GREAT LAKES FISHERY COMMISSION

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Genetic Identification of Sea Lamprey Populations in the Great Lakes

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ABSTRACT

Sea lamprey (Petromyzon marinus) ammocoetes collected from ten tributaries and one bay of the Great Lakes were electrophoretically analyzed for genetic variability at 25 enzyme loci. Chi-square analysis indicated that a significant degree of population structuring occurs among lampreys within Lake Superior and Lake Huron. Cluster analysis of genetic distances generally grouped collections that were in close geographical proximity to each other. A significant correlation was detected between genetic and geographic distances among collections from Lake Superior. It is suggested that sea lamprey control emphasis might shift from individual streams to population regions in order to minimize the rate of reestablishment subsequent to chemical treatment.

SUMMARY

1. Sea lamprey (Petromyzon marinus) ammocoetes collected from locations in Lakes Superior, Huron and Ontario were electrophoretically analyzed for genetic variability at 25 enzyme loci.

2. Genotypic frequencies within samples at the four polymorphic loci (*AGP*, *MDH-1*, *PGI-2*, and *PGM-1*) were close to Hardy-Weinberg expectations.

3. Overall heterogeneity chi-square tests of allelic frequencies at each locus for all samples revealed highly significant differences ($P < 0.005$).

4. Significant differences in allelic frequencies were also observed in separate comparisons of Lake Superior and Lake Huron collections.

5. Cluster analysis of genetic distances between collections revealed two separate clusters: Lake Superior - Lake Huron samples and Lake Ontario - Oneida Lake - Lake Champlain collections. The genetic distinctiveness between these groups suggest lampreys do not freely intermingle between the upper Great Lakes and Lake Ontario.

6. Within the Lake Superior - Lake Huron cluster, samples geographically proximate were usually similar.

7. Rank correlation of genetic and geographic distances among Lake Superior samples was statistically significant ($r = 0.48$, $p < 0.005$).

8. The genetic data presented suggest that multiple populations of sea lampreys exist within the lake basins of Superior and Huron.

9. Detailed analysis of sea lamprey population structure in Lake Huron is not possible since data are available from only three collections.

10. The existence of several lamprey populations within each of the Great Lakes basins would allow the adoption of a stock concept approach to management that could increase control emphasis.

INTRODUCTION

The invasion, colonization, and population expansion of sea lampreys (Petromyzon marinus) in the Great Lakes during the 1940's and 1950's temporarily corresponded to sharp declines in commercially important fish stocks; notably the lake trout (Salvelinus namaycush) and the lake whitefish (Coregonus clupeaformis) (Smith 1968; Lawrie and Rahrer 1972; Christie 1974; Pycha and King 1975). Much of this decline has been atributed to the predatory nature of sea lamprey adults, which cause mortality of prey fish through a process of attachment and feeding with a circular suctorial mouth. This predatory phase extends for 12 to 20 months until the adult lampreys ascend tributary streams, spawn, and die. Larval lampreys (ammocoetes) remain in the tributaries for three to eleven years or more before transformation and migration to the lake.

An intensive management program to reduce the sea lamprey populations began in 1953 with the installation of electrical barriers in streams to block spawning runs (Lawrie 1970; Smith 1971; Smith et al. 1974; Smith and Tibbles 1980). Control measures became much more effective when the selective toxicants, TFM (3-trifluoromethyl-4-nitrophenol) and Bayer 73 (2',5-dichloro-4'nitrosalicylanilide) were used against the ammocoetes in streams. Application of these lampricides at intervals of three to four years to Great Lakes tributaries continues to be the predominant tool used in sea lamprey control.

The control program is organized around a survey system that gathers data on the abundance of ammocoetes in tributary streams. The basic management units for population control are those streams with high densities of ammocoetes nearing the transformation life stage. The geographical corresponsence between these streams and the populations in the lake itself

is unknown. Adoption of a "stock concept management approach" (Loftus 1976) may increase the effectiveness of lamprey control.

Electrophoretic studies on lamprey population structure in the Atlantic coastal drainages and the Great Lakes have found the animals to be genetically distinguishable between widespread geographic localities. Brussard et al. (1981) found genetic distinctiveness among lampreys collected from the Finger Lakes of New York, Hudson River, Delaware River, Lake Ontario, and Lake Superior. Krueger (1980) determined that statistically significant genetic differences occurred among lampreys from Lake Superior, Oneida Lake, Lake Champlain, and the Bay of Fundy at one or more of four polymorphic allozyme loci. The present study was undertaken to determine whether genetically identifiable populations of sea lamprey have become established in the Great Lakes.

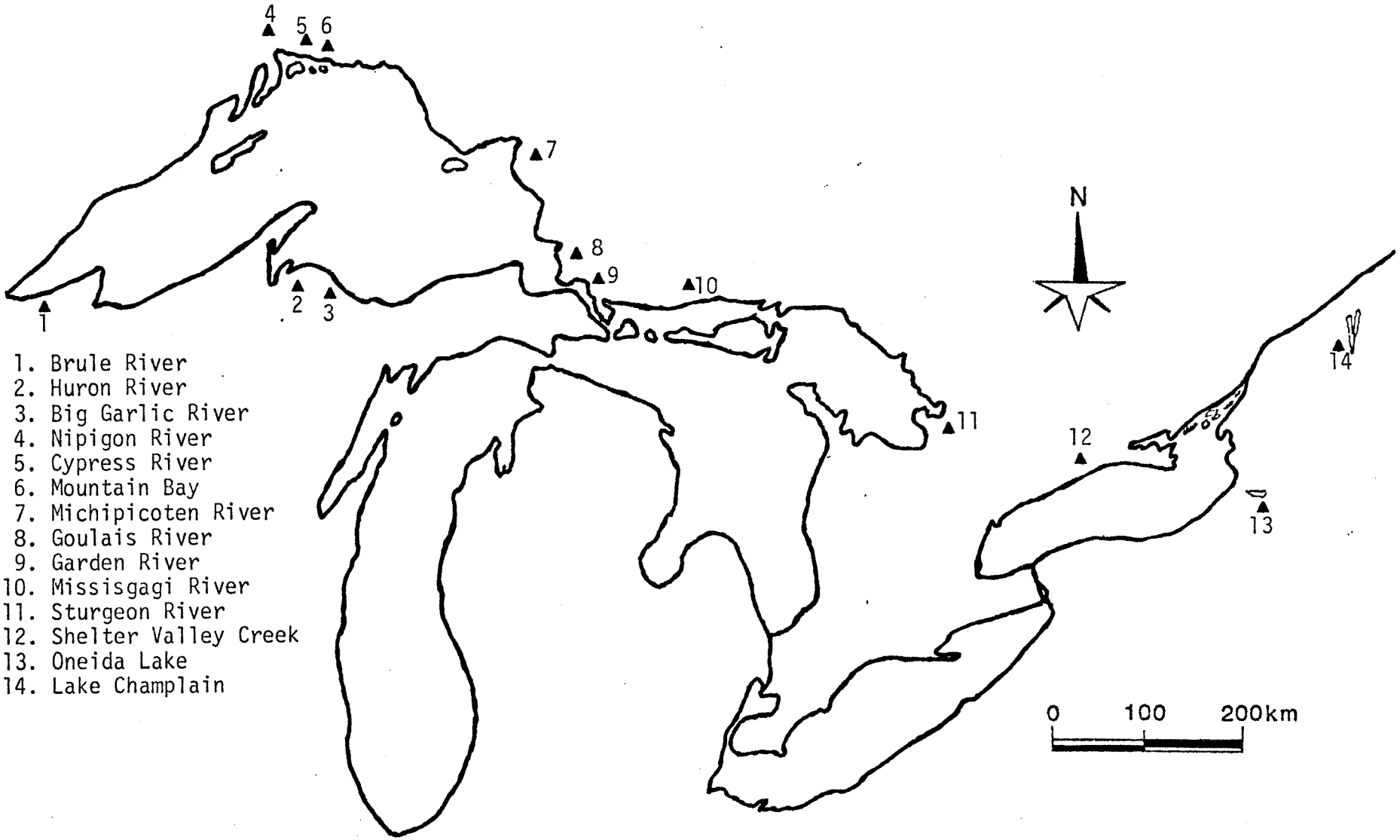
MATERIALS AND METHODS

Sea lamprey ammocoetes from ten tributaries and one bay of the Great Lakes were collected during chemical treatment or by electrofishing (Fig.1). Also included in this report for comparison purposes are those data from the Brule (Nebagamon) River, Oneida Lake (Fish Creek) and Lake Champlain (Lewis Creek) which have been previously reported (Krueger 1980). All specimens used in this analysis were frozen as soon as possible after collection and stored at -20°C.

Starch gel electrophoresis was conducted on lamprey muscle tissue according to the procedures given by Krueger (1980). The nomenclature for specifying enzymes, loci, and alleles is that proposed by Allendorf and Utter (1979). Gels were stained for sixteen enzymes encoded by 25 gene loci: adenosine deaminase (ADA-1,2), alpha-glycerophosphate dehydrogenase (AGP), aspartate aminotransferase (AAT-1,2), creatine phosphokinase (CPK-1,2), glucose-6-phosphate dehydrogenase (G6PDH), glyceraldehyde-3-phosphate dehydrogenase (GAPDH-1,2), lactate dehydrogenase (LDH), malate dehydrogenase (MDH-1,2,3), malic enzyme (ME), peptidase (PEP-1,2), peroxidase (PER-1,2) 6-phosphogluconate dehydrogenase (6PGD), phosphglucose isomerase (PGI-1,2), phosphoglycerate kinase (PGK), phosphoglucomutase (PGM-1), and sorbitol dehydrogenase (SDH). Among these loci, four were demonstrably polymorphic; AGP, MDH-1, PGI-2, and PGM-1. Electrophoretic expression of ME and PER has been reported by Brussard et al. (1981); the remaining enzymes have been described by Krueger (1980). The buffer systems of Ridgway et al. (1970) and Whitt (1970) were used to resolve PER and ME, respectively.

Overall heterogeneity chi-square tests of the genetic data followed that described by Snedecor and Cochran (1967). Genetic distances (Nei 1978) were calculated for all pairs of collection locations based on the four polymorphic loci. The matrix of genetic distances was subjected to cluster

Figure 1. Larval lamprey collection locations.



analysis using the BMDP-1M program (Dixon and Brown 1979). Geographic distances between sample locations were measured as the shortest distances via lake shoreline. Spearman's rank correlation coefficient (Conover 1971) was computed to examine the relationships between genetic characteristics and geographical distance.

RESULTS AND DISCUSSION

Genotypic frequencies within samples at the four polymorphic loci (*AGP*, *MDH-1*, *PGI-2*, and *PGM-1*) were close to Hardy-Weinberg expectations (Tables 1-4); of 61 comparisons only three deviated significantly ($P < 0.05$). The deviant comparisons occurred in lampreys from the Huron River and Brule Rivers at *AGP*, and in fish from the Garden River at *PGM-1*. Heterozygote deficiencies occurred in each of these cases which may suggest that further population substructuring may occur at these locations.

Overall heterogeneity chi-square tests of allelic frequencies at each locus were performed to test the null hypothesis that lamprey samples were drawn from a common population (Table 5). Comparisons of all samples revealed highly significant differences ($P < 0.005$) at each of the four polymorphic loci. Separate comparisons were also made for samples from Lake Superior and Lake Huron drainages. Significant differences ($P < 0.05$) in allelic frequencies occurred among collections from Lake Superior at *PGM-1* and among collections from Lake Huron at *MDH-1* and *PGM-1*. These results suggest that multiple populations of sea lamprey exist within the Lake Superior and Lake Huron basins. Subsequent analysis of ten additional collections from the Lake Superior basin has continued to support this conclusion (Krueger and Spangler 1980 STOCS M.S.).

Genetic distances (Nei 1978) were calculated to further analyze the electrophoretic data. Cluster analysis of the genetic distances between the sea lamprey collections revealed two separate clusters: Lake Superior - Lake Huron samples and the "Eastern" collections (Fig. 2). The genetic distinctiveness between these groups suggest lampreys do not freely intermingle between upper Great Lakes and Lake Ontario. The grouping of lakes Superior and Huron collections probably reflects the relatively recent presumed common origin of

Table 1. *AGP*(alpha-glycerophosphate dehydrogenase) phenotypes, sample sizes, and allelic frequencies in sea lampreys.

Sample Location	Phenotypes			Total	Allelic Frequency	
	100/100	*100/146*	*146/146*		*100*	*146*
Lake Superior						
Brule River	21	13	7	41	0.67	0.33
Huron River	18	13	9	40	0.61	0.39
Big Garlic River	9	23	8	40	0.51	0.49
Goulais River	10	15	4	29	0.60	0.40
Michipicoten River	16	20	4	40	0.65	0.35
Mountain Bay	5	8	5	18	0.50	0.50
Cypress River	4	16	5	25	0.48	0.52
Nipigon River	11	20	8	39	0.54	0.46
Lake Huron						
Garden River	8	18	6	32	0.53	0.47
Mississagi River	10	16	14	40	0.45	0.55
Sturgeon River	5	7	11	23	0.37	0.63
Lake Ontario						
Shelter Valley Creek	11	20	8	39	0.54	0.46
Oneida Lake						
Fish Creek	5	16	10	31	0.42	0.58
Lake Champlain						
Lewis Creek	24	11	0	35	0.84	0.16

Table 2. *MDH-1* (Malate dehydrogenase) phenotypes, sample sizes, and allelic frequencies in sea lampreys.

Sample Location	Phenotypes				Allelic Frequency	
	-100/-100	*-100/-165*	*-165/-165*	Total	*-100*	*-165*
Lake Superior						
Brule River	45	17	0	62	0.86	0.14
Huron River	28	11	1	40	0.84	0.16
Big Garlic River	33	4	3	40	0.87	0.13
Goulais River	31	8	1	40	0.87	0.13
Michipicoten River	27	11	2	40	0.81	0.19
Mountain Bay	10	7	1	18	0.75	0.25
Cypress River	13	12	0	25	0.76	0.24
Nipigon River	24	14	1	39	0.79	0.21
Lake Huron						
Garden River	21	10	1	32	0.81	0.19
Mississagi River	33	7	0	40	0.91	0.09
Sturgeon River	20	17	2	39	0.73	0.27
Lake Ontario						
Shelter Valley Creek	32	6	1	39	0.90	0.10
Oneida Lake						
Fish Creek	31	0	0	31	1.0	0.0
Lake Champlain						
Lewis Creek	30	0	0	30	1.0	0.0

Table 3. *PGI-2* (phosphoglucose isomerase) phenotypes, sample sizes, and allelic frequencies in sea lampreys.

Sample Location	Phenotypes						Allelic Frequency		
	100/100	*100/92*	*92/92*	*100/122*	*122/122*	Total	*100*	*92*	*122*
Lake Superior									
Brule River	67	3	0	0	0	70	0.98	0.02	0.0
Huron River	37	2	0	1	0	40	0.96	0.03	0.1
Big Garlic River	36	2	0	2	0	40	0.95	0.02	0.03
Goulais River	40	0	0	0	0	40	1.0	0.0	0.0
Michipicoten River	40	0	0	0	0	40	1.0	0.0	0.0
Mountain Bay	17	0	0	1	0	18	0.97	0.0	0.03
Cypress River	25	0	0	0	0	25	1.0	0.0	0.0
Nipigon River	37	2	0	0	0	39	0.97	0.03	0.0
Lake Huron									
Garden River	32	0	0	0	0	32	1.0	0.0	0.0
Mississagi River	39	0	0	1	0	40	0.99	0.0	0.1
Sturgeon River	39	0	0	0	0	39	1.0	0.0	0.0
Lake Ontario									
Shelter Valley Creek	30	0	0	9	0	39	0.88	0.0	0.12
Oneida Lake									
Fish Creek	19	0	0	9	3	31	0.76	0.0	0.24
Lake Champlain									
Lewis Creek	26	0	0	4	0	30	0.93	0.0	0.07

Table 4. *PGM-1* (phosphoglucomutase) phenotypes, sample sizes, and allelic frequencies in sea lampreys.

Sample Location	Phenotypes			Total	Allelic Frequency	
	100/100	*100/148*	*148/148*		*100*	*148*
Lake Superior						
Brule River	23	19	0	42	0.77	0.23
Huron River	16	18	6	40	0.62	0.38
Big Garlic River	13	21	6	40	0.59	0.41
Goulais River	8	13	8	29	0.50	0.50
Michipicoten River	21	14	5	40	0.70	0.30
Mountain Bay	6	8	4	18	0.55	0.45
Cypress River	5	15	5	25	0.50	0.50
Nipigon River	11	22	6	39	0.56	0.44
Lake Huron						
Garden River	16	9	7	32	0.64	0.36
Mississagi River	20	18	2	40	0.72	0.28
Sturgeon River	8	15	14	37	0.42	0.58
Lake Ontario						
Shelter Valley Creek	32	7	0	39	0.91	0.09
Oneida Lake						
Fish Creek	29	2	0	31	0.97	0.03
Lake Champlain						
Lewis Creek	28	2	0	30	0.97	0.03

Table 5. Chi-square comparisons of allelic frequencies among sea lamprey collections. Data for alleles *PGI-2* (*90*) and (*122*) were combined.

Comparison	Locus			
	AGP	*MDH-1*	*PGI-2*	*PGM*
Lake Superior Samples				
X^2	13.3	7.3	8.2[1]	19.1
d.f.	7	7	7	7
p	<0.10	<0.45	<0.35	<0.01
Lake Huron Samples				
X^2	2.9	8.9	1.8[1]	15.7
d.f.	2	2	2	2
p	<0.25	<0.05	<0.45	<0.005
All samples				
X^2	50.9	45.3	93.2	120.8
d.f.	13	13	13	13
p.	<0.005	<0.005	<0.005	<0.005

[1]Expected frequencies in some cells were less than one causing inflated X^2 values.

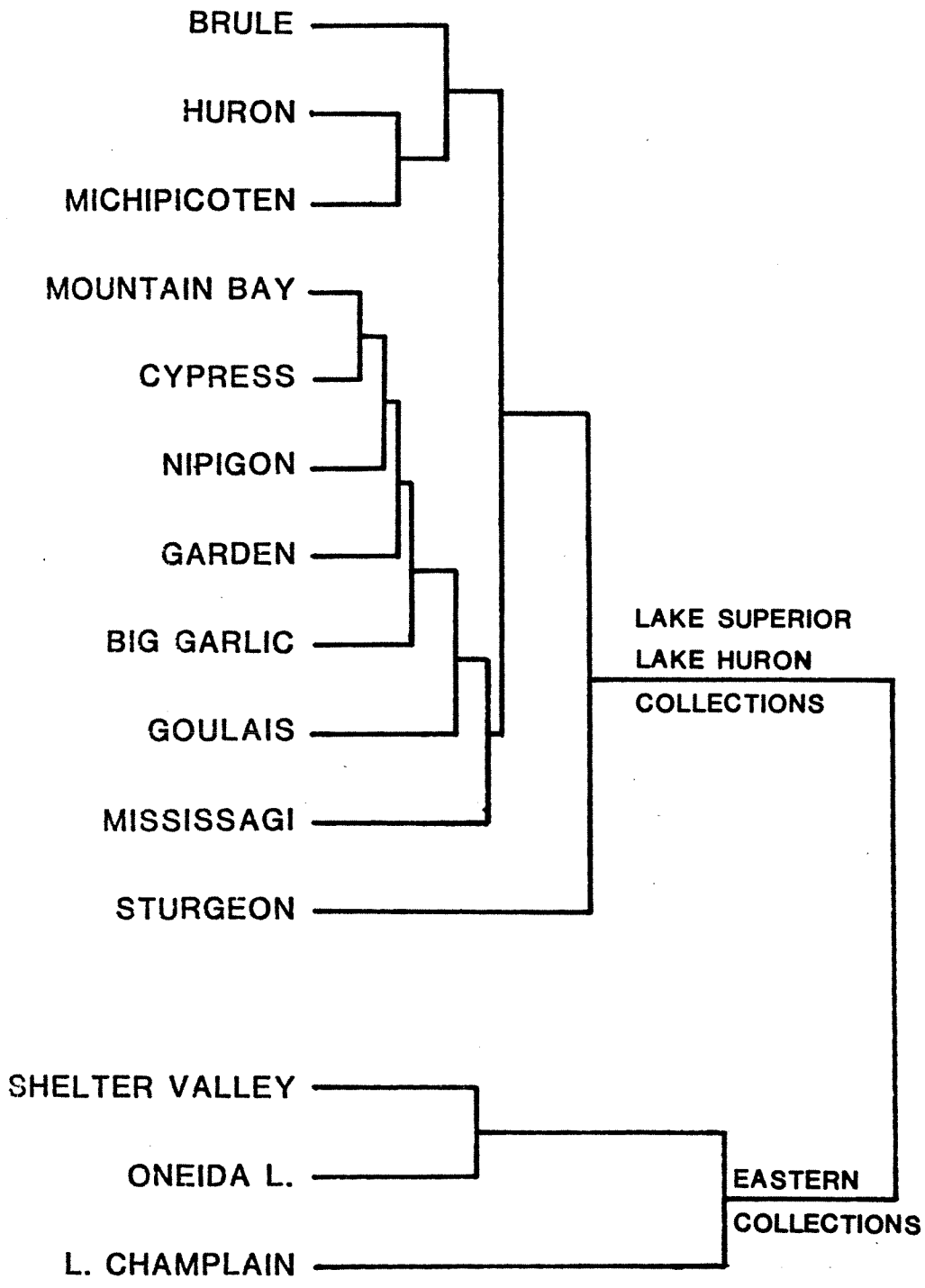
these populations. Within this upper Great Lakes group, collections geographically proximate were usually genetically similar (e.g. Mountain Bay, Cypress River, and Nipigon River, Fig. 1 and 2). Rank correlation of genetic and geographic distances among Lake Superior samples was statistically significant ($r = 0.48$, $p < 0.005$).

The genetic data presented suggest that multiple populations of sea lampreys exist within the lake basins of Superior and Huron. Within Lake Superior these populations appear to be geographically organized with lampreys from streams within a region being genetically similar. Several populations of sea lamprey probably also exist in Lake Huron; however, further analysis of the population structure is not possible since data are available from only three collections.

Genetic differences may have become established through founding errors during initial colonization and maintained by homing of spawning adults or restricted dispersal away from natal areas. If this is the case, migration and subsequent mating or genetic exchange between regions is apparently limited since it is unlikely that these differences would persist if lampreys freely intermingled and bred within the Lake Superior basin. Tagging studies in the Great Lakes have shown that lampreys are capable of traveling long distances (Applegate and Smith 1951; Smith and Elliot 1953; Moore et al. 1974). These studies, however, have not addressed the question of whether or not spawning runs in streams are comprised of adult lampreys with an admixture of natal origins. Recently, pheromones have been implicated as playing an important role in sea lamprey migration and reproductive behavior (Teeter 1980). The ability to detect trace quantities of chemical substances by spawning adults could facilitate a homing behavior.

The existence of several lamprey populations within each of the Great Lakes basins would allow the adoption of a stock concept approach to management

Figure 2. Cluster analysis of genetic distance coefficients calculated between lamprey collection locations.



(Loftus 1976) that could increase control effectiveness. Control emphasis might shift from individual streams to population regions. Each of the streams located within a region, including minor lamprey producers, would be chemically treated simultaneously. This management approach should decrease the probability for recolonization if adult dispersal from adjacent regions is limited.

On the basis of the genetic data presented and those reported elsewhere (Krueger and Spangler 1980 STOCS M.S.), preliminary geographical delimitation of such management zones is possible for most of Lake Superior; however, data are lacking from the Black and Thunder Bay areas of this lake.

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