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ILLINOIS NATURAL HISTORY SURVEY

Identification of Parental Strains of Lake Trout Eggs Captured During Spawning in Lake Michigan, 1996

Final Report to
U.S. Fish and Wildlife Service Fishery Resources Office
1015 Challenger Ct.
Green Bay WI 54311

Center for Aquatic Ecology

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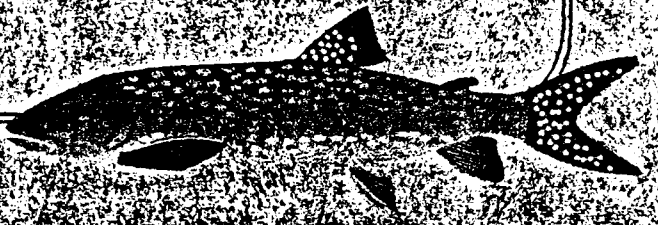
November 1996



Aquatic Ecology Technical Report 96/12

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Introduction

Native lake trout (*Salvelinus namaycush*) were extirpated from Lake Michigan in the late 1950's. Prior to that time they provided a valuable sport and commercial fishing industry for the four states bordering the lake. The decline and eventual extinction of lake trout has been attributed to a combination of overfishing, predation by sea lamprey (*Petromyzon marinus*), and physical degradation of spawning habitat. A program to restore a self-perpetuating population of lake trout to Lake Michigan has been underway since 1965. Restoration strategies include suppression of lamprey populations, creation of refuges to protect trout from exploitation, and annual stocking of yearling or fingerling lake trout (Holey et al. 1995). In the past decade, up to five million lake trout have been stocked in the lake each year. The survival of lake trout after stocking has been adequate to develop an important sport fishery in the lake. Assessment surveys conducted by the Illinois Department of Conservation (now Department of Natural Resources), Wisconsin Department of Natural Resources, and the U. S. Fish and Wildlife Service have found aggregations of mature lake trout at several sites around the lake. The first evidence of spawning by stocked lake trout was documented in Grand Traverse Bay and the southeastern shoreline in the 1970s (Peck 1979, Jude 1981, Wagner 1981). Since that time little additional evidence of spawning has been found in Lake Michigan, despite extensive efforts to find eggs at Clay Banks and Julian's Reef on the west side of the lake. However, in 1992 we collected eggs at several sites along the southwestern shore, and in the spring of 1993 through 1996 we collected hatched fry from a breakwall on the Indiana shore (Marsden 1994). A small number of eggs was also collected on Julian's Reef in the fall of 1995 (Marsden and Janssen in review).

The goal of the fisheries agencies involved in lake trout management is to reestablish naturally reproducing lake trout populations. The optimal strategy to accomplish this goal would be to stock fish from the same genetic strain(s) that were once present in Lake Michigan. Only two remnants of the original Lake Michigan genetic strains exist. The Lewis Lake strain (= Wyoming strain; Holey et al. 1995) originated from gametes collected in northern Lake Michigan in the late 1800s and stocked in Lewis Lake in Yellowstone Park in the late 1800s

(Krueger et al. 1983). The Green Lake strain contains genetic material from trout from the midlake reef complex in Lake Michigan, and is presumed to represent a deep-water spawning strain (Holey et al. 1995, Kincaid et al. 1993). Both of these strains have been stocked in Lake Michigan; however, the majority of fish stocked in the lake have been Lake Superior strain.

In the absence of pure stocks of native strains, the next best stocking strategy for rehabilitation is to identify the strains which successfully reproduce, and focus stocking effort on those strains. This objective requires acquisition of genetic data from potential parental strains and wild fry produced in Lake Michigan, and analysis of the data using second generation mixed stock analysis to identify the lineages of the fry (Marsden et al. 1989). In previous work in Lake Ontario, we determined that no detectable strain-specific selection takes place between the egg and fry stages in the wild, so eggs, which are much easier to collect than fry, can be used to obtain genetic data in place of fry (Grewe et al. 1994). In 1995, we used the second-generation mixed-stock analysis method to determine the parental strain origins of wild-spawned lake trout eggs collected in southern Lake Michigan in the fall of 1994 (which comprised the 1995 year class; Marsden and May 1995). The purpose of this study was to conduct a similar analysis of fry collected in 1996 to replicate the previous work and determine whether there is temporal stability in the parental population of the fry at the Port of Indiana site.

Methods

Sample collections

One hundred and twelve naturally spawned and hatched lake trout fry were collected from the outer west side of the Port of Indiana breakwall using fry traps in the spring of 1996 (Chotkowski and Marsden 1996). Eighty-six fry were frozen immediately in the field in liquid nitrogen for genetic analysis. All samples were shipped on dry ice to the Genomic Variation Laboratory at the University of California, Davis, CA, and stored at -80°C.

Allozyme analysis

Genetic analysis was performed using horizontal starch-gel electrophoresis of allozymes (May 1992). During a previous study, an initial screening of 102 loci had revealed polymorphisms at 18 loci in lake trout; the tissues, enzymes, and buffers used are described in Krueger et al. (1989). All fish in this study were examined at these 18 polymorphic loci (Table 1). Allozyme nomenclature follows the system of Shaklee et al. (1990). Allozyme analysis of samples of lake trout from each of the strains stocked into Lake Michigan had previously been conducted in the Cornell Laboratory for Ecological and Evolutionary Genetics (Krueger et al. 1989, Kincaid et al. 1993).

Parental strain identification

Parental strains of the fry were identified using second-generation mixed-stock analysis (Marsden et al. 1989). This analysis employs the method developed by Grant et al. (1980). Second-generation analysis estimates the strain composition (i.e., proportion of pure-strain and hybrid fry types) in a mixture of F_1 individuals. The strain composition of the parental population can then be derived from these estimates (Marsden et al. 1989). The earliest maturing lake trout are usually 4-year old males, although mature 3-year old males are occasionally seen. If we use the conservative estimate of maturity at five years, then a given year class of eggs or fry would primarily be produced by fish stocked as yearlings at least four or more years previously. Thus, fish stocked through 1991 could have produced fry year classes prior to and including 1996. Strains which could have contributed to the fry were the Clearwater, Superior, Seneca, Manitou, Jenny, Jenny x Lewis, Lewis, and Green Lake strains (Table 2). The Lake Michigan "strain", which was produced using gametes from feral fish and is therefore a mixture of strains, was first stocked in 1983 and comprised 0.07% of the fish stocked through 1991. We did not include this "strain" in the baseline data because it is likely genetically similar to one or more of the pure strains and would confound the model. Any contribution of this "strain" to the fry will most likely be attributed to the strain or strains which were primary contributors to the "Lake Michigan strain". For the same reason we did not include the Lake Ontario "strain", which was stocked first in 1990 and comprised 0.64% of the total stockings through 1991. We did not have baseline genetic data from the pure Jenny and Lewis lake strains, but only the Jenny

x Lewis lake cross. Contributions from the Jenny and Lewis pure strains will likely be clustered with the Jenny x Lewis cross. The Green Lake strain has had a checkered history, described in detail by Kincaid et al. (1993). Fish stocked prior to 1977 were progeny of the original Green Lake strain, of which the 84-DOM group (Kincaid et al. 1993) is the closest remaining descendent. Kincaid et al. also sampled four groups of Green Lake strain fish (86A-WILD, 86B-WILD, 87-WILD, and 88-WILD) which were hatchery-reared progeny of feral fish which bore fin clips identifying them as Green Lake strain. These fish are most closely related to the Green Lake strain fish stocked after 1988. We ran the mixed-stock analysis twice, once using the 84-DOM group and once using the combined WILD groups in the baseline samples. We then ran the model again, omitting the Green Lake strain from the baseline samples (see Discussion).

The accuracy of mixed-stock analysis is directly related to the magnitude of genetic differences between the baseline samples (heterogeneity of stocks). To predict how well the mixed-stock analysis model should be able to differentiate component fry types, we used allozyme data with Nei's index (Nei 1972) to calculate genetic distances between the parental strains. A dendrogram was constructed based on the Unweighted Pair Group Method of Analysis (UPGMA) cluster analysis using the 18 polymorphic loci (Figure 1).

Results

Acid phosphatase (formerly methylumbelliferyl phosphatase) could not be resolved in the fry samples; allelic frequencies for the remaining 17 loci are given in Table 1 with the frequencies for the 1995 year class of fry.

Mixed stock analysis of the 1996 year class of fry using the domestic and wild Green Lake strains both indicated that approximately 50% of the parental population was Superior strain and 15% was Seneca strain (Table 3). Analysis using the wild Green Lake strain apportioned 26% of the parental population to the Green Lake strain, whereas analysis using the domestic Green Lake strain apportioned the remaining parental population among the Clearwater, Green, and Manitou

strains. Parental contributions to the 1995 and 1996 year classes were similar using the wild Green Lake strain in the analysis; using the domestic Green Lake strain, Seneca and Superior strains had the highest contributions to both year classes, but Green Lake strain contributed more to the 1995 year class and Clearwater strain contributed 9% to the 1996 year class and was absent in the 1995 year class. The primary fry types differed considerably between years and between analyses (Table 3). Fry types which appeared most consistently in high frequencies were pure-strain Superior fry, Green x Seneca hybrids, and Seneca x Superior hybrids.

The accuracy of the mixed stock analysis model is decreased by a number of factors, including high similarity among learning samples, low mixture sample sizes, and missing learning samples. The UPGMA analysis indicated that, of the potential parental strains, the wild Green Lake and Superior strains were the most genetically similar (genetic distance = 0.003; Figure 1; see discussion in Kincaid et al. 1993). Therefore, we can predict that the mixed-stock analysis model will have the most difficulty resolving fry produced by these strains. This similarity likely accounts for the large proportion of fry attributed to Green x Superior hybrids in the analysis using wild Green Lake strain, which were attributed to pure-strain Superior in the analysis using domestic Green Lake strain. Even this potential confusion between two parental strains does not entirely explain the lack of consistency between year classes and between models (i.e., analyses using domestic versus wild Green Lake strain). The resolution problems caused by learning sample similarities are exacerbated by small sample sizes (i.e., when each component stock is represented by less than 50 individuals in the mixture; see Marsden et al. 1989). Thus, the low sample size of the 1996 year class (N=86) may be problematic, particularly considering that we lacked data in the 1996 mixture from one locus (ACP-1*); we also lacked data for almost half the individuals, due to poor resolution, for the highly variable loci PEP-PAP-1* and PEP-PAP-2* (Table 1).

Considering the above problems, we re-analyzed the data by only including in the model the strains which were likely to have been present and reproductively mature in 1994 and 1995. Given the high mortality rates of stocked fish (Holey et al. 1995), we conservatively set the reproductive ages between 6 and 15 years, i.e., only fish stocked between 1981 and 1990 (Tables

3 and 4). This excludes Green Lake strain from the model, as we can likely disregard the tiny number (522) of Green Lake strain fish which were stocked in 1989. When we analyzed the wild fry after removing Green Lake from the learning samples, both year classes were estimated to be comprised of 83-97% Superior strain. The variance estimates in this analysis were much lower than in the analyis which included Green Lake strain (Table 4). No fish were rejected by the model as unidentifiable when the Green Lake strain was omitted; this simply means that there were no fish with genotypes that could not be assigned to other strains in the model.

Discussion

The large majority (86%) of lake trout stocked into Lake Michigan through 1991 were Lake Superior strain (Table 2). Six percent of the remaining trout were Green Lake strain, and only 1.6% were Seneca strain (Table 2). An additional 5.3 million lake trout were stocked experimentally as unmarked fry by the University of Wisconsin-Madison, mostly in the northern portion of Green Bay; as the percentage of unmarked fish captured as adults has remained low, it is presumed that recruitment of these fish into the adult population was negligible (Holey et al. 1995). Based on stocking frequencies alone, we would expect a high contribution of Superior strain to naturally produced year classes. However, the Seneca strain has a history of successful reproduction throughout much of Lake Ontario which is in disproportion to the numbers stocked (Marsden et al. 1989, Perkins et al. 1995). Seneca strain also appears to reproduce successfully on shallow reefs, despite the fact that its native lake lacks shallow spawning areas. Thus, we might expect Seneca Lake strain to also perform well on a shallow reef in Lake Michigan. *A priori*, we would also predict that the Green Lake and Lewis Lake strains might be unusually successful in Lake Michigan, as these strains contain the only surviving remnants of the original Lake Michigan lake trout genome (Holey et al 1995, Kincaid et al. 1993). However, stocked fish belonging to these strains are likely to be too old or too young to have been significant contributors to the spawning population inb 1994 and 1995. By 1994, any surviving Green Lake strain trout were 18 years old and the oldest Lewis Lake fish were five years old (Table 2).

Analysis of the first year class of wild fry (1995) suggested that Seneca and Green Lake strains were, in fact, making a significant contribution to the fry (Marsden and May 1995). Addition of a second year class to the analysis produced inconsistent results between year classes and between models. Problems may be caused by small sample size in the 1996 year class, poor resolution of two enzymes, and confusion by the model between closely related strains (Superior and Green). The most conservative analysis, in which Green Lake strain was omitted from the model, indicated that the majority of the fry in both year classes were produced by Lake Superior strain. Estimates produced by this analysis indicate that the strain composition of the parental population in both years closely matches both the proportion of strains stocked in the whole lake. Compared with the strain composition of trout stocked in the southern portion of the lake (Illinois and Indiana waters only), however, there was a smaller contribution of Seneca Lake fish in the parental population than expected (Table 4); this is marked contrast to the behavior of Seneca Lake strain in Lake Ontario (Perkins et al. 1995). Future work in Lake Michigan should include analysis of larger samples of wild-caught fry, and analysis of several groups of fry from different years and (if possible) different reefs so that patterns in parental strain contributions can be observed. In addition, genetic data from the Lewis Lake strain should be included in the learning samples, as this strain has been stocked in large numbers since 1990 (Table 2).

Acknowledgments

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Literature Cited

Chotkowski, M. A., and J. E. Marsden. 1996. Lake trout research on Lake Michigan. Annual report to the Illinois Department of Natural Resources. Illinois Natural History Survey Technical Report 96/9 22 pp.

Grant, W. S., G. B. Milner, P. Krasnowski, and F. M. Utter. 1980. Use of biochemical genetic variants for identification of sockeye salmon (*Onchorhyncus nerka*) stocks in Cook Inlet, Alaska. Can. J. Fish. Aquat. Sci. 37:1236-1247

Grewe, P.M., Krueger, C.C., Marsden, J.E., Aquadro, C.F., May, B. 1994. Hatchery origins of naturally produced lake trout fry captured in Lake Ontario - temporal and spatial variability based on allozyme and mitochondrial DNA data. Trans. Am. Fish. Soc. 123:309-320

Holey, M. E., R. W. Rybicki, J. E. Marsden, G. W. Eck, D. Lavis, M. L. Toneys, T. Trudeau, E. H. Brown, Jr., and R. M Horrall. 1995. Progress toward lake trout restoration in Lake Michigan. J. Great Lakes Res. 21 (suppl. 1):384-399.

Jude, D. J., S. A. Klinger, and M. D. Enk. 1981. Evidence of natural reproduction by planted lake trout in Lake Michigan. J. Great Lakes Res. 7:57-61

Kincaid, H. L., C. C. Krueger, and B. May. 1993. Preservation of genetic variation in the Green Lake strains lake trout derived from remnant domestic and feral populations. N. Am. J. Fish. Soc. 13:318-325

Krueger, C. C., R. M. Horrall, and H. Gruenthal. 1983. Strategy for the use of lake trout strains in Lake Michigan. Wisconsin Department of Natural Resources, Admin. Report 17, Madison, WI.

Krueger, C. C., J. E. Marsden, H. L. Kincaid and B. May. 1989. Genetic differentiation among lake trout strains stocked into Lake Ontario. Trans. Am. Fish. Soc. 118:317-330.

Marsden, J. E. 1994. Spawning by stocked lake trout on shallow, inshore reefs in south-western Lake Michigan. J. Great Lakes Res. 20:377-384

Marsden, J. E., and B. May. 1995. Parental strain analysis of wild lake trout fry collected in southwestern Lake Michigan. Project report to the US Fish and Wildlife Service. Illinois Natural History Survey Technical Report 95/12 10pp.

Marsden, J. E., and J. Janssen. in review. Evidence of lake trout spawning on a deep reef in Lake Michigan: validation of an egg-collection method. J. Great Lakes Res.

Marsden, J. E., C. C Krueger, and B. May. 1989. Identification of parental origins of naturally produced lake trout fry in Lake Ontario: application of mixed-stock analysis to a second generation. N. Am. J. Fish. Manage. 9:257-268.

May, B. 1992. Starch gel electrophoresis of allozymes. In: Molecular Genetic Analysis of Populations: A Practical Approach. A. R. Hoelzel, ed. Oxford Univ. Press. pp 1-27 and 271-280.

Nei, M. 1972. Genetic distance between populations. Am. Nat.106:283-292.

Peck, J. W. 1979. Utilization of traditional spawning reefs by hatchery lake trout in the upper Great Lakes. Mich. Dept. Nat. Res., Fish. Rep. no. 1871. 33p

Perkins, D. L., J. Fitzsimons, J. E. Marsden, C. C. Krueger, and B. May. 1995. Differences in reproduction among hatchery strains of lake trout at eight spawning areas in Lake Ontario: genetic evidence from mixed stock analysis. J. Great Lakes Res 21(suppl. 1):364-374

Shaklee, J.B., F.W. Allendorf, D.C. Morizot, and G.S. Whitt. 1990. Genetic nomenclature for protein-coding loci in fish. Trans. Am. Fish. Soc. 119:2-15.

Wagner, W. C. 1981. Reproduction of planted lake trout in Lake Michigan. N. Am. J. Fish. Manage., 1:159-164.

Table 1. Allelic frequencies for 18 polymorphic protein loci in 135 wild lake trout fry hatched from eggs collected in 1994 and 86 wild lake trout fry collected in 1996 in Lake Michigan.

Enzyme	IUBNC number	Locus	Allele	Year class 1995	1996
acid phosphatase	3.1.3.2	ACP-1*	-100	0.993	-
			-140	0.007	-
			N	134	0
aspartate aminotransferase	2.6.1.1	AAT-1,2*	100	0.490	0.568
			85	0.510	0.432
			N	130	81
fumarase	4.2.1.2	FH-1,2*	100	0.910	0.90
			90	0.090	0.10
			N	132	82
glycerol-3-phosphate dehydrogenase	1.1.1.8	G3P-1*	100	0.966	0.983
			35	0.034	0.017
			N	134	86
glucose-6-phosphate isomerase	5.3.1.9	GPI-1*	100	0.985	0.983
			200	0.015	0.017
			N	133	86
L-lactate dehydrogenase	1.1.1.27	LDH-B3*	100	0.996	1.000
			78	0.004	0.000
			N	133	86
malate dehydrogenase	1.1.1.37	sMDH-B3,4*	100	0.985	0.965
			144	0.015	0.035
			N	134	86
malic enzyme	1.1.1.40	mMEP-2*	100	0.989	0.959
			115	0.011	0.041
			N	134	85
peptidase with phenyl-alanyl-proline	3.4.11-13	PEP-PAP-1*	100	0.295	0.443
			179	0.675	0.523
			138	0.030	0.034
			N	117	44
		PEP-PAP-2*	100	0.000	0.011
			179	1.000	0.989
			N	117	44
phosphoglycerate kinase	2.7.2.3	PGK-1*	-100	1.000	0.994
			-167	0.000	0.006
			N	134	86

Table 3. continued.

Enzyme	IUBNC number	Locus	Allele	Year class 1995	1996
phosphoglucomutase	5.4.2.2	PGM-2*	100	0.989	0.988
			150	0.011	0.012
			N	134	86
		PGM-3,4*	100	0.451	0.372
			94	0.510	0.551
			91	0.039	0.077
			N	127	84
superoxide dismutase	1.15.1.1	sSOD-2*	100	1.000	0.953
			85	0.000	0.047
			N	133	86

Table 2. Lake trout strains stocked into Lake Michigan prior to 1991. Lake Michigan (L. Mich.) and Lake Ontario (L. Ont.) strain fish are the progeny of fish stocked in each lake, and are likely a mixture of strains. The two pairs of rows at the bottom show the totals and proportions of each strain stocked within given time periods.

Year stocked	Superior	Green	Clearwater	Seneca	Jenny	Jenny x Lewis	Lewis	Manitou	L. Mich	L. Ont
1960	-	-	112,778	-	-	-	-	-	-	-
1961	-	-	94,823	-	-	-	-	-	-	-
1962	-	-	72,936	-	-	-	-	-	-	-
1963	-	-	-	-	-	-	-	-	-	-
1964	-	-	-	-	-	-	-	-	-	-
1965	1,273,878	-	-	-	-	-	-	-	-	-
1966	1,551,800	164,990	-	-	-	-	-	-	-	-
1967	1,705,660	177,805	-	-	-	-	-	-	-	-
1968	1,430,710	445,190	-	-	-	-	-	-	-	-
1969	1,760,590	239,215	-	-	-	-	-	-	-	-
1970	1,640,000	320,000	-	-	-	-	-	-	-	-
1971	2,128,145	115,400	-	-	-	-	-	-	-	-
1972	2,656,160	220,000	-	-	-	-	-	-	-	-
1973	2,110,450	293,700	-	-	-	-	-	-	-	-
1974	1,397,100	515,000	260,250	-	-	-	-	-	-	-
1975	1,305,374	886,000	235,713	-	-	-	-	-	-	-
1976	1,694,500	693,300	-	-	-	-	-	-	-	-
1977	2,327,000	-	47,500	-	-	-	-	-	-	-
1978	2,539,400	-	-	-	-	-	-	-	-	-
1979	2,321,173	-	13,900	-	-	-	-	-	-	-
1980	2,791,300	-	-	-	-	-	-	-	-	-
1981	2,395,020	-	-	-	33,000	-	-	-	-	-
1982	2,644,720	-	-	-	-	-	-	-	-	-
1983	2,130,090	-	31,480	-	-	-	-	-	31,480	-
1984	1,544,620	-	20,440	-	-	-	-	-	20,440	-
1985	3,126,339	-	-	453,704	-	-	-	-	-	-
1986	2,476,832	-	-	349,786	-	234,388	-	-	-	-
1987	1,871,400	-	-	24,984	-	-	-	-	-	-
1988	2,477,550	-	-	20,800	49,417	-	-	-	-	-
1989	4,622,296	522	-	27,223	175,091	-	-	287,965	-	-
1990	310,332	-	-	149,473	423,565	-	237,346	-	-	196,378
1991	977,456	-	-	-	-	-	1,588,166	-	-	213,853
1992	814,245	45,153	-	-	151,400	-	2,145,477	-	-	268,590
1993	484,902	253,202	-	-	-	-	1,716,900	-	-	242,831
1994	1,639,355	637,878	-	-	-	-	1,576,600	-	-	-
1960-91	55,209,895	4,071,122	889,820	1,025,970	681,073	234,388	1,825,512	287,965	51,920	410,231
percent	85.64	6.31	1.38	1.59	1.06	0.36	2.83	0.45	0.08	0.64
1981-90	23,599,199	522	51,920	1,025,970	681,073	234,388	237,346	287,965	51,920	196,378
percent	89.5	0.0	0.2	3.9	2.6	0.9	0.9	1.1	0.2	0.7

Table 3. Estimated parental strain contributions to 135 and 86 wild lake trout fry from the 1995 and 1996 year classes, respectively, in Lake Michigan. Wild = analysis using the wild Green Lake strain in the baseline; domestic = analysis using the domestic Green Lake strain in the baseline. A dash indicates absence of a strain contribution; an asterisk indicates estimates which were more that two standard deviations from zero. Cwl= Clearwater Lake, Jen = Jenny Lake, Grn = Green Lake, Man = Lake Manitou, Sen = Seneca, Sup = Superior.

	with Green Lake wild				with Green Lake domestic			
	1995		1996		1995		1996	
Fry type	Contrib.	S.D.	Contrib.	S.D.	Contrib.	S.D.	Contrib.	S.D.
Sup x Sup	0.001	0.001	0.393	0.212	0.366*	0.134	0.501*	0.132
Sen x Sen	-	-	0.040	0.038	0.014	0.071	0.055	0.051
Grn x Grn	0.005	0.015	0.002	0.007	-	-	-	-
Cwl x Cwl	-	-	-	-	-	-	-	-
Jen x Jen	-	-	-	-	-	-	-	-
Man x Man	-	-	0.039	0.041	-	-	0.066	0.058
Sup x Sen	0.434*	0.091	-	-	0.204	0.193	0.081	0.158
Sup x Grn	0.531*	0.095	0.057	0.216	-	-	-	-
Sup x Cwl	-	-	0.008	0.031	-	-	0.023	0.116
Sup x Jen	-	-	-	-	0.013	0.033	-	-
Sup x Man	-	-	-	-	0.008	0.043	0.002	0.004
Sen x Grn	-	-	0.222*	0.095	0.288*	0.088	0.059	0.084
Sen x Cwl	-	-	-	-	-	-	-	-
Sen x Jen	-	-	-	-	-	-	0.016	0.062
Sen x Man	-	-	-	-	-	-	0.033	0.065
Grn x Cwl	-	-	0.238*	0.094	-	-	0.136	0.101
Grn x Jen	-	-	-	-	-	-	-	-
Grn x Man	-	-	-	0.001	0.108	0.069	0.001	0.008
Cwl x Jen	-	-	-	0.001	-	-	0.027	0.028
Cwl x Man	0.029	0.023	-	-	-	-	-	-
Jen x Man	-	-	-	-	-	-	-	-
Proportion of each strain in parental population								
Superior	0.483		0.426		0.478		0.554	
Seneca	0.217		0.151		0.260		0.150	
Green	0.270		0.261		0.198		0.098	
Clearwater	0.015		0.123		-		0.093	
Jenny	-		-		0.006		0.022	
Manitou	0.015		0.039		0.058		0.084	

Table 4. Estimated parental strain contributions to 135 and 86 wild lake trout fry from the 1995 and 1996 year classes, respectively, in Lake Michigan, when Green Lake strain is omitted from the parental strain population. The proportion of each strain stocked between 1981 and 1990 is given for comparison. A dash indicates absence of a strain contribution; an asterisk indicates estimates which were more that two standard deviations from zero. Cwl= Clearwater Lake, Jen = Jenny Lake, Man = Lake Manitou, Sen = Seneca, Sup = Superior.

	1995		1996		Stocked proportions, 1981 through 1990	
Fry type	Contrib.	S.D.	Contrib.	S.D.	whole lake	IL and IN
Sup x Sup	0.965*	0.035	0.834*	0.086		
Sen x Sen	-	-	0.025	0.024		
Cwl x Cwl	-	-	-	-		
Jen x Jen	-	-	-	-		
Man x Man	-	-	0.089	0.059		
Sup x Sen	0.003	0.006	-	-		
Sup x Cwl	-	-	-	-		
Sup x Jen	0.031	0.039	0.042	0.057		
Sup x Man	-	-	0.010	0.051		
Sen x Cwl	-	-	-	-		
Sen x Jen	-	-	-	-		
Sen x Man	-	-	-	-		
Cwl x Jen	-	-	-	-		
Cwl x Man	-	-	-	-		
Jen x Man	-	-	-	-		
Superior	0.982		0.861		0.896	0.873
Seneca	0.002		0.025		0.039	0.126
Clearwater	-		-		0.002	-
Jenny	0.016		0.021		0.026	-
Manitou	-		0.094		0.011	-
other					0.026	0.001

Figure 1. Dendrogram generated by UPGMA cluster analysis of Nei's (1972) genetic distance coefficients based on 18 protein loci in lake trout.