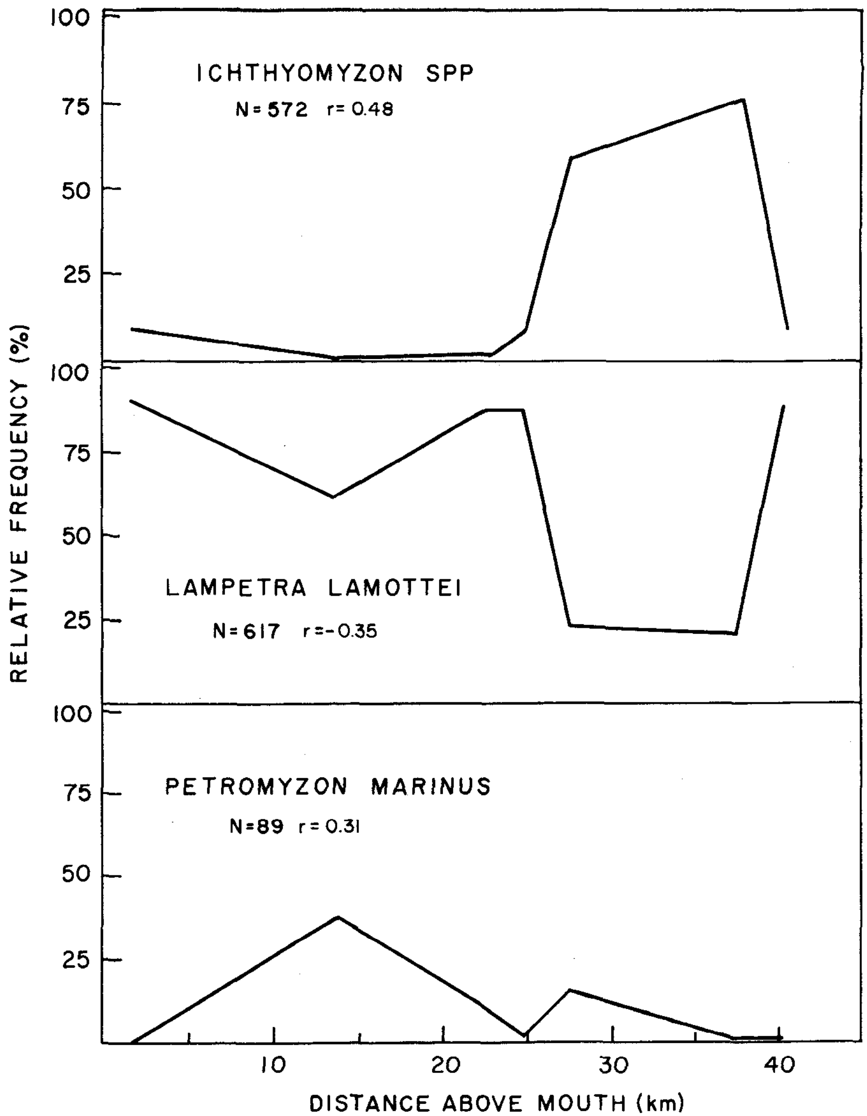

Figure 9. Longitudinal distribution of larval lampreys (percentage collected at different stations) in the Little South Branch of the Pere Marquette River. The four stations in the lower river (lower 30 km) were sampled during the initial lampricide treatment in 1964, whereas the three stations in the upper river (untreated except for the lower 3 km) were sampled in 1973-74.

the Little South Branch of the Pere Marquette River, and also conformed to a reversed temperature gradient in the stream. Species composition of the total collection of 1,409 larvae taken at the six stations in the lower river was 2% *Ichthyomyzon,* 44% *L. lamottei,* and 54% *P. marinus,* as

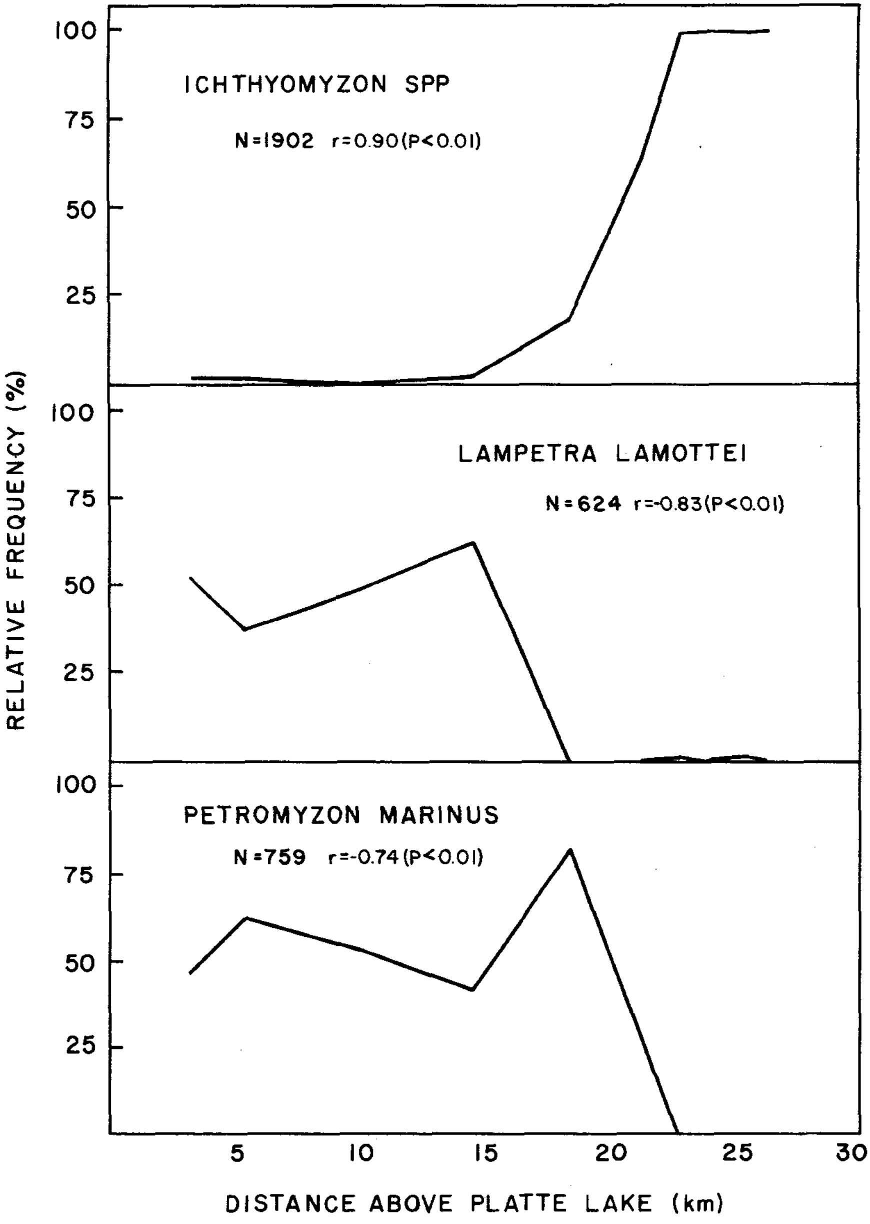

Figure 10. Longitudinal distribution of larval lampreys (percentage collected at different stations) in the main stream of the Platte River, 1960-75. A permanent fish weir was erected about 16 km above Platte Lake in 1967, blocking further upstream migration of lampreys.

opposed to that of the total collection of 1,876 larvae from the five stations *in the* upper river, which consisted of *99.7% Ichthyomyzon, 0.3% L. lamottei,* and no *P. marinus.* There was a highly significant correlation between species composition and distance above the stream mouth.

Since the only adult forms of *Ichthyomyzon* observed or captured in the upper stream were fossor, and the habitat there (warmwater lake outlet) is typical for this species, it is likely that all the *Ichthyomyzon* larvae were of this species. *Ichthyomyzon castaneus* has been taken from the main stream below Platte Lake, but there were no reports of I. *castaneus,* or of lamprey parasitism on fishes, upstream from Platte Lake (Walter C. Houghton and Bernard Ylkanen personal communications).

Rifle River

The Rifle River discharges into Saginaw Bay (Lake Huron). It has an average summer low flow of 3 m^3/s and a basin area of 1,006 km^2. Its headwaters and upper main stream lie principally on the Northern Upland and are essentially coldwater habitat (Hendrickson and Doonan 1972a, 1972b). The lower main stream, however, traverses the flat, clayey Saginaw Bay Lowland Plains and is chiefly warmwater habitat. Maximum daily temperatures in the lower river during April 19 to August 22, 1973, ranged from 0.6 to 6.1 Celsius degrees (mean difference 2.9 Celsius degrees) higher than in the upper river. As in the Pere Marquette River main stream, the upper Rifle River *(L. lamottei-P. marinus* zone), compared with the lower river *(Ichthyomyzon* zone), featured a higher gradient, more riffles, and greater bottom stability with less shifting sand (Table 4).

The four lampreys in this stream-I. *fossor, I. unicuspis, L. lamottei,* and *P. marinus-occurred* in longitudinally restricted ranges in relation to physical features of the stream, as did the species in the Pere Marquette and Platte Rivers. *Lampetra lamottei* and *P. marinus* predominated in the upper river, and were replaced by *Ichthyomyzon* in the lower river (Fig. 11) *Ichthyomyzon* were numerically dominant in 9 of 10 samples taken at the five stations in the lower 38 km; the total collection (by electrofishing and with lampricide) of 2,168 larval lampreys comprised 61% *Ichthyomyzon,* < 1% *L. lamottei,* and *39% P. marinus.* Conversely, of 19 samples collected at the 10 stations in the upper 55 km, 17 were dominated by *P. marinus* and *2* by *Ichthyomyzon.* The combined catch of 5,001 larvae contained 11% *Ichthyomyzon,* 17% *L. lamottei,* and *72% P. marinus.* There was a highly significant correlation between the relative abundance of each species and distance from the stream mouth. The total of 129 adult *Ichthyomyzon* collected from, or observed in, the main stream during 1967-75 consisted of *9% fossor* and 91% *unicuspis,* suggesting that most of the larvae were *unicuspis.* The distributional pattern of lampreys in the Rifle River matched generally the one in the main stream of the Pere Marquette River, except that in the upper Rifle, *P. marinus* was relatively more abundant than *L. lamottei.*

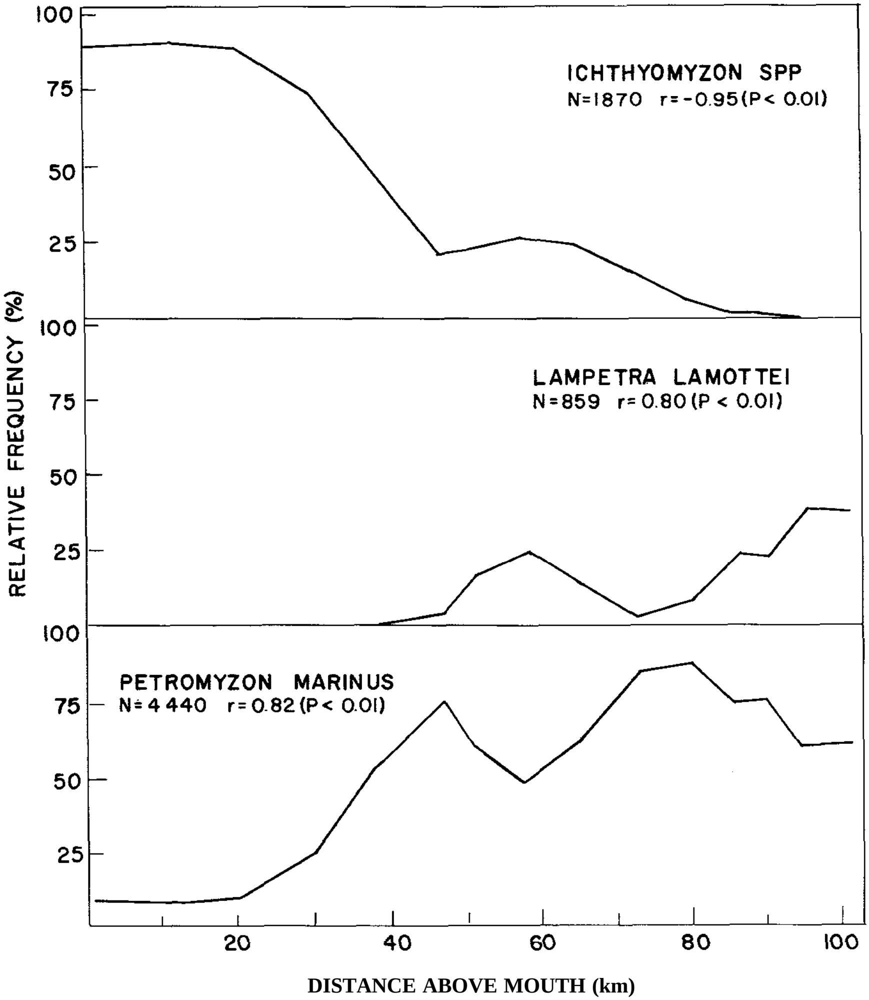

Figure 11. Longitudinal distribution of larval lampreys (percentage collected at different stations) in the main stream of the Rifle River, 1968-1969.

Inter-petromyzontine Associations

Major factors influencing differences in the species composition of lamprey populations among streams (Tables 1 and 5) were the presence or absence of dams, and differences in habitat preferences, habits, and migratory capacities of the lamprey species. Streams with highly diverse habitats contained more species than streams with less diversity, and distribution patterns within streams reflected the spatial arrangement of habitats. Thus, small, simple, environmentally homogeneous streams often contained one species or none, and large, complex, heterogeneous streams often contained three or four.

The lamprey species were geographically sympatric but tended to be ecologically separated, except that I. *castaneus* and *I. unicuspis,* whose ranges did not overlap, used similar stream habitats for reproduction and mu-series. Consequently there were no stream populations that contained all five species. That the populations of different species were separated was clearly evident. Of the total stream territory occupied by larval lampreys, 22% of 100 streams, 60% of 840 tributaries, and about 48% of 10,931 km of stream contained only one species (Table 5). An additional 5 streams, 18 tributaries, and 358 km of stream were inhabited by the larvae of one genus *(Ichthyomyzon),* in which species were unknown. Two-species populations were the most common in stream systems (33% of the lamprey-producing streams), whereas single-species populations were the most common in tributaries of streams (27% of the lamprey-producing tributaries). Furthermore, single-species populations occupied more linear kilometers of stream (52% of the total linear kilometers of lamprey-inhabited streams) than the multi-species populations. Four-species populations were the least common.

Intrastream segregation varied according to the suddenness of change in physical habitats. Where habitat division was indistinct (e.g., along a slowly changing environmental gradient from the headwaters to the mouth of a stream, as in the main channels of the Pere Marquette and Rifle Rivers), segregation was subtle, and shifts in species presence and dominance changed gradually to conform to changes in the environment. The middle river separated the uppermost, coldwater, *L. lamottei* habitat from the lowermost, warmwater *Ichthyomyzon* habitat. On the other hand, at the common boundary of two extremely diverse habitats, species populations were truncated and segregation was abrupt. This was demonstrated in two Pere Marquette River tributaries. Warmwater Bray Creek, a lake outlet that contained a monospecific population of I. *fossor,* joins the upper Baldwin River, a spring-fed coldwater section that was inhabited by a monospecific population of *L. lamottei.* These two populations did not overlap, each being confined to its special habitat. Habitats where these two species did overlap may be thermally transitional.

The parasitic lampreys as a group exhibited greater sympatry than did the nonparasitic lampreys (Table 5); 93% of the streams and 92% of the tributaries occupied by parasitic lampreys were inhabited by two or more species, as compared with 85% of the streams and 44% of the tributaries inhabited by nonparasitic lampreys. These differences reflect the tendency of the nonparasitic species to occupy headwaters allopatrically and main streams sympatrically, and the parasitic species, partilcularly *I. castaneus* and *I. unicuspis,* to avoid small streams and the headwaters and small tributaries of large streams.

Lampetra lamottei occurred more frequently in single-species popula&ions than the other species. It existed alone in 12 (17%) of 73 streams, 433 (60%) of 726 tributaries, and 3,845 (45%) of 8,496 km of stream. Of these 433 tributaries, 425 were components of 34 streams containing two

Table 5. Lamprey associations by the number of species (or genera) in streams of Michigan's Lower Peninsula.
[I = Ichthyomyzon spp., Ic = I. castaneus, If = I. fossor, Iu = I. unicuspis, Ll = Lampetra lamottei, Pm = Petromyzon marinus.]

Species or genus[a]	Number of streams	Number of tributaries			Kilometers of stream[b]			Number of stations		
		Below dams	Above dams	Total	Below dams	Above dams	Total	Below dams	Above dams	Total
One species										
Ic	5	7	11	18	188	170	358	79	78	157
Ic	0	0	2	2	2	126	128	4	8	12
If	3	10	44	54	187	947	1,134	31	82	113
Iu		0	0	0	15	0	15	8	1	9
Ll	12	227	206	433	1,211	2,634	3,845	614	359	973
Pm	6	19	0	19	150	0	150	147	0	147
Total	27	263	263	526	1,753	3,877	5,630	883	528	1,411
Two species										
I^c + Ll		10	28	38	66	398	464	72	134	206
I^c + Pm	**4**	8	0	8	70	0	70	73	0	73
*zc + **If***	**0**	0	3	3	0	190	190		5	6
*zc + **Ll***	**0**		4	5	3	82	85	2	15	17
Ic + Pm	**0**	*0*	0	0	0	0	*0*	3	0	3
If + Iu	**2**	*0*	0	0	11	200	211		2	**3**
If + Ll		7	39	46	116	851	**967**	21	68	**89**
If + Pm	2	5	0	5	44	0	44	18	0	18
Iu + Ll	0	0	**1**	1	0	14	14	0	0	**0**
Iu + Pm	0	*0*	**0**	0	35	0	35	8		**8**
Ll+Pm	28	127	0	127	952	0	952	481	8	481
Total	38	158	75	233	1,297	1,735	3,032	680	224	904

Three species										
Ic + Il Pm	8	35	0	35	397	0	397	214	0	214
Ic + If, Ll	1	0	9	9	34	726	760	1	10	11
Ic + I. Pm	0	0	0	0	0	0	0	0	0	0
Ic + Ll, Pm	2	5	0	5	205	0	205	25	0	25
If + Iu, Ll	0	1	3	4	0	72	72	0	3	3
If + Iu,Pm	4	5	0	5	100	0	100	11	0	11
If + Ll, Pm	1	16	0	16	134	0	134	24	0	24
Iu + Ll, Pm	2	0	0	0	34	0	34	9	0	9
Total	18	62	12	74	904	798	1,702	284	13	297
Four species										
Ic + If, Ll, Pm	10	4	0	4	362	0	362	6	0	6
Iu + If, Ll, Pm	7	3	0	3	205	0	205	3	0	3
Total	17	7	0	7	567	0	567	9	0	9
No lampreys	137	473	216	689	4,003	4,721	8,724	1,263	469	1,732
Grand Total	237	963	566	1,529	8,524	11,131	19,655	3,119	1,234	4,353

[a]No five-species populations found.
[b]Linear distance.
[c]Species unknown, no adult forms.

or more species. Because of its abundance and widespread distribution, *L. lamottei* was also one of the most common affiliates of other lamprey species (Table 6).

The strongest mutual association between any two species, on the basis of number of streams and tributaries occupied by both, was that between *L. lamottei* and *P. marinus;* they cohabited 58 streams and 190 tributaries. Of these, 28 streams and 127 tributaries contained no other species. In kilometers of stream occupied, however, *L. lamottei* overlapped somewhat more with I. fossor than with *P. marinus* (Table 5). The comparatively high degree of overlap between *L. lamottei* and *P. marinus* probably reflects their selection of common habitats, superior adaptability to prevailing habitats, broad distribution, and general numerical abundance. The 28 streams inhabited exclusively by *L. lamottei* and *P. marinus* are small, coastal systems scattered along the western and northeastern shoreline, and 20 (71%) are in the Lake Michigan drainage. Generally, *P. marinus* overlapped exclusively with *L. lamottei* in the smaller, cooler streams and tributaries; and with both *L. lamottei* and *Ichthyomyzon* in main stream habitat and the warmer, larger tributaries. Exclusive overlapping of *P. marinus* and *Ichthyomyzon* was restricted almost entirely to streams that lacked *L. lamottei;* and with the exception of the Bear and Crystal Rivers, all are in the Huron-Erie drainage. Most heterospecific populations not containing *P. marinus* occurred in sections upstream from dams which stopped spawning runs.

According to stream kilometers inhabited, overlapping between *Ichthyomyzon* and *L. lamottei* was greater in the Lake Michigan watershed (76%) than in the Huron-Erie watershed (24%); likewise, *Ichthyomyzon* and *P. marinus* overlapped more in the Lake Michigan drainage (59%) than in the Huron-Erie drainage (41%). However, 79% of the linear kilometers occupied exclusively by *Ichthyomyzon* and *L. lamottei* were in the Lake Michigan drainage, whereas 93% of the linear kilometers occupied exclusively by *Ichthyomyzon* and *P. marinus* occurred in the Huron-

Table 6. Most common affiliate of each species according to the number of streams, tributaries, and kilometers of stream occupied.

	Most common affiliate		
Species	Streams	Tributaries	Kilometers of stream
Ichthyomyzon spp. (collectively)	*P. marinus*	*L. lamottei*	*L. lamottei*
I. castaneus	*L. lamottei*	*L. lamottei*	*L. lamottei*
I. fossor	*P. marinus*	*L. lamottei*	*L. lamottei*
I. unicuspis	*I. fossor* and *P. marinus*	*I. fossor*	*I. fossor*
Lampetra lamottei	*P. marinus*	*P. marinus*	*I. fossor*
Petromyzon marinus	*L. lamottei*	*L. lamottei*	*L. lamottei*

Erie drainage. This difference reflects largely the poorer representation of *L. lamottei* in the eastern drainage. Among sympatric species, *L. lamottei* and *I. unicuspis* were found together least often-principally because of differences in habitat occupied and the discrete distribution and relatively low abundance of I. *unicuspis.*

Lampreys in Lentic Habitats

Larval lampreys were detected in lakes off the mouths of 22 of 57 streams and tributaries examined (Table 7). Nine of these lentic areas were occupied by *Ichthyomyzon,* 13 by *L. lamottei,* and *20* by *P. marinus.* The presence of *P. marinus* in 18 of these areas has been reported (Great Lakes Fishery Commission 1966-74). Larval lampreys have been collected from similar habitats in other sections of the upper Great Lakes (Thomas 1960, 1962; Great Lakes Fishery Commission 1961-74; Wagner and Stauffer 1962a, 1962b; Hansen and Hayne 1962; Gaylord and Smith 1966; Manion 1969).

Most lacustrine populations were small and limited to areas of less than 5 ha. Because the surveys were oriented toward locating *P. marinus,* most were conducted off the mouths of streams inhabited by this species. Furthermore, by the time the search for lake-dwelling larvae in the study area was begun in earnest (1969), most *P.* marinus-inhabited streams already had been treated with lampricides from one to three times over a 3- to 5-year interval. Possibly, therefore, fewer lentic areas were inhabited, and lampreys when present were less abundant during the surveys than in the precontrol period due to the drastic reduction of populations in source streams by lampricide treatment.

Lake-dwelling populations were composed of a broad array of age classes including metamorphosing individuals. Four metamorphosing I. *fossor* were taken from Ocqueoc Lake about 75 m from the mouth of the upper Ocqueoc River on September 28, 1973. In addition, 83 metamorphosing *P. marinus* were collected off the mouth of six streams: Horton Creek (77), Porter Creek (1), Boyne River (1), Cheboygan River (2), Elliot Creek (1), and Ocqueoc River (1). All were captured during July-October, except one *P. marinus,* which came from the Boyne River delta in April. Hansen and Hayne (1962), who compared stream and lake populations of *P. marinus* larvae in the Ogontz River (a northern Lake Michigan stream) and the area off its mouth, demonstrated that larvae in the lake were larger on the average, and a greater proportion were metamorphosing in the lake than in the stream.

Larvae lived more frequently in embayments and inland lakes than along the open coasts of the Great Lakes, and usually on abrupt dropoffs in relatively deep water, rather than in gently sloping shallow areas where waves and water currents agitated the bottom. Lamprey habitats featured predominantly soft to semi-soft substrates, depths of 1 to 16 m, and bottom temperatures ranging from 5” to 23” C. But the lacustrine habitat associated with Carp Lake River, which supported sparse populations of

Table 7. Distribution of larval lampreys off the mouth of streams in the Lower Peninsula of Michigan (1969-75) and some physical characteristics of the habitat.
[*I* = *Ichthyomyzon* spp., *Ll* = *Lampetra lamottei*, and *Pm* = *Petromyzon marinus*; numbers in parentheses correspond to stream numbers in Table 1 and Fig. 1.]

Great Lakes drainage, stream, and tributary	Basin	Number of surveys	Species	Principal bottom materials[a]	Water temperature at bottom[b] (°C)	Depth (m)	Maximum distance from mouth (m)
LAKE MICHIGAN							
Carp Lake River (2)	Cecil Bay	2	*Ll,Pm*	G,R,S	18-19	3	270
Big Stone Creek (3)	Big Stone Bay	1		G,R	19	1-2	225
Wycamp Creek (7)	Lake Michigan	1		G,R,S	19	2	90
Bear River (14)	Little Traverse Bay	3	*I,Pm*	S,SI,G	18-19	1-3	250
Pine River tributaries (16)	Lake Charlevoix						
Shelson Creek		1		G,S,SI		o-1	20
Horton Creek		7[c]	*Ll,Pm*	S,SI,D	14-23	1-8	270
Boyne River		6[c]	*Ll,Pm*	S,SI	5-22	3-11	75
Porter Creek		7[c]	*Ll,Pm*	S,SI	5-23	1-16	90
Jordan River		3[c]	*Ll,Pm*	S,SI	14-20	2-5	60
Monroe Creek		3[c]	*Ll,Pm*	S,SI	18	1	35
Medusa Creek (17)	Grand Traverse Bay	1		G,R,S	19	1-2	70
Inwood Creek (19)	Grand Traverse Bay	1		G,R,S	13	3	90
Elk River (32)	Grand Traverse Bay	2		S	19-23	3-13	1,200
Acme Creek (35)	Grand Traverse Bay	2[c]		S,SI	22-23	1-8	790
Mitchell Creek (37)	Grand Traverse Bay	1	*Pm*	S,SI	21-22	1-3	135
Boardman River (38)	Grand Traverse Bay	4[c]	*I,Pm*	S,SI,D	8-18	3-15	45
Boardman River (38)	Boardman Lake	1	*Ll,Pm*	S,SI,D	19	1-2	195
Cedar Creek (40)	Grand Traverse Bay	1		S,G	19	1	60
Belanger Creek (44)	Grand Traverse Bay	1		S,G	19	2	30
Leland River (50)	Lake Michigan	2		R,S,SI	19-23	2	0
Shalda Creek (52) (Good Harbor Creek)	Good Harbor Bay	2		S	19-21	0-6	225
Shetland Creek	Little Traverse Lake	1		S,SI	21	o-2	30
Crystal River (53)	Sleeping Bear Bay	1		S	18	3	90
Platte River (56)	Platte Bay	2[c]		S,G,R	12-23	2-5	450
Platte River (56)	Loon Lake	4[c]	*Pm*	S,SI,D	10-20	1-13	360
Platte River (56)	Platte Lake	2		S,SI	14-19	1-3	1,190
Betsie River (57)	Betsie Lake	1		S,SI	18-19	1-2	450

Herring Creek (58)	Herring Lake	1		S,G	22	1-6	**65**
Manistee River (61)	Manistee Lake	2	*I,Pm*	S,SI,D	19-21	1-7	**90**
Little Manistee River	Manistee Lake	2	*Ll*	S,SI	20-22	1-5	45
Pere Marquette River (68)	Pere Marquette Lake	1		S,SI	19-20	5-6	180
Stony Creek (72)	Stony Lake	1		S,SI		4	25
Muskegon River (78)	Muskegon Lake	1		SI	19-21	4-8	630
Galien River (109)	Lake Michigan	1		S,SI	21	4	0
State Creek (111)	Lake Michigan	1		S	19	4	90
LAKE HURON							
Mill Creek (2)	Straits of Mackinac	1		**R,G,S**	20		120
Cheboygan 266-20 Creek (3)	Straits of Mackinac	1		R,G,S	21	2	30
Cheboygan River (9)	Straits of Mackinac	2	*Pm*	S,SI	20	3-8	90
Pigeon River	Mullett Lake	1	*Ll*	S,SI	20	2	135
Sturgeon River	Burt Lake	3[c]	*I,Ll,Pm*	S,SI,D	16-21	1-8	135
Maple River	Burt Lake	1		**D,P**	18-19	1-2	70
Elliot Creek (10)	Duncan Bay	2	*Ll,Pm*	S,SI	19-21	1	0
Greene Creek (13)	Lake Huron	1		**S,R**	19-21	1-5	180
Mulligan Creek (15)	Lake Huron	1	*Pm*	**S,R,G**	20	1-3	120
Carp Creek (18) (Black Mallard Creek)	Hammond Bay	1		S,R	19	2	60
Ocqueoc River (20)	Hammond Bay	2	*I,Ll,Pm*	S,CS,D	19-20	2-3	450
Ocqueoc River (20)	Ocqueoc Lake	2	*I[d],Ll,Pm*	S,SI,D	13-14	1-5	60
Mud Creek	Orchard Lake	1		S,SI,D	16-19		9
Trout River (24)	Lake Huron	1		**R,G**	21	3	120
Swan River (26)	Swan Lake	1		C	24		
Little Trout River (27)	Lake Huron	1		R	16	4	90
Devils River (38)	Thunder Bay	2	*I,Pm*	**S,G**	14-17	1-3	225
Mill Creek (42)	Lake Huron	1		S,SI,R	19		25
Au Sable River (44)	Lake Huron	2		S	9-19	5-6	790
Pine River	Van Etten Lake	1		S,SI	20-21	1-2	
East Au Gres River (47)	Lake Huron	1	*I,Pm*	S,SI	22	2-4	235
LAKE ERIE							
St. Clair River (6)	Lake St. Clair	1	*I*	S,SI,D	18-20	2-6	2,500

[a]C = clay; CS = clayey silt; D = detritus; G = gravel; P = peat; R = rubble; S = sand; SI x silt.
b Taken during survey; may vary considerably when conditions and seasons are different.
[c]Surveyed during different seasons.
[d]Includes metamorphosing I. fossor.

L. lamottei and *P. marinus,* was principally gravel, rubble, and hard-packed sand. Furthermore, Thomas (1962) reported that larvae inhabiting areas off stream mouths in Lake Superior lived in all bottom types, sometimes not even burrowing into the bottom but, instead, lying under "various articles," including strips of bark. Thomas collected larval lampreys as far as 2,500 m from the presumed source stream.

Low concentrations of dissolved oxygen in summer were a limitation in thermally stratified lakes. Larvae did not inhabit the oxygen-depleted (< 1 ppm) hypolimnia in Loon Lake (Platte River system) and Ocqueoc Lake (Ocqueoc River system), though they were generally numerous in the shallower strata.

The tendency to move into lakes did not differ materially among species; the number of lentic areas inhabited by different species was proportional to their presence, distribution, and abundance in the associated streams. All streams contributing to lake populations of larval lampreys, other than the Manistee River, contained spawning gravel in the lowermost l-3 km. Downstream movements, therefore, whether resulting from intrinsic or extrinsic factors, or both, did not necessarily cover great distances, although the exact origin of larvae was not determined. Mass downstream movements of larval lampreys were documented in the Carp Lake River (Applegate 1961) and the Big Garlic River, a Lake Superior stream (Manion and McLain 1971). Larvae of *L. lamottei* and *P. marinus* were more abundant off the mouths of Horton and Porter Creeks than in the streams proper. Heavy siltation and slack current in the lower reaches may be unsuitable for these species, causing them to move farther downstream and eventually into lakes. As mentioned earlier, *L. lamottei* and *P. marinus* largely avoided the lower main channels of the Pere Marquette and Rifle Rivers. Thomas' (1962) observations of larval lampreys in Lake Superior tributaries similarly indicated that many larvae passed the slow, silty lower reaches and moved into lacustrine zones. The absence or general scarcity of larvae in lakes, despite their abundance in connecting streams, suggests that most lentic habitats were generally unfavorable. Tibbles (1967) believed that larval lampreys migrated into 13 small Lake Superior tributaries from lake-dwelling populations originating from other streams. Other factors in lakes, such as sedimentation, current inconstancy (direction and velocity), and bottom compactness and instability may be limiting. Bear River, which was blocked by a dam near its mouth, was the only system with a lentic population of *P. marinus* but no stream population. Larvae were confined to the boat harbor at the mouth of the stream and apparently did not range into the large off-mouth embayment of Little Traverse Bay.

Reproductive Behavior

Spawning behavior and habitat have been described for *I. castaneus* (Case 1970), I. fossor (Reighard and Cummins 1916; Hankinson 1932), *L. lamottei* (Gage 1893, 1928; Dean and Sumner 1898; Young and Cole 1900;

Reighard 1903), and P. marinus (Gage 1893, 1928; Surface 1899; Hussakof 1912; Coventry 1922; Applegate 1950; Wigley 1959; Manion and McLain 197 1); however, such information for I. unicuspis is scant. On the basis of observations of 1,359 lampreys (all species) engaged in spawning activity, information for the present study was collected on the number of lamprey nests, dates, water temperature, and the width, depth, and discharge of streams (Table 8). The spawning seasons of the five lampreys overlapped. *Lampetra lamottei* began spawning earliest in the season (April 20) and *P. marinus,* which had by far the most protracted season (beginning as early as May 27), spawned latest (as late as September 2). Gage (1928) reported, however, that overlapping of the spawning periods of *L. lamottei* and the landlocked *P. marinus* in New York occurred infrequently and "only in years when the season is unusual." Coinciding with earlier spawning, stream temperatures were lower for *L. lamottei* (mean 14.1° C) than for the other lampreys (range of means 18-18.3° C). It is worth noting that the mean water temperature (18.2° C) for *P. marinus* spawning, determined in the present study, corresponds to the optimum constant water temperature (18.3° C) required for the successful development of *P. marinus* embryos, which Piavis (1961) delimited in laboratory experiments.

Continuous water temperatures were monitored in sections of the Au Sable, Platte, and Pere Marquette Rivers during April-August 1973 to coincide with observations of lamprey spawning.

Twenty-two spawning I. *fossor* were observed in seven nests on June 13 in the South Branch of the Pine River, tributary of the Au Sable. Temperatures ranged from 16.5° to 20.5° C (daily mean 18° C) on June 13, after a general warming trend that began in mid-May, and reached a maximum daily peak of 21.5° C on June 11 and a mean daily peak of 20° C on June 12. Spawning occurred in a shallow, pool-riffle, high-gradient stretch of the stream. Nests were inconspicuously located in interstices beneath large stones (18-36 cm in diameter), and spawning lampreys were unobtrusive-as had been observed by Reighard and Cummins (1916). Thirteen spawning I. *fossor* were also observed on a small patch of gravel in a washed-out area beneath a submerged log in a predominately sandy, sluggish stretch in the upper Big South Branch of the Pere Marquette River on July 6, 1967. Elsewhere, however, I. *fossor* spawned prominently in the open, in poorly defined nests in shallow riffle areas-as Hankinson (1932) had also observed. For two nests in which sex ratio was determined, 11 males and 2 females were in one and 3 males and 1 female in the other. The latter nest was also occupied by one female I. unicuspis.

In McDuffee Creek, a small (0.3 m^3/s) headwater tributary of the Pere Marquette, 43 *L. lamottei* were observed building nests and spawning during May 9-23, 1973. Mean daily water temperatures ranged from 9.5° to 13.5° C during the peak spawning period of May 9-15. Initial spawning followed a general increase in stream temperatures that began on April 11 and a secondary warming phase that began in May 3-5. The mean daily water temperature rose from 8.5° (range 7-11°) on May 3 to 13.5° C (range 11.5-15.5°) on May 9.

In 1973, the spawning of *P. marinus* began in the Platte River on May

Table 8. Spawningdata (ranges in parentheses) for five species of lampreys in the Lower Peninsula of Michigan. [Water temperature recorded with a hand thermometer.]

Species	Spawning lampreys		Number of nests	Mean number of lampreys per nest	Peak spawning period	Water temperature (°C)		Characteristics of spawning area (stream)		
	Total number observed	Number in nests				Number of readings	Mean	Width (m)	Depth (cm)	Flow **(m^3/s)**
Ichthyomyzon castaneus	59	13	10	**1.3 (1-4)**	early June (May 28-June 25)	17	18.3 (15.6-22.2)	6.5-43	40-90	1.1-54
I. fossor	134	20	3	**6.7 (3-13)**	late May to mid-June (May 26-July 6)	8	18.0 (12.8-23.3)	3.5-8	10-61	0.1-0.6
I. unicuspis	77	69	31	**2.2 (1-10)**	early June (May 23-June 26)	33	18.3 (12.8-22.8)	3.5-30	10-61	0.1-4.2
Lampetra lamottei	357	94	36	**2.6 (1-9)**	early May (April 20-June 26)	28	14.1 (6.7-20.6)	1.5-18	15-61	0.1-5.2
Petromyzon marinus	732	732	298	**2.4 (1-10)**	late May to mid-June (May 27-Sept. 2)	262	18.2 (11.1-26.1)	1.5-43	15-90	0.01-54

29 following first, a 6-day warming period (May 18-23) in which the mean daily water temperatures increased from 10.5° to 16° C and, later, a 6-day thermally stable period (May 24-29) in which mean daily temperatures ranged from 15° to 15.5° C. Spawning continued through June 18. A total of 51 spawning lampreys were observed, of which 84% were counted during May 3 l-June 11, when mean daily water temperatures ranged from 15° to 23.5° C. The recording thermometer was located 1.2-1.8 km upstream from the spawning area, immediately above the outflow from a cool, spring-fed tributary (Brundage Creek), in a reach with temperatures 0.5 to 2 Celsius degrees higher than those at the spawning site.

Observations of the spawning habits of I. unicuspis were emphasized in the present study, since the literature was limited to two short accounts by Trautman (1957) and Scott and Crossman (1973). Trautman wrote that they spawned in nests "they build in the sand- and gravel-bottoms of riffles of moderate-sized streams which have moderate gradients," and suggested (as reported by Hall 1963) that the parasitic species of *Ichthyomyzon* may spawn more often at night than do other lampreys. Scott and Crossman reported that they "ascend larger rivers where they construct shallow nests in gravelly riffles." In the present study, 82% of the I. *unicuspis* spawners were counted in the Rifle River, where surveys were most intensive. They spawned throughout the day and into dusk, at least as late as 8:30 P.M. (on May 23). No effort was made, however, to determine whether spawning occurred after dark. Although one I. *unicuspis* was found in a nest about 73 km above the river mouth, spawners in the Rifle River were more common in the lower 30 to 50 km (⅓ to ½) of the main stream; none were found in the otherwise suitable headwaters or tributaries. This distribution of nests coincided well with the dispersion of *Ichthyomyzon* larvae (Fig. 11). Since 81% of all nests occupied by *I. unicuspis* spawners also contained other lamprey species, it could not be ascertained which of these nests, if any, were constructed solely by *I. unicuspis*. Details were recorded, however, on May 23 and June 1, 1972, for two nests occupied exclusively by I. *unicuspis*. Each nest contained 10 lampreys, and was located in a shallow (45-50 cm) riffle area with moderate to rapid current. The nest observed on May 23 was built at the upper end of a riffle; it had a diameter of 30 cm, a cavity depth of 8-15 cm and, unlike the nests of *P. marinus* (Applegate 1950), contained no downstream rim. The nest checked on June 1 was a poorly defined depression constructed among submerged sticks, twigs, and a beer can on the upstream side, and partly beneath a large boulder (diameter 50 cm). In the Rifle River, the average depth of 11 nests that were occupied by I. *unicuspis* (10 of which were shared with *P. marinus)* was 38 cm (range 23-79 cm) and the average cavity depth was 8 cm (range 2.5-15 cm). These nests varied from 33 to 122 cm in diameter (mean 66 cm), and were 2 to 13 m (mean 7 m) from the nearest stream bank.

The sex of 25 of 26 Z unicuspis on 14 nests in the Carp Lake, Pine, and Rifle Rivers was determined. Five nests were occupied by one male, three by two males, one by three males, one by one female, one by one male and one female, one by one male and two females, one by two males and two females, and one by one male and one unidentified individual. Of these nests, 11 were also occupied by *P.* marinus and 1 by I. fossor spawners.

Notwithstanding their tendency to occupy different stream habitats, the spawning areas of the different species overlapped, except, of course, for those of I. castaneus and I. unicuspis, the two species that were geographically separated. Moreover, as indicated above, spawning lampreys of different species were associated in many nests (Table 9). *Petromyzon marinus* was the most common reproductive associate, occurring in all but one of the nests containing more than one species. However, these data were biased in favor of *P. marinus* sightings, because surveys for spawning lampreys were generally most intensive in the main stream habitats used heavily by this species. It appeared that the native species capitalized on the availability and abundance of *P. marinus* nests, because most shared nests were of typical *P. marinus* construction. Nest associates appeared compatible, and there was no indication of antagonistic encounters between species. Interspecific mating was not witnessed, but the possibility of accidental cross fertilization cannot be dismissed. Piavis et al. (1970) experimentally demonstrated hybridization among the five species of lampreys inhabiting the study area. Their hybrid crosses almost routinely produced embryos through stage 8, and some produced larvae. Hybridization, or the possibility of hybridization, in lampreys was noted by Hubbs and Trautman (1937); Starrett et al. (1960); Rembiszewski (1968); and Huggins and Thompson (1970). Nests occupied

Table 9. Interspecific communal spawning of lampreys observed in streams of the Lower Peninsula of Michigan, 1965-7.5.
[Ic = Ichthyomyzon castaneus; If= I. fossor; Iu = I. unicuspis; Ll = Lampetra lamottei; and *Pm = Petromyzon marinus.]*

Species association	Lake basin and river	Number of nests	Ratio of species by nest[a]
Two species			
Ic, Pm	Michigan: Pine, Platte, Muskegon	5b	1:2 (2); 1:6; 1:? (2)
If, Iu	Huron: Pine	1	4: 1
If, Pm	Huron: Devils	c	c
Iu, *Pm*	Michigan: Carp Lake Huron: Devils, East Au Gres, Rifle	21	1:1 (2); 1:2 (2); 1:3; 1:4 (2); 1:5 (2); 1:6; 1:10; 2:1 (2); 2:3 (3); **2:5; 2:9;** 3:1; 3:4; 5:1
Ll, Pm	Michigan: Carp Lake, Pine, Pentwater	5	**1:1;** 1:2; 1:6; 2:2; 2:?
Three species			
Zc, Ll, Pm	Michigan: Betsie	1	4:2:?
Zu, Ll, Pm	Michigan: Carp Lake	3	1:5:6; **2:2:2; 2:4:2**

[a]Sex of individual lampreys was not determined in most nests. Number of nests (when more than one) shown in parentheses.
b An additional eight nests were observed in the Muskegon River, but the lampreys were not counted.
c Not recorded.

by more than one species were observed for only short periods in the present study, and identification of the progeny was not attempted. Furthermore, of the many thousands of larval lampreys collected in 1957-75, none were identified as hybrids.

In 22 nests containing a total of 59 spawning *P. marinus,* 13 were occupied by 1 male and 1 female, 2 by 1 male and 2 females, 1 by 1 male and 3 females, 2 by 1 female and 2 males, 3 by 2 males and 2 females, and 1 by 3 males and 2 females. Of three nests with one male and one female *P. marinus,* two were also occupied by a single I. *castaneus* (one was a female) and the third nest by a single *I. unicuspis.*

DISCUSSION

The results of this study suggest that the geographic distribution and spatial segregation of larval lamprey populations in Michigan's Lower Peninsula result primarily from the complex relationship among the behavorial characteristics of the five species, their differences in ecological tolerance, and the availability of preferred stream habitats.

The distribution of larval populations was broadly correlated with major physical regional subdivisions. Larvae reached maximum density and were more continuously distributed in comparatively high-quality, uniformly flowing streams, best represented by those on the interior upland in the northern half of the Lower Peninsula, including and northward from the Muskegon River of the Lake Michigan drainage and the Tittabawassee River (Saginaw River system) of the Lake Huron drainage. Large populations occurred in most of these streams, but particularly in the Pine, Platte, Betsie, Big Sable, Manistee, Pere Marquette, White, Muskegon, Cheboygan, Ocqueoc, Thunder Bay, Au Sable, East Au Gres, and Rifle Rivers. On the other hand, larvae were less abundant and more discretely distributed in the southern half of the Lower Peninsula. This contrast was previously reported for *P. marinus* (Lawrie 1970). There, the greater preponderance of impervious surface formations (ground moraines and lake beds), as well as man-related deleterious factors that resulted from urbanization, agriculture, and industry contributed to unfavorable stream conditions such as intermittent and unstable flows, high and widely fluctuating stream temperatures, bottom instability, and pollution. These conditions were most severe in the southeastern area. Accordingly, lampreys were scarcest there. Larval lampreys were likewise sparse in most clayey lowland streams, even in those on the periphery of the Northern Upland. Streams subject to occasional or periodic intermittency were unsuitable for perpetuating populations of nonparasitic lampreys, but produced and sustained larvae of the migratory species during periods of favorable flow. Hence, monospecific populations of *P. marinus* were found occasionally in small, clayey lowland streams like Cheboygan 266-20, Beaugrand, Johnny, Schmidt, and Middle Lake Creeks. Likewise, *I. unicuspis* occurred alone in Birch Creek.

The differential distribution of larval lampreys was broadly correlated with such physical factors as stream size (discharge, length, and channel size), water temperature, gradient, bottom composition and stability, turbidity, and principal water source (groundwater or surface). The explicit factors that separated the species were not delimited. Studies dealing with the habitats of larval lampreys and the difficulty in delimiting their precise physical and chemical properties were reviewed by Hardisty and Potter (1971).

The habitat preferences of *P. marinus* indicate that this species is ecologically intermediate between the *Ichthyomyzon* congeners and *L. lamottei*. It occupied a wider range of stream and habitat types than either *I. castaneus* or I. *unicuspis,* but was not found, or was scarce, in available coldwater habitats dominated by *L. lamottei* and warmwater habitats occupied by I. *fossor*. Furthermore, in streams where linear zonation was developed, the principal inhabitants were typically *P. marinus* in the middle section, *L. lamottei* in the cold headwaters, and *Ichthyomyzon* in the lower reaches.

Whether spatial segregation of sympatric species was caused by selective processes (genetically encoded differential habitat selection) or interactive processes (competition) was not determined. Both methods have been advanced in explaining spatial separation among sympatric stream fishes (Lindroth 1955; Kalleberg 1958; Saunders and Gee 1964; Nilsson 1967; Everest and Chapman 1972; Gibbons and Gee 1972). Hubbs and Trautman (1937) hypothesized that competition was the probable reason for the displacement of *I. unicuspis* by *P. marinus* in Lake Ontario and the Finger Lakes, but that lampreys in Michigan mainly avoided each other through the selection of different habitats. Scott and Crossman (1973) mentioned the probability of competition between *I. castaneus* and *I. unicuspis* for spawning grounds and food, but suggested that this may be circumvented by differences in habits and habitats. Reasons for the apparently complete allopatry of *I. castaneus* and *I. unicuspis* in the Lower Peninsula drainage are not fully understood. Hubbs and Trautman (1937) suggested that the mutual avoidance of *Ichthyomyzon* species was due chiefly to competition and the resulting population pressure. *Ichthyomyzon castaneus* may have penetrated into the Saginaw Bay-Lake Huron drainage in postglacial time, but was absorbed by the more dominant *I. unicuspis*. In the present study, there was little direct evidence that the absence or scarcity of one species was caused by the presence or numerical dominance of another. Since each species tended to occupy the same habitat in sympatry that it occupied in allopatry, I suggest that selective segregation was the more important cause of spatial segregation among these lampreys.

Dams were important in preventing species from expanding their range into (or surviving in) inland reaches. This was particularly true of the migratory species, but especially of *P. marinus, whose* invasion came after the erection of most dams. Trautman (1957) ascribed the drastic reduction of *I. unicuspis* in Ohio waters of Lake Erie in part to dams. In the Lower Peninsula, the more migratory *I. unicuspis* was less common above dams than was *I. castaneus* (Table 5).

Other factors that were probably important in influencing distributional patterns and relative abundance of larval lampreys were the migratory habits, dispersive capacity, size and duration of spawning runs, reproductive potential, and downstream dispersal of species.

The parasitic lampreys, being more migratory, have a distinct advantage in extending and replenishing their range more rapidly. This was undoubtedly a major factor in the phenomenal spread of *P. marinus* throughout the upper Great Lakes in the short period since its initial discovery there in the 1920's (Dymond 1922). Studies by Smith and Elliott (1953) and Moore et al. (1974) demonstrated that parasitic-phase *P. marinus* dispersed widely. Interchange between the Great Lakes was common, and lampreys traveled as far as 628 km from the point of tagging and release. In *I. castaneus* and I *unicuspis,* however, this edge in mobility was somewhat nullified by their narrow habitat selection-particularly their preference for the lower sections of main branches, which were typically the most severely degraded portions of streams. Siltation and pollution were mentioned as possible decimating factors for *I. castaneus* and *I. unicuspis* by Hall and Moore (1954), Trautman (1957), Bailey (1959), and Starrett et al. (1960). The general exclusion of I. *castaneus* and *I. unicuspis* from headwaters also may be due in part to the inability of these species to move long distances against stream currents during spawning migrations. Being smaller, these species may be weaker swimmers than *P. marinus* (Beamish 1974). However, this factor does not account for their absence from small streams, or from small tributaries in the lower reaches of rivers.

The nonparasitic lampreys, on the other hand, would have difficulty in spreading from one river system to another, as Young (1962) suggested, because of their nonmigratory behavior. I believe that the absence of *L. lamottei* from a major portion of the northern Lake Huron drainage, particularly where highly favorable habitats exist (as in the Au Sable River system, for example) is due to its limited capacity for dispersal. *Ichthyomyzon fossor* inhabits this region but may have migrated there through headwater transfer routes during an early postglacial period, when conditions favored its expansion but not that of *L. lamottei,* such as during the xerothermic stage, a period when the Lower Peninsula was somewhat warmer and drier than today (Dorr and Eschman 1970). Indeed, the occurrence of I. *fossor* as disjunct populations and its affinity for areas of poor natural drainage and warmwater habitats suggest that this species may have been more abundant and widespread in an earlier period.

Synchronization of the spawning run with optimal stream conditions (such as, temperature and flow) for spawning and, later, for embryonic development must be of considerable importance in the establishment of larval populations. In a number of streams and tributaries, only one year class of a species was found during the entire study period. Obviously a species such as *P. marinus,* which was abundant and has a protracted spawning period (Table 8), was favored in streams where suitable conditions existed for only short periods, or sporadically. *Petromyzon marinus* was a disproportionately large component of spawning runs when compared with native lampreys (Shetter 1949; Applegate 1950; Applegate and Smith 1950; Applegate et al. 1952a). These factors and the great dispersive powers of *P. marinus* also probably contributed to its occupancy of a comparatively wide variety of habitats.

Possibly the weak representation of *P. marinus* larvae in the southern half of the Lower Peninsula was caused in part by generally small spawning runs. The higher larval densities and greater frequency of year classes of *P. marinus* in small streams on the Cheboygan Lowland than in streams of similar size and with equal or better habitat that are scattered along most of the Lake Michigan coast suggest that spawning runs are larger and more protracted in the Cheboygan Lowland than they are along the Lake Michigan shore. The size of these runs was probably associated with concentration centers of parasitic-phase or prespawning-phase lampreys in the lakes. Shetter (1949) and Applegate (1950) reported that *P. marinus* spawning was heaviest in tributaries to northern Lake Michigan and northern Lake Huron. However, the absence or rare occurrence of larval populations in some streams was probably related more to the absence or scarcity of favorable environments than to the characteristics of spawning runs. Applegate (1950) did not believe that extensive spawning would ever occur in the southeastern drainage, because of the sluggish currents, siltation, and a paucity of gravel there.

Species differences in reproductive capacity must also have been important in affecting the relative abundance of larvae in heterospecific populations. There is a wide range in the potential fecundity of species: average egg counts reported by Hardisty (1971) were 2,580 for I. fossor; 19,000 for *I. unicuspis; 2, 339* for *L. lamottei;* and 61,000 for *P. marinus.* Manion (1972) reported the mean estimated number of *eggs* for *P. marinus* as 68,599. Possibly because of the greater fecundity of *P. marinus,* its larvae were more abundant in some areas than the larvae of other lamprey species.

Species dominance and distributional patterns also may have been influenced by the downstream movement of larvae. Such dispersal may act to redistribute populations from upstream to downstream sections of river systems. Whether these migrations occur commonly on a large scale in all lamprey streams is largely conjectural. Hardisty and Potter (1971) described the intrastream distribution of larval lampreys as a function of the distance upstream that adults migrate to spawn and the largely passive but continuous downstream drift of larvae. Referring to this downstream drift as "flushing," they mentioned that it will "ensure" the distribution of nonparasitic lampreys into the lower reaches, but they admitted its dependence on the hydrographical patterns, bottom type, and current velocity of the stream. The longitudinal zonation of sympatric species described in the present report, however, does not indicate such major redistributions. Downstream dispersal in streams such as the Pere Marquette, Platte, and Rifle Rivers was either slight, or the species were differentially intolerant of habitats in the middle and lower courses.

There is no evidence that lampreys spawn in the Great Lakes or in tributary inland lakes. Colonization of lentic waters by larval lampreys is a consequence of their downstream travel. The proximity of lake-dwelling larvae to nearby nursery streams strongly supports the hypothesis of Hansen and Hayne (1962) that such colonies are a natural extension of stream populations. That the larvae cannot only survive but metamorphose to adult stages in lakes attests to the great adaptability of lampreys. Probably their absence off the mouths of many lamprey-producing streams is due mainly to limited downstream passage and unfavorable lake habitats. Since most lentic areas sampled were within 1.6 km of the mouth of lamprey streams, the possibility also exists that populations may have been present in areas beyond this distance. Although Wagner and Stauffer (1962b) reported that nearly all larval lampreys taken from 10 of 22 areas in the Great Lakes proper came from areas within 0.4 km from the mouth of the nearest source stream, they collected some larvae 2 km away. Moreover, in Batchawana Bay of Lake Superior, *P. marinus* larvae were found inhabiting areas up to 3.4 km from the Batchawana River mouth (Thomas 1962). The distance that lake-dwelling larval lampreys disperse may be affected mostly by the suitability of the habitat in areas immediately off the mouths of source streams and the size of the population, such that dispersal to more distant habitats would be greatest where conditions near the stream mouth were the most inhospitable or larval densities were high.

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