Transactions of the American Fisheries Society 133:674–691, 2004
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Genetic Diversity of Wild and Hatchery Lake Trout Populations: Relevance for Management and Restoration in the Great Lakes

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Abstract.—The biological diversity of lake trout *Salvelinus namaycush* in the upper Great Lakes was historically high, consisting of many recognizable morphological types and discrete spawning populations. During the 1950s and 1960s, lake trout populations were extirpated from much of the Great Lakes primarily as a result of overfishing and predation by the parasitic sea lamprey *Petromyzon marinus*. Investigations of how genetic diversity is partitioned among remnant wild lake trout populations and hatchery broodstocks have been advocated to guide lake trout management and conservation planning. Using microsatellite genetic markers, we estimated measures of genetic diversity and the apportionment of genetic variance among 6 hatchery broodstocks and 10 wild populations representing three morphotypes (lean, humper, and siscowet). Analyses revealed that different hatchery broodstocks and wild populations contributed disproportionally to the total levels of genetic diversity. The genetic affinities of hatchery lake trout reflected the lake basins of origin of the wild source populations. The variance in allele frequency over all sampled extant wild populations was apportioned primarily on the basis of morphotype ($\theta_{MT} = 0.029$) and secondarily among geographically dispersed populations within each morphotype ($\theta_{ST} = 0.024$). The findings suggest that the genetic divergence reflected in recognized morphotypes and the associated ecological and physiological specialization occurred prior to the partitioning of large proglacial lakes into the Great Lakes or as a consequence of higher contemporary levels of gene flow within than among morphotypes. Information on the relative contributions of different broodstocks to total gene diversity within the regional hatchery program can be used to prioritize the broodstocks to be retained and to guide future stocking strategies. The findings highlight the importance of ecological and phenotypic diversity in Great Lakes fish communities and emphasize that the management of wild remnant lake trout populations and the restoration of extirpated populations should recognize and make greater use of the genetic diversity that still exists.

The lake trout *Salvelinus namaycush* of the upper Great Lakes (Lakes Michigan, Huron, and Superior) were historically abundant and biologically diverse. The size of the Great Lakes basin, the heterogeneous nature of lake habitats, and contributions from multiple isolated and phylogenetically distinct Pleistocene glacial refugia (Wilson and Hebert 1996) promoted geographical and ecophenotypic variation among lake trout populations (Brown et al. 1981; Goodier 1981; MacLean et al. 1981). Discrete lake trout populations were historically differentiated on the basis of spawning time and location, body type and coloration, and occupancy of different water depths (Goodier 1981). As many as 12 phenotypes are believed to have existed in Lake Huron alone (Eshenroder et al. 1995), and many more were thought to have been present in Lake Superior, particularly around Isle Royale (Rakestraw 1968). Numerous anecdotal accounts describe the diversity of lake trout populations in Lake Michigan, Lake Huron, and Lake Superior, adding testimony to the importance of different lake trout stocks to the historical Great Lakes fish community structure (Thomson 1883; Goode 1884).

Habitat degradation from pollution and eutrophication, overfishing, and the invasion of the sea lamprey *Petromyzon marinus* decimated lake trout populations throughout the upper Great Lakes

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Received January 22, 2003; accepted November 10, 2003

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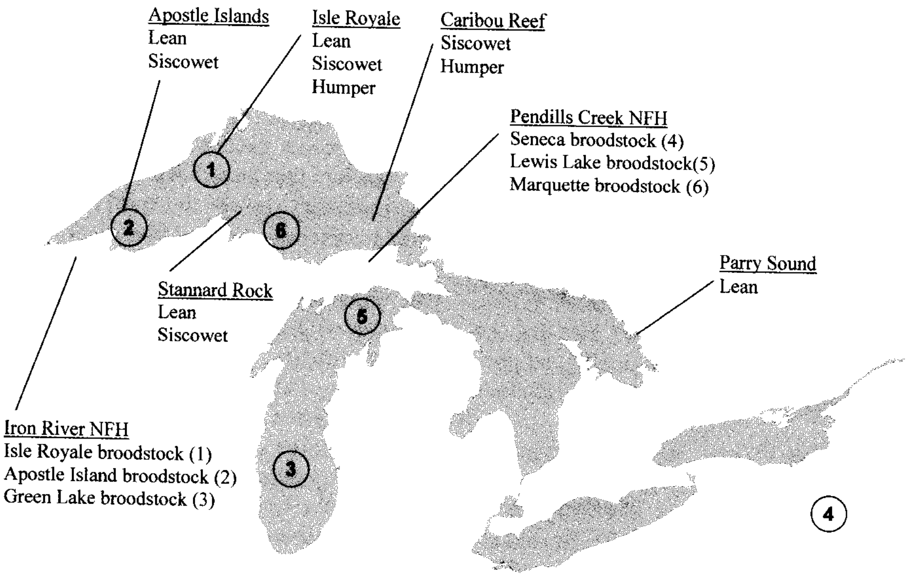


FIGURE 1.—Locations of origin (1 = Isle Royale, 2 = Apostle Islands, 3 = Green Lake, 4 = Seneca Lake, 5 = Lewis Lake, and 6 = Marquette) for hatchery broodstocks and wild populations and morphotypes (humper, lean, or siscowet) of lake trout sampled. The abbreviation NFH stands for National Fish Hatchery.

(Cornelius et al. 1995; Eshenroder et al. 1995; Hansen et al. 1995; Holey et al. 1995). By the early 1950s, wild lake trout populations were completely extirpated from Lake Michigan (Eschmeyer 1957) and U.S. waters of Lake Huron (Eshenroder et al. 1995). Remnant wild populations survived in Georgian Bay of Lake Huron (Berst and Spangler 1973) and in Lake Superior around Isle Royale, the Apostle Islands, Caribou Reef, and Stannard Rock (Figure 1; Rahrer 1965; Swanson and Swedberg 1980; Curtis 1990; Hansen et al. 1995).

Of the diversity that once existed, only three recognized morphotypes, defined on the basis of phenotypic and life history characteristics, remain (lean, siscowet, and humper; review in Krueger and Ihssen 1995; Figure 1). Lean lake trout have a streamlined shape and inhabit inshore waters (<70 m). Lean lake trout spawn in shallow nearshore waters (<18 m) during the months of October and November (Goode 1884). Siscowet lake trout are characterized by a robust body and higher body fat content and inhabit deeper offshore waters (70–150 m) (Goode 1884; Eschmeyer and Phillips 1965). Siscowets in spawning condition have been captured throughout the year (Eschmeyer 1957; Bronte 1993). Humper lake trout reside near isolated offshore reefs (or "humps") commonly surrounded by water deeper than 100 m (Rahrer 1965). Phenotypically, humper lake trout are intermediate to leans and siscowets, and possess intermediate levels of body fat (Eschmeyer and Phillips 1965). Humper lake trout are generally smaller, mature at smaller sizes than leans and siscowets, are long-lived (Rahrer 1965; Burnham-Curtis and Bronte 1996), and spawn in September (sometimes as early as August [Rahrer 1965]). All three morphotypes occur only in Lake Superior (Goodier 1981). Remnant lean lake trout populations occur within Georgian Bay of Lake Huron (Berst and Spangler 1973).

In 1955, the Great Lakes Fishery Commission was established to facilitate efforts to control the sea lamprey and restore the Great Lakes fish community structure, including lake trout (Fetterolf 1980). A major emphasis of the lake trout restoration effort has been on stocking offspring from domestic lake trout hatchery strains (Fetterolf 1980) and conserving remnant populations. Currently, progeny from six broodstocks that are maintained in the U.S. Fish and Wildlife Service hatchery system are annually stocked into U.S. waters of the upper Great Lakes (Figure 1; Krueger and Ihssen 1995).

The six hatchery broodstocks and wild lake trout populations of Lake Superior represent the remaining stocks available for restoration efforts in U.S. waters of the upper Great Lakes (Figure 1; Appendix 1). The selection of source stocks to develop broodstocks was based on political considerations, the life history traits of source populations, source population availability, and desires to maximize use of the available genetic and ecological diversity of lake trout populations still existing within the Great Lakes basin (Krueger et al. 1983). All of the broodstocks currently used for restoration efforts were developed from natural lean lake trout populations, as lean lake trout were preferred by sport and commercial fisherman (Krueger et al. 1983). Preference for the lake trout phenotype of greatest recreational and economic value precluded the development of broodstocks from the full complement of ecologically and phenotypically differentiated forms (i.e., siscowets and humpers).

The need to identify and incorporate existing biological and genetic diversity into conservation and restoration programs for fish species has been widely advocated (MacLean et al. 1981; Burnham-Curtis et al. 1995; Meffe 1995; Minckley 1995; Beardmore et al. 1997). However, conservation programs often do not recognize or utilize the diversity present across populations of a given species (i.e., discrete stocks) due in part to sociological, economic, and political factors (Hynes et al. 1981; Brannon 1993). Restoration efforts should work to identify, conserve, and utilize a more complete complement of the biological and genetic diversity of imperiled fish species (Krueger et al. 1981; Meffe 1995; Anders 1998).

Previous studies have described the levels of genetic diversity within and relationships among hatchery broodstocks and wild lake trout populations (review in Krueger and Ihssen 1995). Previous research, based primarily on protein allozymes, has documented significant differences in allele frequency among wild populations within and between lake trout morphotypes in Lake Superior (Dehring et al. 1981; Ihssen et al. 1988). Ihssen et al. (1988) found significant differences in allele frequency between geographically distant lean lake trout populations in Lake Superior. Dehring et al. (1981) found that different lake trout morphotypes (siscowets and humpers) surveyed within a given location were more similar in allele frequency than were different populations of the same morphotype sampled from across the Lake Superior basin. Krueger et al. (1989) also found significant differences in allele frequency between lean and siscowet morphotypes sampled from the same region of Lake Superior. Hatchery broodstocks developed from lean populations across the Great Lakes region also differ significantly in allele frequency (Krueger et al. 1989). In general, previous genetic studies of lake trout populations have primarily evaluated either hatchery or wild populations separately. Hatchery broodstocks and wild populations have not been thoroughly evaluated simultaneously in a management context.

This project used highly polymorphic microsatellite loci that have been shown to possess high discriminatory power in resolving relationships among contemporary and historical lake trout populations (Page et al. 2003; Guinand et al. 2003). Our objectives were to (1) quantify the genetic diversity within and among hatchery and wild lake trout populations in the upper Great Lakes, (2) identify populations of conservation priority based on their relative contributions to genetic diversity, and (3) resolve genetic affinities among morphotypes and geographically disjunct lake trout populations. The implications of genetic data for ongoing and future lake trout management and restoration are discussed.

Methods

Sample collection.—Six hatchery strains and remnant wild populations representing all three remaining lake trout phenotypes were sampled. All hatchery broodstocks were sampled in the fall of 1998 during routine spawning activities by hatchery personnel from the Pendill's Creek/Hiawatha National Forest Fish Hatchery in Michigan and Iron River National Fish Hatchery in Wisconsin (Figure 1; Table 1). The geographic origins of each broodstock and historical information on broodstock development are provided in Figure 1 and Appendix 1, respectively. Samples consisted of fin clips (~1 cm^2) that were removed from caudal fins and stored individually in high-salt buffer (4 M urea, 0.2 M NaCl, 0.1 M tris-HCl, 0.5% Sarcosine, and 10 mM EDTA). Fin clips were stored at -20°C until analyzed.

The remnant wild lake trout populations sampled represent the remaining vestiges of wild lake trout in the U.S. waters of Lake Superior and all of Lake Huron. Ten wild lake trout populations were sampled from four locations in Lake Superior and one in Lake Huron (Table 1; Figure 1) during summer (late June to August) and/or fall (October and November). Low sample sizes for some localities (Apostle Islands and Stannard Rock) were supplemented with archival scale samples collected in 1991 and 1993 that were obtained from the same locations by the Wisconsin Department of Natural Resources' Bayfield Field Station. Lake trout designated as originating from Caribou Island were collected from a reef complex near Caribou Island. To provide comparative population

TABLE 1.—Wild and hatchery populations of lake trout sampled.

Location	Morphotype	Number	Year[a]	Tissue type
		Wild		
Lake Superior				
Isle Royale	Lean	70	1991, 1993, 1995	Liver, scales
	Siscowet	94	1991, 1993, 1995	Liver, scales
	Humper	55	1995	Liver, fin
Apostle Islands	Lean	67	1991, 1993, 1995	Liver, scales
	Siscowet	63	1991, 1993, 1995	Liver, scales
Stannard Rock	Lean	85	1995	Liver
	Siscowet	64	1995	Liver
Caribou Island[b]	Siscowet[c]	67	1995	Liver
	Humper	72	1995, 1998	Liver, fin
Lake Huron				
Parry Sound (Georgian Bay)	Lean	50	2000	Fin
		Hatchery		
Lake Michigan				
Lewis Lake	Lean	200	1998	Fin
Green Lake	Lean	166	1998	Fin
Lake Superior				
Apostle Islands	Lean	200	1998	Fin
Isle Royale	Lean	200	1998	Fin
Marquette	Lean	200	1998	Fin
Seneca Lake	Lean	200	1998	Fin

[a] Wild populations sampled in late summer or fall.

[b] Samples were collected from a large complex of reefs surrounding Caribou Island.

[c] Caribou Island siscowet samples supplemented with individuals from nearby siscowet populations (Grand Marais and Whitefish Point, Michigan).

samples of lake trout phenotypes within and across locations, samples of siscowets from adjoining areas along the southeastern shore of Lake Superior (between Grand Marais and Whitefish Point, Michigan) were included with the Caribou Island siscowet samples. Tissue samples were preserved in ethanol, and scales were preserved dried and/or stored at −20°C.

Samples from some localities might represent admixtures given that a number of lean lake trout from each population were collected during the summer months (late June to August) and not during the fall spawning season (October and November). Population admixture could reduce our ability to elucidate differences in allele frequency among lake trout populations. To evaluate the possibility that samples were admixtures, we tested for significant deviations in genotypic frequencies from expectations under Hardy-Weinberg equilibrium using Fisher's exact tests in GENEPOP (Raymond and Rousset 1995). Nominal significance levels ($\alpha = 0.05$) were adjusted for multiple testing with sequential Bonferroni methods (Rice 1989).

DNA extraction.—DNA extraction of liver and fin tissue was performed by means of proteinase K digestion and a modified Puregene extraction protocol (Gentra, Inc.). The DNA was resuspended in 50 μL of tris-EDTA buffer (10 mM tris-HCl [pH 8.0], 1 mM EDTA). Fluorometry was used to determine DNA concentrations; RNase (2 μL of a 20 mg/μL solution) was added to each sample. One hundred nanograms of DNA was used for each polymerase chain reaction (PCR).

A Chelex procedure was utilized for DNA extraction from scale samples. Scales (3–5) were added to 250 μL of a suspension of 5% Chelex and 10 mM tris-HCl (pH 7.5–8.0). Scales were digested overnight with 3 μL of proteinase K. Proteinase K was subsequently inhibited at 95°C for 5 min, and samples were centrifuged at 12,000 × gravity for up to 10 min. The supernatant was then removed, and 2.5 μL of supernatant was used for each PCR.

Microsatellite screening.—Nine polymorphic microsatellite markers were assayed (Table 2). Polymerase chain reactions were performed in 25-μL volumes with concentrations recommended by the respective authors. The PCR profiles involved a single 2-min denaturing step at 94°C followed by 30 cycles of a 1-min denaturing step at 94°C, a 1-min annealing step at various temperatures (Table 2), and a 1-min extension step at 72°C. The

TABLE 2.—Microsatellite loci used in the analysis of the genetic structure of wild and hatchery lake trout populations of the upper Great Lakes.

Locus	Annealing temperature (°C)	Primer sequence (5′–3′)[a]
Ogo1a[b]	52	F: GAT CTG GGC CTA AGG GAA AC R: ACT AGC GGT TGG AGA ACC C
Ogo1c[b]	48	F: CAA TCG CTC TCT CGC TAC ACT R: CGC AAG CCC AAA CAG ATA A
Oneμ9[c]	54	F: CTC TCT TTG GCT CGG GGA ATG TT R: GCA TGT TCT GAC AGC CTA CAG CT
Oneμ10[c]	46	F: ATG GGG AAC AGA AGA GGA AT R: CTG TAG GTG TGA AAT GTA TTT AAA
Scou19[d]	46	F: CTT GAA ATT AGT TAA ACA GC R: CAA AAC TAC CCA ATA ATC
Sfo1[e]	60	F: ACC ATA ACC CCC CAC CAC R: GTC CCT CCG TGG CAG ATT
Sfo12[e]	60	F: GGT TTT GAA GAG TGA CAG R: CCC GTT TCA CAA TCA GAG
Sfo18[e]	56	F: TGG TGT ATC CTG CTG TTT TCT R: TGG AAT GTG TGT CTG TTT TCT
Ssa85[f]	56	F: AGG TGG GTC CTC CAA GCT AC R: ACC CGC TCC TCA CTT ATT C

[a] F = forward, R = reverse.
[b] Olsen et al. (1998).
[c] Scribner et al. (1996).
[d] Taylor et al. (2001).
[e] Angers et al. (1995).
[f] O'Reilly et al. (1996).

profiles for DNA extracted from scales required 35 cycles. The PCR products were screened by means of 6% polyacrylamide gels. Products were visualized by a Hitachi FMBIO II Multi-View scanner and associated software. Microsatellite fragments were sized manually using 20-base-pair internal lane standards. Two or more individuals of known genotype were evenly spaced among the samples to be screened as an additional means of standardization in scoring across gels.

Statistical analysis.—Measures of genetic diversity (allele frequencies, heterozygosities, and the average number of alleles) were estimated for all wild populations and broodstocks with BIOSYS I (Swofford and Selander 1981). Since individual populations can contribute disproportionately to measures of total diversity across all of the populations surveyed (Petit et al. 1998), we estimated the levels and partitioning of genetic diversity within and among hatchery and wild populations using the program CONTRIBUTE (Petit et al. 1998). This program estimates the relative contributions (C_t) of population (k) to total gene diversity (Nei 1973) across all populations surveyed (n) by comparing the total diversity of all populations to the diversity excluding the kth population. The relative contribution of the kth population to total diversity was apportioned into estimates of the diversity within the kth population (C_s) and the genetic divergence or uniqueness of the kth population from other populations (C_d). Population divergence or uniqueness was expressed as the mean pairwise differentiation of the kth population from all other populations (G_{St}; Nei 1973).

The relative contributions of populations based on allelic diversity or richness (adjusted for population differences in sample size) were also estimated. Populations were evaluated on the basis of their contributions to overall allelic richness (C_{rt}), which was assessed (1) as a relative measure of the number of alleles observed (C_{rs}) and (2) according to whether populations possessed alleles not present in other populations (C_{rd}). Analyses were performed separately for hatchery broodstocks, wild lean populations, and all wild Lake Superior populations (across all morphotypes).

Components of allelic variance were estimated among individuals (F), among individuals within populations (f), and among populations (θ_{ST}). Estimates of the variance in allele frequency for all loci were derived for hatchery and wild populations separately with the program FSTAT (Goudet 2000). Since lake trout populations consist of different morphotypes, an additional estimate of the variance among morphotypes (θ_{MT}) was calculated for wild populations in Lake Superior. Significance tests were performed using permutations (N = 1,000). Hierarchical analysis of the wild populations of Lake Superior lake trout was performed using the program GDA (Lewis and Zaykin 2001). The rejection level for the null hypothesis that estimates of genetic variation were equal to zero was set at 0.05. Where appropriate, the rejection level was adjusted for multiple comparisons by means of a sequential Bonferroni method (Rice 1989). The genetic relationships among the populations evaluated were visualized as a consensus tree based on Cavalli-Sforza and Edwards chord distances (1967) generated in the program PHYLIP (Felsenstein 2002). The tree was generated by performing 1,000 bootstrap resamplings over loci using Seqboot, Neighbor, and Consense software implanted in the program PHYLIP.

Results

Contributions to Genetic and Allelic Diversity

Estimates of observed average heterozygosity for wild populations were consistently lower than those expected under Hardy-Weinberg equilibrium (Appendix 2). However, tests for population admixtures revealed evidence of an admixture (specific data not shown) only for the Caribou Reef siscowet population. Observed average heterozygosity was typically greater among hatchery broodstocks (range = 0.370–0.445; Appendix 3) than among wild populations (range = 0.355–0.398; Appendix 2). Allelic richness (r) ranged from 2.38 to 3.59 and was also typically greater among hatchery broodstocks than among wild populations (Table 3). Analysis of the contribution of individual populations to total genetic diversity revealed that several groups contributed disproportionately to that diversity (C_t; ranges = −0.040 to +0.051; Table 3). A number of groups (e.g., the Seneca Lake and Lewis Lake broodstocks and the Isle Royale and Stannard Rock wild lean lake trout) contributed greatly to total diversity due to their larger levels of intrinsic diversity (C_s; range = −0.147 to +0.014) and divergence (C_d; range = −0.012 to +0.151), while other groups (e.g., the Marquette broodstock and Caribou Island humpers) were characterized by comparatively high levels of total allelic richness (C_{rt}; range = −0.021 to +0.058), intrinsic allelic richness (C_{rs}; range = −0.042 to +0.024), and presence of unique alleles (C_{rd}; range = −0.025 to +0.051).

Genetic Differentiation among Broodstocks and Wild Populations

Analyses of genetic variance conducted for hatchery and wild populations separately revealed that the magnitude of the interpopulation (or broodstock) variance in allele frequency differed (Table 4). The variance was greater among hatchery broodstocks (mean θ_{ST} = 0.058, $P < 0.01$) than among wild populations (θ_{ST} = 0.024, $P < 0.01$). Within Lake Superior, the variance between morphotypes (θ_{MT} = 0.029; $P < 0.01$) was greater than that among geographic locales for each morphotype (θ_{ST} = 0.024; $P < 0.01$). The variance among wild populations was greater when wild populations from all lakes (i.e., including Parry Sound lean lake trout) were analyzed (θ_{ST} = 0.033).

As demonstrated by the neighbor-joining tree (Figure 2), the genetic affinities among wild populations and broodstocks were based primarily on lake basin of origin (broodstocks and wild populations) and morphotype. The Seneca Lake broodstock and Parry Sound lean lake trout population were the most genetically distinct groups. Broodstocks developed from the same basin were genetically more similar to each other than to broodstocks developed from other basins. The differences in allele frequency across all wild populations were most notable among populations from different basins (i.e., the Parry Sound population from Lake Huron and populations from Lake Superior; Figure 2). Within Lake Superior, genetic relationships among populations were best explained by morphotype irrespective of location of origin.

Discussion

Population levels of genetic diversity are most completely characterized based on multiple measures (Petit et al. 1998), including the relative contributions to total allelic diversity or richness and the divergence from other populations. Allelic richness is an important diversity measure because populations subjected to bottlenecks or to prolonged periods of low effective population size may retain high levels of heterozygosity while losing large numbers of alleles (Petit et al. 1998). As was observed in this study, populations can contribute disproportionately to one or both measures (Table 3). Population contributions to total diversity and allelic richness can be used to prioritize management strategies for remnant wild lake trout populations as well as for broodstock perpetuation and stocking to maintain the current genetic diversity and to maintain or create stock structure.

TABLE 3.—Components of genetic diversity (Petit et al. 1997) estimated for lake trout hatchery broodstocks, wild lean lake trout populations, and all wild lake trout morphotypes of Lake Superior. Components are defined as follows: $r(82)$ = the allelic richness rarefaction number ($2N$), where N is the smallest sample size of all populations surveyed within each category; h_k = expected heterozygosity; G_{ST} = the average relative divergence of the kth population from the other populations; C_t = the contribution of the kth population to total diversity; C_s = the contribution of the kth population to total diversity based on k's own diversity; C_d = the contribution of the kth population to total diversity due to k's allelic divergence or uniqueness; C_{rt} = the contribution of the kth population to total allelic richness; C_{rs} = the contribution of the kth population to total allelic richness due to k's own allelic richness; and C_{rd} = the contribution of the kth population to total allelic richness due to k's allelic divergence or uniqueness.

Sample	$r(82)$	h_k	G_{ST}	C_t	C_s	C_d	C_{rt}	C_{rs}	C_{rd}
Hatchery broodstocks									
Lewis Lake	3.27	0.448	0.063	0.014	0.013	0.001	0.058	0.007	0.051
Seneca Lake	2.38	0.449	0.110	0.051	0.014	0.038	−0.021	−0.042	0.020
Apostle Islands	3.37	0.411	0.038	−0.015	−0.003	−0.012	0.001	0.013	−0.012
Marquette	3.59	0.373	0.050	−0.028	−0.020	−0.008	0.000	0.024	−0.025
Green Lake	2.88	0.419	0.041	−0.011	0.000	−0.011	0.001	−0.020	0.021
Isle Royale	3.46	0.410	0.046	−0.012	−0.004	−0.009	0.013	0.018	−0.004
Wild lean lake trout									
Isle Royale	3.12	0.426	0.014	0.004	−0.147	0.151	0.010	0.021	−0.011
Stannard Rock	2.82	0.436	0.024	0.037	0.023	0.013	−0.007	−0.028	0.021
Apostle Islands	3.04	0.387	0.019	−0.040	−0.035	−0.005	0.018	0.008	0.011
All wild lake trout									
Isle Royale									
Lean	3.04	0.426	0.031	0.006	0.002	0.003	−0.009	0.001	−0.010
Siscowet	3.15	0.425	0.020	0.001	0.002	−0.001	−0.002	0.005	−0.003
Humper	2.86	0.417	0.029	−0.001	0.000	−0.001	0.000	−0.006	0.006
Apostle Islands									
Lean	2.97	0.387	0.030	−0.008	−0.009	0.001	−0.003	−0.002	0.002
Siscowet	2.99	0.407	0.020	−0.004	−0.003	−0.001	−0.003	−0.001	−0.002
Stannard Rock									
Lean	2.76	0.436	0.031	0.007	0.005	0.002	−0.003	−0.010	−0.007
Siscowet	2.94	0.437	0.024	0.005	0.005	−0.001	0.002	−0.027	0.005
Caribou Island									
Siscowet	3.13	0.412	0.018	−0.004	−0.002	−0.002	−0.001	0.005	−0.006
Humper	3.28	0.416	0.025	−0.001	−0.001	0.000	0.016	0.010	0.006

Genetic Diversity within and among Wild Populations

Two hypotheses have been proposed to explain how genetic diversity is partitioned among wild lake trout populations from Lake Superior. The lake trout populations of the Great Lakes and eastern Canada are believed to have originated from three Pleistocene glacial refugia (the Beringian, Mississippian, and Atlantic; Wilson and Hebert 1996). As lake trout recolonized the Great Lakes, the populations and preexisting morphotypes may have segregated on the basis of physiological adaptations. Phenotypic variation among lean, siscowet, and humper lake trout probably reflects long-standing adaptations to local environmental regimes. Experimental evidence indicates that physiological differences (e.g., gas retention [Ihssen and Tait 1974] and fat content [Eschmeyer and Phillips 1965]) among lake trout morphotypes are hereditable and not plastic responses to the environments occupied. Further, the lean and siscowet morphotypes have been found to exhibit distinct forage preferences (Harvey et al. 2003). The reproductive isolation of lake trout morphotypes is probably mediated (spatially and temporally) by the occupation of different habitats (water depth, temperature, and pressure), tendencies to spawn at different times of the year (which are related to water temperature), and fidelity to spawning sites.

An alternative hypothesis proposes that genetic diversity is mainly partitioned spatially across the lake basin (i.e., that genetic affinities among populations are a function of geographic proximity) rather than among morphotypes. The presence of the same morphotype in geographically disparate locales represents either phenotypic plasticity or convergent evolution. Subpopulations within a lake region (across all morphotypes) share common and recent ancestry or are experiencing gene flow at different rates within and between mor-

TABLE 4.—Summary of F-statistics partitioning genetic variation in allele frequency within and among hatchery and wild populations of lake trout from the upper Great Lakes. The statistics reflect the allelic variance among all individuals (F), among individuals within populations (f), among populations within hatchery broodstocks and morphotypes (leans, humpers, and siscowets; θ_{ST}), and among lake trout morphotypes (θ_{MT}); $P < 0.05$ *, $P < 0.01$ **.

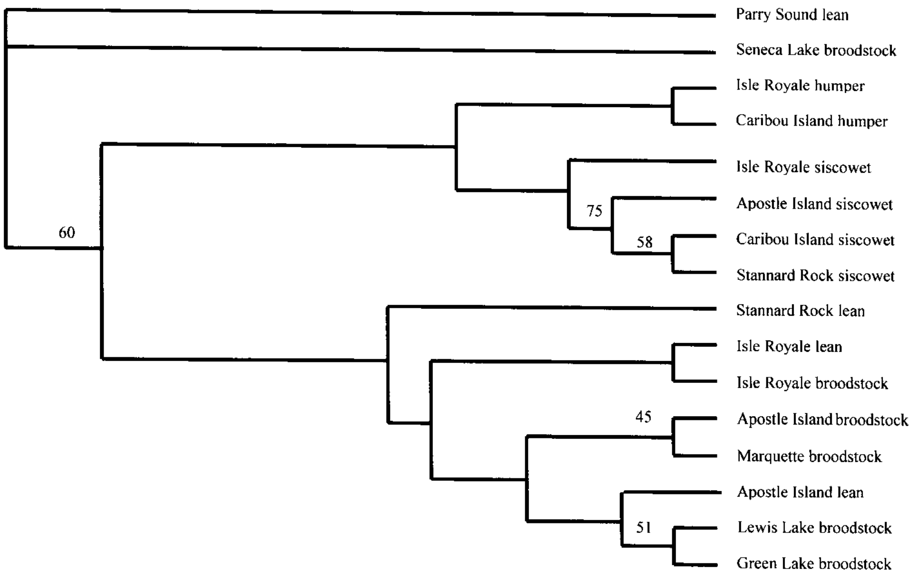
Population and mean	Locus	F-statistic			
		F	f	θ_{ST}	θ_{MT}
Hatchery (N = 6)	*Sfo18*	−0.012	−0.086	0.068**	
	Sfo1	0.073*	−0.226	0.094**	
	Oneμ9	0.055	0.051	0.004**	
	Oneμ10	−0.054	−0.116	0.055**	
	Ogo1a	0.086*	−0.029	0.111**	
	Scou19	0.023	−0.005	0.028**	
	Ssa85	0.006	−0.056	0.059**	
	Sfo12	0.014	−0.020	0.033**	
	Ogo1c	0.538**	0.501*	0.074**	
Mean		0.081**	0.002	0.058**	
		(0.000, 0.259)	(−0.062, 0.205)	(0.043, 0.082)	
Wild (Lake Superior; N = 9)	*Sfo18*	0.091**	0.028	0.065**	0.086**
	Sfo1	0.115**	0.080*	0.039**	0.050**
	Oneμ9	0.015	−0.002	0.017**	0.019**
	Oneμ10	−0.038	−0.051	0.013**	0.011
	Ogo1a	0.043	0.030	0.014**	0.015**
	Scou19	0.046*	0.034	0.013**	0.018**
	Ssa85	−0.026	−0.045	0.019**	0.024**
	Sfo12	0.022	0.016	0.007	0.007
	Ogo1c	0.657**	0.647**	0.029**	0.031**
Mean		0.103**	0.082**	0.024**	0.029**
		(0.011, 0.312)	(−0.010, 0.296)	(0.014, 0.040)	(0.017, 0.051)
All wild[a]	All wild[2]	0.078**	0.103**	0.033**	
		(0.012, 0.312)	(−0.009, 0.291)	(0.017, 0.042)	

[a] Includes Parry Sound population from Lake Huron.

photypes. This hypothesis is supported by previous genetic studies employing allozymes that documented significant differences in allele frequency among widely dispersed populations within a given morphotype (review in Krueger and Ihssen 1995). For example, analyses of lake trout populations from Isle Royale, Stannard Rock, and Caribou Island revealed that the genetic differences among populations of the same morphotype across Lake Superior were greater than those among morphotypes from within the same location (Dehring et al. 1981). Similarly, based on allozyme data, northern Lake Superior lean lake trout populations differed significantly from southern Lake Superior populations (Ihssen et al. 1988).

Our analyses revealed that morphotype represents a fundamental source of variance among wild lake trout populations in the Lake Superior basin. Populations of the same morphotype collected from across Lake Superior were more similar in allele frequency than they were to other morphotypes sampled from the same location (θ_{MT} = 0.029); however, comparative structuring based on geographic location exists (θ_{ST} = 0.024; Table 4; Figure 2). For example, the allele frequencies of Caribou Island siscowets were more similar to those of Isle Royale siscowets than they were to those of Stannard Rock lean lake trout or Caribou island humpers. Lean and siscowet populations also possessed greater genetic affinities with other geographically proximate lean and siscowet populations than with distant populations (Figure 2), which is consistent with the results of an allozyme analysis of Lake Superior lean lake trout populations performed by Ihssen et al. (1988). Therefore, our microsatellite data support the hypothesis that the morphotypes diverged genetically prior to recolonization or that the higher contemporary levels of gene flow are realized more within than between morphotypes.

Population genetic structuring resolved by both allozyme and microsatellite genetic markers has been found to be concordant in studies of several fish species (Sanchez et al. 1996; Scribner et al. 1996, 1998). Inconsistencies between allozyme and microsatellite genetic markers in resolving population genetic structure have been attributed to the higher levels of variation (and accordingly finer resolution) of microsatellite markers (Goudet et al. 1996; Ruzzante et al. 1999; Shaw et al. 1999) or factors related to the nonneutrality of allozyme markers (Avise 1994; Dufresne et al. 2002). The



Parry Sound lean
Seneca Lake broodstock
Isle Royale humper
Caribou Island humper
Isle Royale siscowet
Apostle Island siscowet
Caribou Island siscowet
Stannard Rock siscowet
Stannard Rock lean
Isle Royale lean
Isle Royale broodstock
Apostle Island broodstock
Marquette broodstock
Apostle Island lean
Lewis Lake broodstock
Green Lake broodstock
60
75
58
45
51

FIGURE 2.—Neighbor-joining trees representing the genetic divergence among lake trout hatchery broodstocks and wild lake trout populations based on Cavalli-Sforza and Edwards (1967) chord distances. Numbers represent bootstrap values over 1,000 replicates that exceed 40%.

differences between our results and those of previous studies may also be due to differences in sampling strategy. The lake trout samples collected by Dehring et al. (1981) were collected in the spring (May), typically the point when Lake Superior lean lake trout have migrated the greatest distances from their spawning sites (Rahrer 1968). Given the high probability that the lean lake trout populations sampled represented admixtures of populations, Dehring et al. (1981) pooled all lean samples for analysis. This pooling may have confounded resolution of the genetic relationships among lake trout morphotypes. Further, all of the lake trout samples assayed by Dehring et al. (1981) were collected by commercial fishermen. Inconsistencies among fisherman in classifying morphotypes may have also confounded the analyses, potentially increasing the genetic similarity between morphotypes (Dehring et al. 1981).

Given our broad geographic coverage and current knowledge of lake trout movements and spawning behavior, we believe that although some of our samples were collected in the summer (late June to August) these samples represent geographically distinct populations. Evaluations of lake trout migration patterns found that most (94%) of the lean lake trout collected at an Apostle Islands spawning site and tagged were recovered within 80 km of the site of tagging and all of the lake trout recaptured during the following August were within 40 km of the spawning site (Rahrer 1968). Our most proximal sites were approximately 100 km apart. Further, humper lake trout have been found to be sedentary, possessing strong affinities for certain reef sites (Lawrie and Rahrer 1973). Humpers have also been observed in spawning condition as early as August in the waters surrounding Isle Royale (Burnham-Curtis 1993) and in October near Caribou Island (Hansen et al. 1995). Siscowets have a very protracted spawning period, and individuals in spawning condition have been collected from early spring (April; Bronte 1993) to late fall (November; Eschmeyer 1955). Given that most direct observations of lake trout movement did not exceed intersite distances and that spawning periods coincided with our sampling dates, we believe that the sampling of admixed populations was unlikely. If present, sampling artifacts and population admixture would have detracted from our ability to reject the null hypothesis of no structure.

Our findings of significant differences in allele frequency argue strongly for restricted gene flow among leans, siscowets, and humpers, even when these morphotypes exist in close proximity. Reproductive isolation most likely results from other spatial (water depth) and temporal (temperature-dependent) segregation during spawning. Each morphotype represents a significant component of the overall genetic diversity of wild Lake Superior lake trout. The Isle Royale humper population, for example, possessed unique alleles (C_{rd} = 0.006; Table 3) despite a low allelic richness (r = 2.86), which is characteristic of a reproductively isolated population subjected to genetic drift (i.e., low allelic diversity but high divergence from other populations). Our data are consistent with mark–recapture data of humper lake trout (reviewed in Dehring et al. 1981) corroborating evidence of the restricted movement of this lake trout morphotype (Burnham-Curtis and Bronte 1996). Genetic affinities among widely dispersed humper populations probably reflect common ancestry.

Wild populations were also geographically structured on a larger spatial scale, namely, by lake basin. The Parry Sound population of Lake Huron was genetically differentiated from all Lake Superior populations (Figure 2). Addition of the Parry Sound population to the analysis of Lake Superior populations increased the overall variance among wild populations (from θ_{ST} = 0.024 to θ_{ST} = 0.033; Table 4).

Morphotypes contribute fundamentally to native fish community diversity in Lake Superior. In light of the evidence of significant genetic differentiation among morphotypes, lake trout morphotypes should be managed as distinct units in a manner similar to that advocated for imperiled Pacific salmon (i.e., Waples 1991). Lake trout management should consider both phenotypic and spatial (stock) genetic differences.

Genetic data could also be used to identify wild populations as sources for the development of new broodstocks. Interest has grown in the development of new broodstocks from lake trout morphotypes other than the lean morphotype (Krueger and Ihssen 1995). The current broodstocks used for restoration efforts in the upper Great Lakes were all originally derived exclusively from wild lean populations. However, the lean populations within Lake Superior represent a small proportion of the overall diversity of wild lake trout in the upper Great Lakes (Figure 2). The methodology and data presented here can provide relative measures of the genetic diversity of wild populations that can be used in conjunction with other criteria to identify wild populations as potential sources for new broodstocks. If maximizing diversity is a desired restoration goal, the development of broodstocks from additional lake trout morphotypes could be considered (Figure 2).

Genetic Diversity within and among Broodstocks

We provide quantitative data showing that the relative contributions of different broodstocks to the total genetic diversity of fish held in captive facilities in the Great Lakes region reflect phylogeographic relationships among the wild progenitor populations (Figure 2) as well as the anthropogenic effects associated with generations of hatchery and management manipulations (Appendix 1). The genetic differences among broodstocks (mean θ_{ST} = 0.058; Table 4) were related to lake basin of origin (Figure 2). Lake trout from different glacial refugia could have contributed to the differences that we observed between lake basins and concomitantly to the broodstocks developed from the populations indigenous to those basins. The Seneca Lake broodstock was the only broodstock developed from fish that were completely isolated from upper Great Lakes lake trout populations, which probably accounts for their comparatively high measures of genetic diversity and divergence. The source of the Lewis Lake broodstock (Lewis Lake, Wyoming) was derived from multiple lake trout populations inhabiting northern Lake Michigan and lake trout from an unknown source (Appendix 1; reviews in Grewe and Hebert 1988 and Visscher 1983). Contributions from multiple sources may account for the Lewis Lake broodstock's high diversity and high contribution to total allelic richness and allelic uniqueness (C_{rt} = 0.058, C_{rd} = 0.051; Table 3). The Marquette broodstock exhibited low levels of genetic diversity (mean observed heterozygosity = 0.374; Appendix 3). The low gene diversity associated with the Marquette broodstock probably reflects this broodstock's long history of domestication (i.e., since 1949; Krueger et al. 1983). However, this broodstock exhibited the highest level of allelic richness (r = 3.59; Table 3) and contribution to total allelic richness based on intrinsic allelic diversity (C_{rs} = 0.024). Lake trout from the Green Lake and Apostle Islands broodstocks were added to the Marquette broodstock in the middle and late 1960s (Krueger et al. 1983), potentially contributing alleles currently present in the Marquette broodstock. Our analysis was consistent with previous studies that found comparatively high numbers of alleles per locus (Ihssen et al. 1988) and mitochondrial DNA haplotypes for the Marquette broodstock and wild lake trout populations sampled near the Marquette broodstock source population (Grewe and Hebert 1988; Wilson and Hebert 1996).

Despite multiple generations of domestication in hatchery environments, the present relationships among broodstocks reflect the genetic relationships of the historical populations within and among lake basins in the upper Great Lakes (Guinand et al. 2003). Thus, the historical genetic diversity (as reflected in the loci examined) associated with lake basin origin has been maintained during the development and perpetuation of these broodstocks.

Broodstock Management Considerations

Maintenance of genetic diversity is an important goal of the Great Lakes lake trout hatchery system (Holey 1997) and is widely embraced when hatcheries are used in a conservation context. Retention of high levels of genetic diversity over generations in adults maintained in hatcheries and in progeny to be released is dependent on adult effective population size and the mating regime (Waples et al. 1990; Busack and Currens 1995; Page 2001). Resources may not allow managers to simultaneously maintain broodstocks of sufficient size to satisfy the mandated objectives of minimizing generational declines in genetic diversity (Holey 1997; Page 2001) and maintaining large numbers of broodstocks. Our data may be used as a means of prioritizing retention or expansion of existing broodstocks, as has been proposed for wild remnant stocks.

To maintain large effective population sizes (Holey 1997)—and consequently genetic diversity—the lake trout hatcheries responsible for stocking within the upper Great Lakes currently maintain large numbers of adults (i.e., hundreds) within each broodstock (D. Bast, U.S. Fish and Wildlife Service, personal communication). Reductions in the numbers of adults across broodstocks could result in concomitant reductions in the effective population sizes of broodstocks. Using information on the genetic affinities among broodstocks (Figure 2) and the relative contributions of each broodstock to total diversity (Table 3), one can set priorities for the retention and consolidation of broodstocks. For example, combining broodstocks with similar ancestry (e.g., those from ancestral source populations from the same basin and geographically proximal locales) and high genetic affinities (Figure 2) may represent one means of maintaining high numbers of adults while preserving what we characterize to be the broodstocks (or broodstock mixtures) that represent the fundamental genetic architecture or genetic discordance within the hatchery system.

Lake trout stocking strategies in the upper Great Lakes have emphasized the simultaneous stocking of fish from multiple broodstocks so as to introduce progeny representing the greatest diversity possible and thereby increase the likelihood that some proportion of the stocked individuals are well matched to the habitats of specific stocking sites (Krueger et al. 1981, 1983, 1995). Due to the generation time of lake trout (6–8 years), this strategy was preferred over sequential stocking and assessment strategies employing one lake trout broodstock at a time (Krueger et al. 1981, 1983, 1995). Further, given the changing nature of the Great Lakes ecosystem, with increasing numbers and diversity of introduced species, contaminants, and other perturbations, adaptation clearly has been a moving target.

Different isolated populations (or broodstocks from genetically distinct source populations) may have evolved different complexes of alleles that interact well within one population but poorly when mixed by crossing adults from different populations. The concurrent stocking of juveniles from multiple and genetically divergent broodstocks (as identified herein) may increase the potential for interbreeding and subsequent loss of the phenotypic and genetic distinctness of the juveniles stocked. If stocked progeny survive to reproduce in nature, interbreeding between individuals from different hatchery broodstocks is likely given that hatchery adult lake trout that are returning to spawn exhibit fidelity for the sites where they were stocked as juveniles (Eshenroder et al. 1995; Hansen et al. 1995). Consideration should be given to the potential genetic consequences of systematic stocking of juveniles from multiple and genetically divergent broodstocks into identical locations (i.e., specific reef sites), especially given the increasing practice of stocking earlier life history stages of lake trout to encourage imprinting of juveniles to stocking sites (e.g., eggs; Bronte et al. 2002). Management decisions regarding the stewardship of domestic populations and the stocking of progeny can potentially produce both inbreeding and outbreeding depression, both of which can reduce the fitness of newly established populations (Lynch 1996).

Summary

The lack of success in restoring viable and self-sustaining populations of lake trout has prompted efforts to reevaluate recovery programs and research needs. Restoration efforts would be best based on biologically sound criteria founded on a greater fundamental understanding of the relationships between the genetic diversity of lake trout broodstocks (both historical and contemporary) and that of extant populations. Our analysis revealed that the genetic affinities among lake trout broodstocks and wild populations were based on basin of origin. The relative contributions of broodstocks and wild populations to genetic diversity were not uniform according to several criteria, including heterozygosity, allelic richness, and degree of genetic differentiation from other populations. The genetic relationships of lake trout hatchery broodstocks can be used as additional criteria guiding broodstock management and stocking efforts. Lake trout morphotypes should be recognized as distinct units for management. Evidence suggests that significant differentiation among natural populations occurs at both the micro- and macrogeographic scales.

Acknowledgments

Support for this project was provided by the Great Lakes Protection Fund, the Great Lakes Fisheries Trust, and the Michigan Sea Grant College Program. Support during analysis and manuscript preparation was provided by the Minnesota Department of Natural Resources (K. Page) and Michigan Department of Natural Resources PERM Program (K. Scribner). Hatchery samples were collected and the backgrounds of lake trout broodstocks provided by members of the Iron River, Pendill's Creek, and Jordan River National Fish Hatcheries, specifically, Dale Bast, Faber Bland, Dave Huntly, Denise Johnston, Crystal LeGault, Dave Radloff, and Rick Westerhof. Thanks to David Anderson, Chuck Bronte, Mark Holey, Jim Peck, Ruth Phillips, Mark Rude, and Steve Schram for providing wild lake trout samples. Thanks to Darryl Bathel, Dave Blick, Michael Donofrio, Randy Eshenroder, Mark Holey, John Huber, and Roger Hugill for the background information they provided on lake trout broodstocks. Comments from three reviewers and the journal editorial staff greatly improved the manuscript.

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Appendix 1: History of Lake Trout Broodstocks Used for Restoration Efforts in the Upper Great Lakes

Domestic broodstocks of lake trout were developed on the basis of the availability of wild remnant lake trout populations and a desire to utilize lake trout stocks native to the Great Lakes (Lawrie and Rahrer 1973; Peck 1975; Lawrie 1978; Swanson and Swedberg 1980; Krueger et al. 1983; G. Curtis, U.S. Geological Survey, Great Lakes Science Center, unpublished data). The Apostle Islands, Marquette, and Isle Royale broodstocks were developed from Lake Superior populations. The Marquette broodstock was developed in 1948 from lake trout populations sampled near Marquette, Michigan, along the southern shore of Lake Superior. At the time the Marquette broodstock was being developed, lake trout populations from southern Lake Superior had collapsed and lake trout populations near Marquette were the only remaining populations available (Lawrie and Rahrer 1973; Peck 1975; Lawrie 1978). The Marquette lake trout broodstock is the oldest of the hatchery broodstocks. The broodstock year-classes surveyed (1987 and 1988) were developed from the original 1948 year-class (Coberly and Horrall 1982; Krueger et al. 1983; Kincaid et al. 1997).

The Apostle Islands and Isle Royale broodstocks were derived in the middle 1990s from remnant wild lake trout populations from the Apostle Islands, Wisconsin, and Isle Royale, Michigan, both in Lake Superior. Like the Marquette broodstock, the Apostle Islands broodstock was developed opportunistically but with a desire to utilize native lake trout that were suspected of having survived the collapse and extirpation of other nearshore Lake Superior lake trout populations (Swanson and Swedberg 1980; Krueger et al. 1983). The Apostle Islands broodstock was developed from reciprocal crosses between two captive year-classes derived from wild Apostle Islands fish in 1985 and 1986 (D. Bast, U.S. Fish and Wildlife Service, personal communication; S. Schram, Wisconsin Department of Natural Resources, personal communication).

Populations sampled from locations around Siskiwit Bay, Isle Royale, between 1981 and 1986 were the progenitors of the Isle Royal broodstock (D. Bathel, Michigan Department of Natural Resources, personal communication). Multiple captive populations developed from five sampling years were reciprocally crossed to produce the two year-classes (1989 and 1993) surveyed in this study (D. Bast, personal communication).

The Green Lake and Lewis Lake broodstocks represent the remaining vestiges of the genetic diversity that historically existed in Lake Michigan. In an effort to develop broodstocks that reflected the phenotypic and behavioral characteristics of the extirpated lake trout populations, feral lake trout from Lewis Lake, Wyoming, and Green Lake, Wisconsin, were sampled to develop the Lewis Lake and Green Lake broodstocks (Coberly and Horrall 1982; Krueger et al. 1983; Visscher 1983; Kincaid 1993; Page 2001). The 1989 and 1991 year-classes of the Lewis Lake broodstock and the 1992 and 1993 year-classes of the Green Lake broodstock were surveyed.

The Seneca Lake broodstock is the only broodstock in the upper Great Lakes derived from a lake trout population outside the Great Lakes basin. The Seneca Lake broodstock was developed to add a deepwater stock to the lake trout hatchery system and because evidence suggested that Seneca Lake lake trout were less prone to mortality from sea lampreys (Krueger et al. 1983; Eshenroder et al. 1995; Holey et al. 1995). The year-classes surveyed (1987 and 1992) were developed from reciprocal crosses of a captive broodstock housed at Allegheny National Fish Hatchery.

Appendix 2: Genetic Variability in Wild Lake Trout

TABLE A2.1.—Estimates of allele frequencies and measures of genetic variability for wild lake trout populations by lake basin of origin.

		Lake Superior									
		Leans			Siscowets				Humpers		
Locus, number, and statistic	Allele	Isle Royale	Apostle Islands	Stannard Rock	Isle Royale	Apostle Islands	Stannard Rock	Caribou Island	Isle Royale	Caribou Island	Lake Huron[a]
Sfo1	108	.036	.057	.000	.113	.109	.207	.091	.000	.034	.000
	110	.882	.877	.942	.780	.813	.716	.848	.979	.932	1.000
	116	.082	.066	.058	.107	.078	.078	.061	.021	.034	.000
N		55	61	75	84	61	64	66	48	67	49
Sfo12	254	.127	.061	.139	.076	.108	.102	.119	.223	.140	.082
	256	.032	.045	.060	.051	.042	.056	.024	.043	.018	.010
	258	.841	.894	.789	.873	.842	.843	.833	.734	.842	.908
	260	.000	.000	.012	.000	.008	.000	.016	.000	.000	.000
	262	.000	.000	.000	.000	.000	.000	.008	.000	.000	.000
N		63	66	83	79	60	54	63	47	57	49
Sfo18	167	.009	.000	.000	.023	.000	.000	.000	.000	.030	.000
	169	.000	.008	.000	.006	.000	.000	.000	.000	.000	.000
	171	.536	.562	.413	.631	.742	.691	.730	.674	.769	.583
	173	.018	.015	.000	.000	.000	.000	.000	.022	.007	.021
	175	.009	.008	.013	.040	.016	.021	.016	.011	.015	.063
	177	.000	.008	.013	.000	.000	.000	.000	.000	.000	.104
	179	.018	.000	.000	.000	.000	.000	.000	.000	.000	.000
	181	.345	.308	.360	.068	.032	.011	.040	.174	.075	.042
	183	.000	.000	.000	.000	.000	.000	.000	.000	.000	.156
	185	.009	.008	.007	.011	.016	.053	.024	.022	.000	.010
	187	.055	.085	.193	.216	.194	.213	.183	.098	.075	.021
	189	.000	.000	.000	.000	.000	.000	.000	.000	.022	.000
	191	.000	.000	.000	.006	.000	.011	.008	.000	.007	.000
N		55	65	75	88	62	47	63	46	67	48
Oneμ9	222	.000	.000	.000	.000	.000	.047	.033	.000	.000	.000
	224	.007	.000	.000	.000	.000	.019	.017	.000	.000	.000
	228	.963	.955	.994	.960	.970	.896	.883	.988	.958	.917
	230	.000	.000	.000	.016	.030	.000	.008	.012	.017	.073
	232	.030	.045	.006	.024	.000	.019	.058	.000	.008	.010
	234	.000	.000	.000	.000	.000	.000	.000	.000	.017	.000
	236	.000	.000	.000	.000	.000	.019	.000	.000	.000	.000
N		67	33	77	62	33	53	60	41	60	48
Oneμ10	174	.731	.902	.705	.769	.811	.816	.793	.793	.683	.802
	178	.269	.098	.267	.231	.189	.184	.207	.207	.258	.198
	182	.000	.000	.027	.000	.000	.000	.000	.000	.058	.000
N		52	46	73	52	46	53	57	41	62	48
Ogo1a	144	.078	.090	.042	.071	.103	.123	.060	.094	.040	.300
	150	.719	.701	.595	.536	.587	.561	.687	.531	.556	.470
	152	.203	.209	.363	.371	.302	.316	.254	.375	.403	.230
	154	.000	.000	.000	.014	.008	.000	.000	.000	.000	.000
	176	.000	.000	.000	.007	.000	.000	.000	.000	.000	.000
N		64	67	84	70	63	57	67	48	62	50
Ogo1c	213	.024	.032	.013	.026	.065	.071	.030	.033	.015	.140
	219	.683	.645	.462	.355	.359	.446	.530	.435	.470	.430
	221	.294	.323	.525	.599	.554	.482	.440	.533	.515	.430
	223	.000	.000	.000	.013	.022	.000	.000	.000	.000	.000
	245	.000	.000	.000	.007	.000	.000	.000	.000	.000	.000
N		63	31	79	76	46	56	67	46	67	50
Scou19	157	.000	.000	.000	.000	.008	.000	.000	.000	.000	.000
	159	.007	.000	.000	.000	.000	.000	.000	.009	.000	.000
	161	.100	.111	.056	.090	.057	.044	.053	.018	.021	.000
	163	.000	.016	.000	.000	.016	.009	.008	.000	.007	.000
	165	.029	.016	.123	.011	.008	.000	.008	.000	.076	.010
	167	.000	.016	.000	.005	.000	.000	.000	.027	.021	.010
	169	.000	.016	.019	.000	.000	.000	.000	.000	.000	.000
	171	.300	.278	.247	.191	.189	.211	.159	.164	.181	.265
	173	.021	.000	.043	.059	.025	.018	.045	.045	.014	.112
	175	.429	.468	.426	.569	.623	.614	.606	.527	.507	.582
	177	.029	.024	.031	.032	.033	.061	.053	.118	.035	.020
	179	.079	.056	.049	.043	.041	.044	.068	.073	.132	.000
	181	.007	.000	.006	.000	.000	.000	.000	.018	.007	.000
N		70	63	81	94	61	57	66	55	72	49

Appendix 2: Genetic Variability in Wild Lake Trout

TABLE A2.1.—Continued.

		Lake Superior									
		Leans			Siscowets				Humpers		
Locus, number, and statistic	Allele	Isle Royale	Apostle Islands	Stannard Rock	Isle Royale	Apostle Islands	Stannard Rock	Caribou Island	Isle Royale	Caribou Island	Lake Huron[a]
Ssa85	126	.125	.045	.065	.033	.008	.043	.037	.076	.125	.000
	132	.000	.000	.000	.000	.000	.004	.000	.000	.000	.000
	134	.456	.604	.600	.658	.658	.664	.567	.446	.463	.510
	136	.118	.112	.147	.083	.133	.069	.149	.087	.051	.000
	138	.301	.239	.188	.225	.200	.224	.246	.391	.360	.490
N		68	67	85	60	60	58	67	46	68	49
Observed heterozygosity		.380	.355	.391	.388	.383	.398	.357	.383	.361	.372
Expected heterozygosity[b]		.427	.387	.436	.425	.407	.437	.412	.418	.414	.402
Mean number of alleles		4.2	4.1	4.9	4.6	4.1	4.0	4.3	3.9	4.6	3.4

[a] Lean lake trout from Parry Sound.

[b] Hardy–Weinberg equilibrium (Nei 1978).

Appendix 3: Genetic Variability in Hatchery Lake Trout

TABLE A3.1.—Estimates of allele frequencies and measures of genetic variability for hatchery strains of lake trout by lake basin of origin.

		Lake Superior			Lake Michigan		
Locus, number, and statistic	Allele	Apostle Islands	Isle Royale	Marquette	Lewis Lake	Green Lake	Seneca Lake
Sfo1	108	.027	.015	.040	.000	.008	.007
	110	.900	.924	.905	.974	.947	.699
	116	.073	.061	.056	.026	.045	.294
N		75	66	63	76	66	68
Sfo12	254	.041	.142	.048	.027	.063	.037
	256	.081	.052	.040	.040	.071	.224
	258	.858	.799	.889	.920	.865	.739
	260	.020	.007	.016	.000	.000	.000
	262	.000	.000	.008	.013	.000	.000
N		74	67	63	75	63	67
Sfo18	169	.000	.010	.000	.000	.000	.000
	171	.562	.510	.599	.366	.465	.748
	173	.008	.019	.000	.000	.025	.022
	175	.044	.055	.041	.004	.005	.204
	179	.000	.000	.000	.009	.000	.000
	181	.228	.271	.275	.451	.449	.026
	183	.062	.010	.005	.112	.000	.000
	185	.003	.039	.005	.045	.000	.000
	187	.083	.081	.068	.013	.040	.000
	189	.008	.006	.009	.000	.015	.000
	191	.003	.000	.000	.000	.000	.000
N		193	155	111	112	99	115

Appendix 3: Genetic Variability in Hatchery Lake Trout

TABLE A3.1.—Continued.

Locus, number, and statistic	Allele	Lake Superior			Lake Michigan		Seneca Lake
		Apostle Islands	Isle Royale	Marquette	Lewis Lake	Green Lake	
Oneμ9	224	.000	.000	.000	.008	.000	.000
	228	.934	.909	.927	.903	.911	.932
	230	.046	.083	.053	.065	.000	.038
	232	.020	.000	.020	.016	.089	.030
	234	.000	.008	.000	.008	.000	.000
N		76	66	75	62	56	66
Oneμ10	170	.000	.000	.000	.007	.000	.000
	174	.807	.846	.893	.601	.827	.750
	178	.193	.154	.107	.392	.173	.250
N		75	65	56	74	55	68
Ogo1a	142	.000	.000	.000	.013	.000	.000
	144	.039	.062	.087	.256	.182	.149
	146	.000	.000	.000	.019	.000	.000
	148	.000	.000	.000	.058	.000	.000
	150	.671	.800	.762	.481	.667	.306
	152	.283	.138	.151	.173	.152	.545
	154	.007	.000	.000	.000	.000	.000
N		76	65	63	78	66	67
Ogo1c	213	.140	.045	.046	.059	.146	.096
	219	.570	.261	.620	.686	.561	.640
	221	.290	.693	.324	.255	.293	.263
N		50	44	54	51	41	57
Scou19	157	.000	.000	.005	.000	.000	.000
	159	.000	.015	.005	.000	.000	.000
	161	.174	.039	.122	.057	.103	.256
	163	.000	.003	.000	.000	.000	.000
	165	.013	.018	.009	.039	.000	.000
	167	.000	.000	.000	.022	.005	.004
	169	.000	.000	.005	.000	.029	.004
	171	.265	.352	.275	.250	.279	.415
	173	.020	.048	.014	.000	.010	.047
	175	.465	.473	.437	.478	.363	.231
	177	.040	.018	.086	.061	.108	.043
	179	.020	.027	.045	.092	.103	.000
	181	.000	.006	.000	.000	.000	.000
	183	.003	.000	.000	.000	.000	.000
N		198	166	111	114	102	117
Ssa85	126	.049	.090	.018	.000	.005	.000
	130	.003	.000	.000	.000	.000	.000
	132	.000	.000	.000	.000	.000	.004
	134	.657	.500	.694	.403	.505	.470
	136	.098	.139	.063	.146	.040	.000
	138	.193	.271	.225	.447	.450	.526
	140	.000	.000	.000	.004	.000	.000
N		194	166	111	113	100	117
Observed heterozygosity		.392	.370	.374	.436	.421	.445
Expected heterozygosity[a]		.411	.410	.373	.448	.419	.449
Mean number of alleles		4.7	4.6	4.7	4.3	3.8	3.4

[a] Hardy–Weinberg equilibrium (Nei 1978).