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Preservation of Genetic Variation in the Green Lake Strain Lake Trout Derived from Remnant Domestic and Feral Populations

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Abstract.—The Green Lake, Wisconsin, strain of lake trout *Salvelinus namaycush* was discontinued as a hatchery brood stock in 1976 after Lake Michigan was stocked with the 1975 year-class. In 1982, a decision was made to restore the Green Lake strain as a production brood stock. Five groups were produced by spawning marked fish that were survivors from the 1976 stocking of southern Lake Michigan. A sixth group was produced from a remnant of the Green Lake brood stock held at the Genoa (Wisconsin) National Fish Hatchery. Hatchery accidents reduced both the number of groups and the effective population number of each group. We studied a procedure for reconstructing a composite Green Lake brood stock from individuals of these six groups. Genetic variability was evaluated by allozyme electrophoresis in five of these groups. Twelve of 18 loci were polymorphic. Allelic frequencies were similar in all five groups; however, significant differences occurred in nine systems. Heterozygosity level (mean ± SE) was lowest in the domestic group (0.119 ± 0.043) and ranged from 0.139 ± 0.043 to 0.166 ± 0.052 in the feral groups. Cluster analysis of genetic distances grouped the four feral groups together, but separate from the domestic group. Progeny from fish captured on Black Can Reef, Lake Michigan, in 1986 and 1988 were the most similar. A modified diallel mating design was developed to produce a composite brood stock from remnant feral and domestic fish. Pooled families from 1991 and 1992 diallel matings will be reared to maturity, then reciprocal crosses of the two year-classes will be made to form the new composite Green Lake brood stock.

Attempts to expand populations of lake trout *Salvelinus namaycush* throughout the Great Lakes have emphasized adapted strains that could survive and reproduce on the historic spawning reefs (Schneider et al. 1983). The Green Lake strain of lake trout was used extensively for the stocking of southern Lake Michigan; more than 4.9 million yearlings were planted from 1966 to 1976 (Brown et al. 1981). In 1976, the Green Lake strain was discontinued as a hatchery brood stock, except 10,900 eyed eggs were transferred from the Jordan River (Michigan) National Fish Hatchery (NFH) to the Crystal Spring (Wisconsin) State Fish Hatchery (SFH). When the Green Lake strain was discovered to be the last representative of the southern Lake Michigan deep-water spawning strains, managers began to examine techniques to recover the strain. Fish from the 1975 and earlier year-classes were present in sport, commercial, and assessment catches from Lake Michigan during the 1980s, but their numbers decreased with each passing year.

In 1983, the Lake Michigan Lake Trout Brood Stock Committee of the Great Lakes Fishery Commission initiated development of a hatchery brood stock of Green Lake strain fish (Krueger et al. 1983). Between 1985 and 1988, feral fish were captured from spawning reefs in southern Lake Michigan and used as parents for a series of progeny lots that were transferred to hatcheries. Fish from these lots were to be the parental stock for the new Green Lake brood stock. The present study served to examine the genetic variability within and among the six Green Lake strain progeny lots, one lot from the 1975 domestic brood stock and five lots from feral brood fish collected in southern Lake Michigan. The objectives were to determine the level of genetic differentiation among the six lots and to design a mating plan to produce a new brood stock from the remnant Green Lake gene pool.

Methods

Background of Green Lake strain.—The Green Lake lake trout strain was developed from repeated stockings of Green Lake, Wisconsin, from 1886 to 1943 with fish from southern Lake Michigan. The source of these fish is believed to have

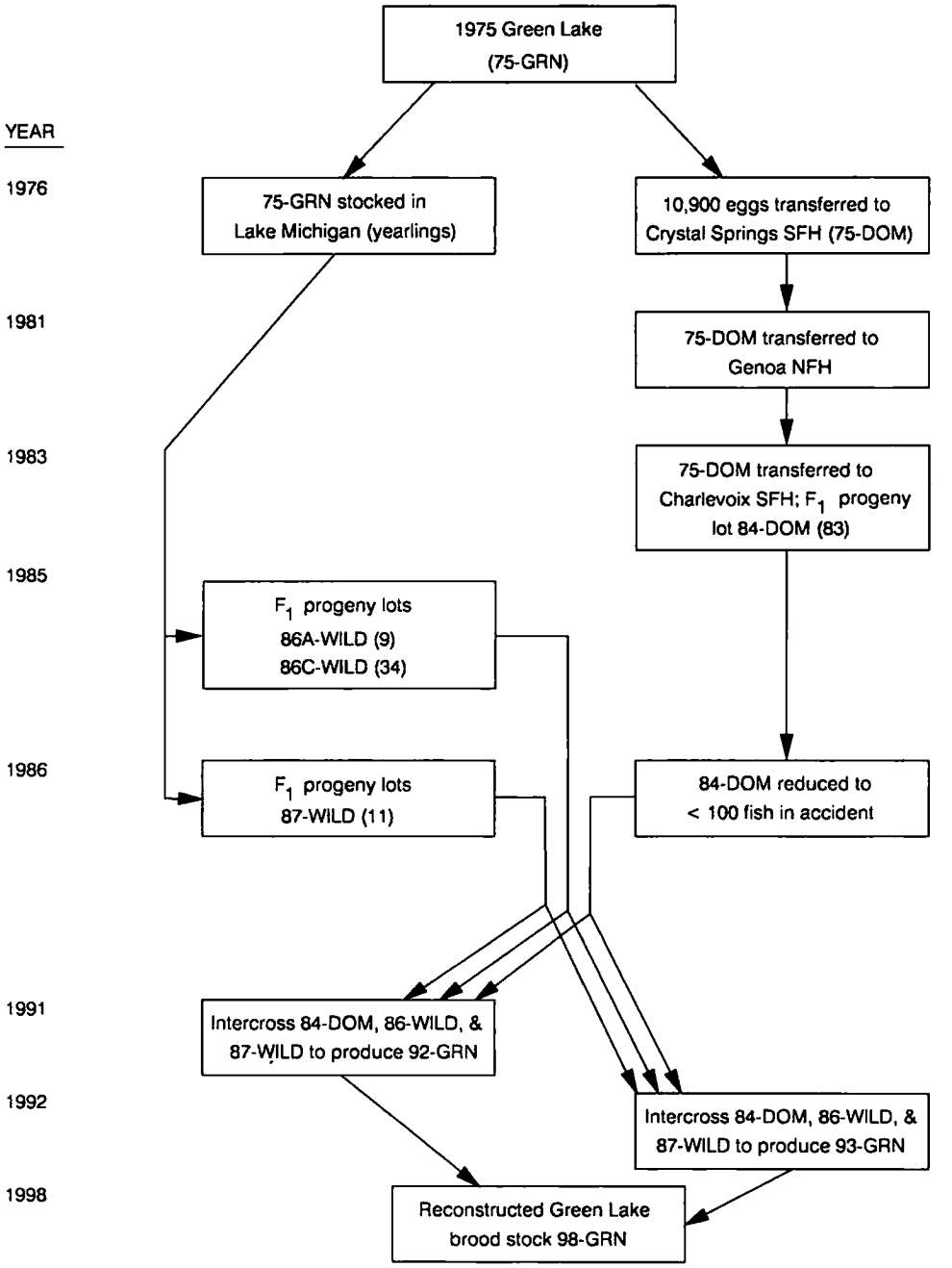

FIGURE 1.—Relationship of current Green Lake feral and domestic groups of lake trout with the 1975 lot and 1998 reconstructed lot. Numbers of parents used to produce feral lots are given in parentheses.

been the deep-water populations from the southern basin (Hacker 1956). The origin of a 1944 group released in Green Lake as fingerlings, however, has been questioned. Krueger et al. (1983) believed the 1944 group was from a Sturgeon Bay (Wisconsin) SFH egg shipment of northern Lake Michigan strains. No lake trout were released in Green Lake between 1945 and 1952, but stocking resumed in 1953 with fish from Lake Superior.

The Green Lake lake trout, as we know it today

(Krueger et al. 1983), was developed from two egg collections from Green Lake fish, in 1958 (59-WILD) and 1959 (60-WILD). Parents of the 1958 group were primarily fish released between 1939 and 1944 and should have been of Lake Michigan origin. The 1959 matings used 78 females, which included one Lake Superior female, and could have included up to eight Lake Superior males (Krueger et al. 1983). The 59-WILD and 60-WILD brood stocks were pooled into a single group in 1971, at which time males from the Apostle Island (Lake Superior) strain may have been added to the brood stock (Krueger et al. 1983). This addition could have been as many as 10% of the total males used to produce the composite group. Fish of the 1972 to 1975 year-classes released in Lake Michigan would have reflected this hybrid contribution from Apostle Island males and would have been the primary source of feral Green Lake fish recovered from the lake and used as parents to produce the 1986 to 1988 groups in this study.

Source of domestic group.—The Green Lake strain (GRN) was discontinued as a hatchery production brood stock in the spring of 1976 when the last 277,300 fish from the 1975 year-class were released in Lake Michigan (Larry Wubbles, Jordan River NFH, personal communication). The 1975 Green Lake lot (75-GRN) was a pooled 2-million-egg spawn from the 59-WILD, 60-WILD, and 65-DOM (domestic) brood stocks at the Marquette (Michigan) SFH that was shipped to the Jordan River NFH. A new Green Lake brood stock (75-DOM) was started when 10,900 eggs from the 75-GRN lot were transferred to the Crystal Spring SFH in 1976 (Figure 1). In May 1981, the 75-DOM was transferred from Crystal Spring to the Genoa (Wisconsin) NFH. In November 1983, the first generation brood stock (84-DOM) was started from the 75-DOM and transferred to Charlevoix (Michigan) SFH as eyed eggs. The 75-DOM fish were moved from Genoa NFH to the Charlevoix SFH in April 1984. The last fish from the 75-DOM group were released in Lake Michigan at Pine River Channel on March 20, 1986. A dewatering accident at the Charlevoix SFH in April 1986, reduced the 84-DOM to 100 fish (Figure 1).

Source of feral groups.—Gametes were collected from sexually mature feral fish on Julian's Reef and Black Can Reef in Lake Michigan from 1985 to 1987. Fish from Julian's Reef were collected by the Illinois Department of Natural Resources and fish from Black Can Reef by the Wisconsin Department of Natural Resources. Initially, only fish from the 1975 Green Lake group were to be used as parents for the new brood stock. These fish could be identified by a unique mark of dorsal and left ventral (DLV) fin clips. Because of the small number of fish collected during the 1985 spawning season, a decision was made to spawn all fish with a total length greater than or equal to 800 mm. These large fish were assumed to be Green Lake strain from year-classes older than 1975 because Green Lake fish had been released in southern Lake Michigan from 1966 to 1976 and each year-class carried unique fin clips. Fish identified as Green Lake strain by either fin clip or size were randomly mated using one or two males per female. Non-DLV fin-clipped fish less than 800 mm were not spawned except in the 86B-WILD group (see Table 1). The 86B-WILD group was reared at the Jake Wolfe (Illinois) SFH; all other fish were spawned and eggs were transferred to the Charlevoix SFH. Altogether, 29 females and 45 males recovered from Lake Michigan were spawned to produce five progeny groups from the 1986 to 1988 year-classes (Figure 1; Table 1).

Sample collection.—In April 1989, forty fish each from the 86A-WILD, 86B-WILD, 87-WILD, and 88-WILD groups were sampled for electrophoretic analysis. The 84-DOM and 86C-WILD groups could not be sampled directly because they contained less than 100 fish. The 84-DOM was sampled by examination of 40 fish from a pooled progeny group (89-DOM) developed from six families (12 parents) spawned in December 1988. These fish were held at the Charlevoix SFH until July 1989, when they reached an average length of 5 cm. The 86C-WILD group was not sampled because fish were immature, and all remaining fish were needed for future brood stock.

The WILD groups were sampled at the hatchery where fish were sacrificed and eye, heart, kidney, and muscle tissues were collected. Tissue samples were placed on dry ice immediately after collection and shipped to Cornell University, where they were stored at −80°C until processing. Forty fish from the 89-DOM group were shipped to Cornell University as whole fish on dry ice and tissue samples were collected at Cornell. Genetic analysis was performed by horizontal starch gel electrophoretic procedures (May et al. 1979, 1980; May 1992). Buffer–tissue–enzyme combinations were described in Krueger et al. (1989).

Statistical analysis.—Average heterozygosity, the G-test, F_{ST} values (estimate of deviation from Hardy–Weinburg proportions due to differentiation among subpopulations), and genetic distance coefficients were used to compare genetic char-

TABLE 1.—Source of brood stock for the 1984–1988 lots of the Green Lake strain.

Group	Year-class	Hatchery location	Source	Parental source (females/males)[a]			Fish with DLV fin clip[b] (%)	Parental information
				Domestic brood	Julian's Reef	Black Can Reef		
84-DOM[c]	1984	Charlevoix	Domestic	44/39			0.0	Domestic brood stock transferred from Genoa NFH to Charlevoix SFH Apr 10, 1984; brood stock planted in Pine River Channel, Lake Michigan, Mar 20, 1986
86A-WILD	1986	Charlevoix	Lake Michigan			3/6	22.2	Wild fish captured Oct 29–31, 1985
86B-WILD	1986	Jake Wolfe	Lake Michigan		3/5		100.0	Wild fish captured Oct 24, 1985
86C-WILD	1986	Charlevoix	Lake Michigan		7/10	5/12	85.3	Wild fish captured from Oct 28 to Nov 8, 1985
87-WILD	1987	Charlevoix	Lake Michigan		3/4	2/2	90.9	Wild fish captured Oct 30 to Nov 6, 1986
88-WILD	1988	Charlevoix	Lake Michigan			6/6	95.5	Wild fish captured Nov 3–5, 1987

[a] Number of fish spawned to produce the group from each parent source.
[b] Percentage of fish used as parents that had identifiable dorsal and left-ventral (DLV) fin clips; clips identified fish from the 1976 stocking of Green Lake strain.
[c] Pooled progeny group (89-DOM) of 84-DOM used for electrophoretic analysis.

acteristics among the sampled lots. Allele counts by locus were compared statistically by contingency table analysis with G-statistics (Sokal and Rohlf 1981). A probability level of $P < 0.05$ was used to reject the null hypothesis that genetic differences among samples were not significant. Genetic distances (Nei 1972) were calculated for each pair of populations over polymorphic loci only. Genetic distance data were analyzed by cluster analysis using the unweighted pair-group method

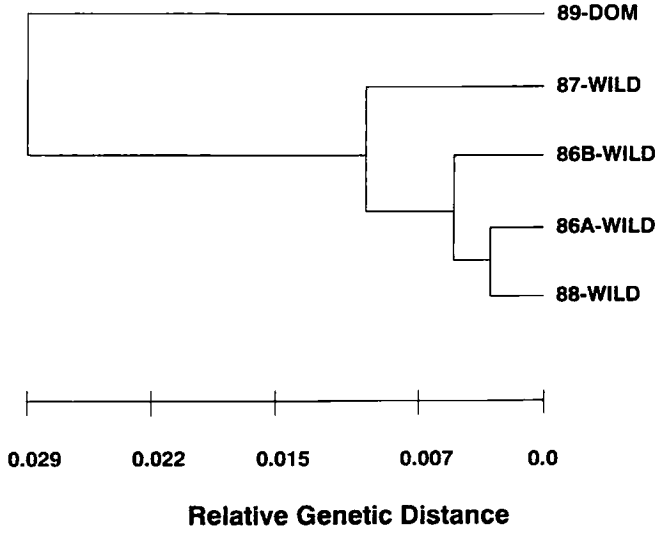

FIGURE 2.—Dendrogram generated by cluster analysis of Nei's (1972) genetic distance coefficients based on 12 polymorphic loci of lake trout from five Green Lake strain progeny groups. See Table 1 for definition of group abbreviations.

TABLE 2.—Allele frequencies and statistics for 12 polymorphic loci of lake trout from five groups of Green Lake strain fish (group identification given in Table 1).

Locus[a]	Allele	Green Lake strain progeny group					F_{ST}[b]	G-test[c]
		89-DOM	86A-WILD	86B-WILD	87-WILD	88-WILD		
Polymorphic loci								
*AAT-1**	*85	0.825	0.438	0.268	0.432	0.413	0.138	59.1**
	*100	0.175	0.563	0.732	0.568	0.588		
*AAT-2**	*85	0.813	0.438	0.256	0.419	0.400	0.138	58.5**
	*100	0.188	0.563	0.744	0.581	0.600		
*ACP-1**	*100	1.000	0.988	1.000	0.878	0.950	0.060	25.1**
	*400	0.000	0.013	0.000	0.122	0.050		
*FH-1**	*100	0.976	0.816	0.805	0.866	0.910	0.036	17.3*
	*90	0.024	0.184	0.195	0.134	0.090		
*FH-2**	*100	1.000	0.829	0.829	0.854	0.987	0.039	25.2**
	*90	0.000	0.171	0.171	0.146	0.013		
*GPI-1**	*100	0.988	1.000	1.000	1.000	1.000	0.010	3.2
	*200	0.012	0.000	0.000	0.000	0.000		
*MDH-4**	*100	1.000	0.988	1.000	1.000	1.000	0.010	3.3
	*144	0.000	0.013	0.000	0.000	0.000		
*PEPD-1**	*100	0.450	0.371	0.276	0.188	0.450	0.039	26.3**
	*179	0.488	0.543	0.553	0.750	0.500		
	*138	0.063	0.086	0.171	0.063	0.050		
*PEPD-2**	*100	0.000	0.000	0.026	0.000	0.013	0.014	5.9
	*179	1.000	1.000	0.974	1.000	0.988		
*PGM-3**	*100	0.378	0.400	0.463	0.276	0.488	0.029	24.7*
	*94	0.622	0.575	0.463	0.724	0.500		
	*91	0.000	0.025	0.073	0.000	0.013		
*PGM-4**	*100	0.366	0.375	0.451	0.250	0.475	0.029	20.0*
	*94	0.634	0.600	0.488	0.737	0.513		
	*91	0.000	0.025	0.061	0.013	0.013		
*sSOD-1**	*100	0.890	1.000	1.000	0.866	1.000	0.078	38.0**
	*85	0.110	0.000	0.000	0.134	0.000		
Heterozygosity								
Mean		0.119	0.163	0.166	0.154	0.139		
SE		0.043	0.051	0.052	0.042	0.043		

[a] Locus nomenclature follows Shaklee et al. (1990). The loci examined and their IUBNC (1984) numbers were aspartate aminotransferase 2.6.1.1 (*AAT-1**, *AAT-2**), acid phosphatase 3.1.3.2 (*ACP-1**), fumarate hydratase 4.2.1.2 (*FH-1**, *FH-2**), glucose-6-phosphate isomerase 5.3.1.9 (*GPI-1**), malate dehydrogenase 1.1.1.37 (*MDH-4**), proline dipeptidase 3.4.13.9 (*PEPD-1**, *PEPD-2**), phosphoglucomutase 5.4.2.2 (*PGM-3**, *PGM-4**), and superoxide dismutase 1.15.1.1 (*sSOD-1**).

[b] Estimate of deviation from Hardy–Weinberg proportions due to differentiation among subpopulations.

[c] Asterisk (*) reflects significance at $P < 0.05$; ** represents significance at $P < 0.01$.

(Sneath and Sokal 1973) and the pool cluster method (Royse and May 1982) to determine the genetic similarities among the five groups (Figure 2). Data analysis was performed with "Genes in Populations," a microcomputer program designed by B. May and C. C. Krueger and written by W. Eng, Cornell University.

Electrophoretic Comparison of Green Lake Groups

Allozyme frequencies for 18 systems, previously identified as polymorphic in lake trout (Krueger et al. 1989), were examined by electrophoretic analysis. Six systems were monomorphic and 12 were polymorphic (Table 2). The groups were genetically heterogenous as significant allele frequency differences were found at 9 loci. Average heterozygosity levels ranged from 0.119 ± 0.043 to 0.166 ± 0.052 (mean ± SE), but none were significantly different from each other (Table 2). The four groups from feral parents were more similar to one another than to the 89-DOM group, and the two groups captured on Black Can Reef (86A-WILD and 88-WILD) showed the greatest similarity (Figure 2). When compared to other populations in the Great Lakes basin, the five Green Lake groups did not cluster together as a single strain (Figure 3). Instead, each feral sample ini-

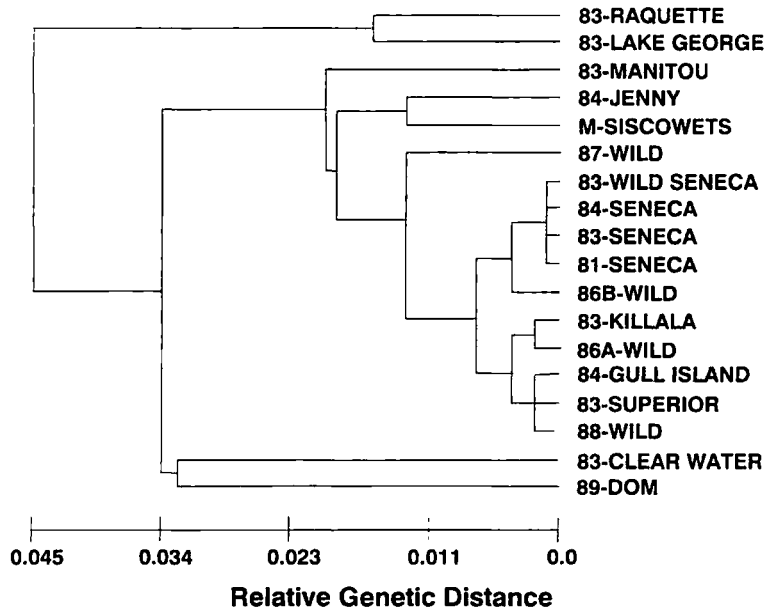

FIGURE 3.—Dendrogram generated by cluster analysis of Nei's (1972) genetic distance coefficients based on 18 polymorphic loci of lake trout evaluated in this study and a study by Krueger et al. (1989) (see latter for description of sample origins). Samples are identified by the last two digits of the year-class from which they were taken and the strain name; M represents mixed year-class. Abbreviations for the Green Lake groups are given in Table 1.

tially grouped with at least one different strain: the 86A-WILD with Killala, the 88-WILD with Superior, and the 86B-WILD with Seneca. The 87-WILD group was intermediate between the other feral groups and 89-DOM. The 89-DOM clustered most closely with the Clearwater strain. The level of differentiation within the Green Lake groups, therefore, approximated the level observed among strains planted in the Green Lake (Krueger et al. 1989).

Discussion

Reasons for Genetic Differences

Allelic frequencies and cluster analysis indicated that the 89-DOM group, derived from the original Green Lake hatchery brood stock, was genetically the most divergent of the five groups examined. The level of differentiation of the 89-DOM relative to the feral groups was as large as any found among lake trout strains (see Figure 3). These differences may have developed in several ways. First, the 75-DOM group was established from a small number of eggs (10,900), indicating that a small, but unknown, number of parents were involved, thus creating a founder effect. The 84-DOM experienced a bottleneck due to hatchery accidents that reduced the total number of fish to less than 100. Selection could have operated when the fish were exposed to furunculosis. The 84-DOM was also exposed to selection for domestication in three hatcheries: Crystal Springs SFH, Genoa NFH, and Charlevoix SFH. The 89-DOM experienced a bottleneck when it was established from only six families. Parents of feral groups were exposed to natural selection in the lake from the yearling stage to maturity. These fish were at least 10 years old and had survived fishing pressure, exposure to the sea lamprey *Petromyzon marinus*, and predation. In addition, they successfully returned to the reef for spawning.

Genetic differences among the four feral groups were caused by the bottleneck and resulting founder effect when each group was established from a small number of parents. Additionally, the 86A-WILD group, developed from females captured at Black Can Reef, grouped with the 88-WILD from the same reef. Finding that fish recovered from Black Can Reef (86A-WILD and 88-WILD) cluster closer to each other than with fish recovered from Julian's Reef (86B-WILD) suggests that natural selection occurred when fish of different genotypes chose different spawning reefs.

A third source of variation could have been failure of the assumption that non-DLV clipped fish

longer than 800 mm were Green Lake strain. Non-DLV fish made up 5 to 78% of the parents for each feral lot except 86B-WILD (Table 1). Other lake trout strains were released in the northern half of the lake, and some of these fish may have migrated to the southern reefs to spawn. The probable mixing of Green Lake and Superior strains in the 60-WILD brood stock may explain the genetic affinity of Black Can Reef fish (86A-WILD and 88-WILD) with fish from Lake Superior (Killala and Superior strains).

The genetic differences observed among the five Green Lake groups, all of which were derived from the 75-GRN lot, emphasize the problems involved in attempting to reestablish or reconstruct a discontinued gene pool. Each group represents a small subset of the original population that has experienced both selection and genetic drift. As a result, no one group by itself accurately represents the total gene pool of the Green Lake strain. A composite of these groups, both domestic and feral, will better represent the original gene pool than any one alone. For reasons discussed above, genetic variability in the original population has now been transferred to genetic divergence among the groups. This among-group divergence can be recaptured in the composite brood stock through interbreeding of the remnant groups.

Development of a Composite Brood Stock

A breeding plan was developed to establish a composite gene pool in two stages. In the first stage, a diallel cross-breeding design is used to combine genetic material from the separate groups into a single progeny lot. In this scheme, fish from each parent group will be reciprocally mated to fish of every other group (Table 3). This procedure is repeated in two consecutive years to produce two separate year-classes in order to increase the effective population size in the first generation. In the second step, the two progeny year-classes are mated in reciprocal combinations to produce the F_2 generation. The breeding plan provides: (1) proportionate parental representation from each group, (2) equal genetic contribution from each family, which increases effective population size above the actual number of founders, and (3) maximum genetic variability.

Preparatory to brood stock development, the 86A-WILD and 86C-WILD groups were pooled and redesignated the 86-WILD. The number of fish in these groups was too small to allow their treatment as separate groups. Furthermore, the 86B-WILD at the Jake Wolfe SFH was dropped from the breeding program because disease certification could not be obtained to transfer fish or gametes for the new brood stock. Each of the groups had experienced one or more bottlenecks in the hatchery, causing the effective population number to be less than expected from the initial number mated. The composite Green Lake brood stock will be developed from the three groups—84-DOM, 86-WILD and 87-WILD. The projected number of brood fish in each group available for the 1991 and 1992 spawning years is shown in Table 4.

The breeding plan will be carried out in three steps starting in fall 1991, when the 87-WILD group reaches maturity. Fish from 84-DOM, 86-WILD, and 87-WILD will be mated in a 3 by 3 diallel mating design to produce four replicates or 36 separate families (Table 3). Fish will be mated one male to one female, and each fish will produce only one family. Parents will be randomly chosen from mature fish on each spawning date irrespective of any physical trait. Every effort will be made to ensure that selection is avoided in the choice

TABLE 3.—Number of families to be produced for pooling into the new composite Green Lake brood stock in fall 1991 and 1992. One female and one male are used to produce one family. In all, 36 families are produced in each year-class.

	Male group		
Female group	84-DOM	86-WILD[a]	87-WILD
84-DOM	4	4	4
86-WILD[a]	4	4	4
87-WILD	4	4	4

[a] Group 86-WILD was created by pooling groups 86A-WILD and 86C-WILD.

TABLE 4.—Expected number of brood fish in three Green Lake strain progeny groups available to develop the new composite Green Lake brood stock.

Group	Year first mature	Number of female parents[a]	Percent of female parents[a]	Expected number available[b]		
				1990	1991	1992
84-DOM	1988	44	69	49	44	40
86-WILD[c]	1990	15	23	27	24	21
87-WILD	1991	5	8	900	810	729
Total		64	100	976	878	790

[a] Number and percentage of female parents used to produce listed progeny groups. See Table 1.

[b] Expected number of fish available in each group during the spawning period and available for use as brood stock based on the current inventory and a 10% annual mortality.

[c] Group 86-WILD was created by pooling groups 86A-WILD and 86C-WILD.

of parents. Each egg lot will be identified and incubated separately. At swim-up, 100 fry from each group will be transferred to a composite group (92-GRN) to establish the 1992 year-class. This procedure will be repeated to produce a second pool to serve as a backup. After the backup group is established, remaining fry can be pooled into production lots. The backup group will be held until the yearling stage before it is added to production groups. Parents in 1991 matings will be identified with fin clips so they can be excluded from matings to produce the 1993 brood stock year-class.

In 1992, a second brood stock year-class will be produced with the procedures outlined for 1991. Fish from the 87-WILD group spawned in 1991 matings will be excluded from 1992 matings. Fish from the 84-DOM and 86-WILD groups may be used to produce a second mating in 1992 after fish not spawned in 1991 have been used. When families reach the swim-up stage, 100 fry will be drawn from each family and transferred to the 1992 composite lot (93-GRN) and backup lots.

The final Green Lake brood stock will be produced by crossbred matings between the 92-GRN and 93-GRN lots when they attain maturity in 1998. One hundred families of 92-GRN males by 93-GRN females and 100 families of 93-GRN males by 92-GRN females will be produced. At the swim-up stage, 100 fry from each of these lots will be pooled to produce the final Green Lake brood stock (99-GRN).

This mating design provides a method for combining genetic material from the remaining Green Lake feral and domestic groups into a single brood stock based on equal representation from each group. Special efforts will be needed in the hatchery to establish these families and to carry them separately to the swim-up stage. The procedure introduces some practices that are different from those normally employed in hatchery spawning and incubation operations, but the procedure is essential if all parents are to contribute equally to the progeny generation. This approach will provide maximum genetic diversity in the final brood stock because all mating combinations among feral and domestic groups will be included and will contribute equally.

Acknowledgments

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