

POPULATION GENETICS OF ISLE ROYALE LAKE TROUT

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Status of Resources

Lake trout (*Salvelinus namaycush*) are native inhabitants of colder deep lakes in northern North America, and were abundant throughout the Laurentian Great Lakes prior to the mid-twentieth century (Scott and Crossman 1973, Baldwin et al. 1979, Eshenroder et al. 1984). Sea lamprey (*Petromyzon marinus*) predation and overfishing contributed to the elimination of lake trout populations in Lakes Ontario, Erie, Huron, and Michigan, though two remaining populations reportedly persist in South Bay of Lake Huron. In Lake Superior, sea lamprey populations had not yet reached maximum abundance when control efforts were combined with stocking programs in an effort to save the remaining lake trout populations (Smith and Tibbles 1981), but not before several locally-adapted populations went extinct (Lawrie and Rahrer 1973). The lake trout in Lake Superior show a high level of within-population genetic diversity, and Isle Royale lake trout are unique among the rest of the Lake Superior lake trout because there has been little, if any, impact of hatchery stocking on the genetic resources there. The genetic characteristics of Isle Royale lake trout likely are little changed from those of the original post-glacial colonists.

Lake Superior lake trout populations are composed of several locally-adapted and morphologically distinct forms (Agassiz 1850, Eschmeyer and Phillips 1965, Rahrer 1965, Rakestraw 1967). Isle Royale lake trout populations historically had the greatest amount of diversity with up to twelve morphological variants of three general phenotypes recognized from various locations around the island (Goode 1884, Rakestraw 1967, Goodier 1981). The different phenotypes have variously supported significant sport and commercial fisheries at Isle Royale (Agassiz 1850, Thomson 1883, Baldwin et al. 1979). The lean phenotype is common to lake trout found throughout the Great Lakes as well as from lakes outside of the Great Lakes basin. Extant populations of siscowet and humper lake trout are unique to Lake Superior, though there

are anecdotal reports of siscowet-like lake trout from northern Lakes Michigan and Huron (Brown et al. 1981, Goodier 1981).

Lean, siscowet, and humper lake trout phenotypes are generally distinguished on the basis of unique facial characteristics, body shape, fat content, depth of capture, and spawning time (Goodier 1981). Lean lake trout have a slender body and low body fat content that ranges from 12-32% of its ash-free dry weight (Eschmeyer and Phillips 1965) and typically inhabit waters to about 70 meters. Spawning time for leans in the Great Lakes occurs from October through November, depending on changes in water temperatures during the autumn turnover (Van Oosten 1944). Siscowet lake trout have a slightly convex snout, a deep robust body, and high body fat content that ranges from 28-85% of ash-free dry weight (Eschmeyer and Phillips 1965). Siscowets typically live at depths from 50 to over 150 meters, and their spawning times vary by population from April through November (Eschmeyer 1955, Bronte 1993, and personal observations). Humper lake trout are recognized by a thin abdominal wall and relatively large eyes (Rahrer 1965), and their fat content is intermediate to that of leans and siscowets (Eschmeyer and Phillips 1965). Humpers were thought to be less widely distributed than leans or siscowets in Lake Superior, however recent observations of humpers in shallow, low-relief areas of the lake suggest that the distribution of humpers is more widespread than originally indicated in published records (C. Bronte, Great Lakes Science Center, Lake Superior Biological Station, personal communication).

Some morphological and physiological differences among populations of lake trout in Lake Superior, such as fat content and swim bladder gas retention, correspond to habitat depth differences and have been shown to be heritable (Eschmeyer and Phillips 1965, Ihssen and Tait 1974). Significant differences in the shape of the opercle bone distinguish siscowets and humpers from lean lake trout (Burnham-Curtis and Smith 1994). Although some differences among the three phenotypes breed true, the significance of morphological differences as species-level differences is still unclear and there are no discrete genetic markers that allow the three types to be discriminated.

Genetic studies of Lake Superior lake trout began with protein electrophoretic analyses conducted by Dehring et al. (1981) and Ihssen et al. (1988). While no discrete genetic

differences among lean, siscowet, and humper populations were uncovered, there was evidence that populations in geographic proximity were more closely related than were populations of a similar phenotype that were geographically distant. Overall genetic diversity of protein electrophoretic characters is low for lake trout throughout their range, and differences between stocks are differences in the frequency of alternate expressions of nuclear genes rather than fixed genetic differences. Studies of mitochondrial DNA (mtDNA) diversity were undertaken to see if mtDNA sequence differences would give more information about stock differentiation (Grewe and Hebert 1988, Grewe 1993, Burnham-Curtis 1993). Sequence variation in lake trout mtDNA revealed three major clonal groups that were hypothesized to represent the colonizing populations from three major glacial refugia (Grewe and Hebert 1988).

Mitochondrial DNA analysis of Isle Royale lake trout which included all three of the extant phenotypes revealed the presence of the three major lake trout clonal types, and the haplotypes were distributed similarly within populations of the three phenotypes (Burnham-Curtis 1993). There was no correspondence between mtDNA haplotype and either geographic locality or phenotype, however, a particular site mutation that is rare outside of Lake Superior, was significantly more frequent among Lake Superior populations. The high frequency of this mutation in Lake Superior suggests that these lake trout populations share a unique evolutionary history. Siscowets appear to be adapted to a deeper existence and possess a consistently higher fat content which may facilitate vertical migration and buoyancy regulation (Thurston 1962). Humpers have characteristics that appear intermediate to the lean and siscowet phenotypes, and may have evolved from isolated populations that remained on offshore reef areas after the last series of post-glacial water level fluctuations about 6500 years ago (Prest 1970, Burnham-Curtis 1993). Ecological adaptations that lead to character divergence could evolve in the absence of genetic differentiation (Utter 1981), but random genetic mutations could eventually become fixed in these populations if segregation in time or place of spawning reduces the potential for populations to interbreed. Observations of lake trout with morphological characteristics intermediate to the lean and siscowet phenotypes suggests that there is interbreeding among some populations, and this is represented in the lack of correspondence of unique mtDNA haplotypes to location or phenotype.

Lake trout populations around Isle Royale show no evidence of reduced genetic diversity from recent declines in population abundance (Curtis 1991, Burnham-Curtis 1993). In contrast, hatchery-raised lake trout stocks and lake trout stocks transplanted to inland lakes show decreased levels of genetic diversity (DeSilva 1989, Grewe et al. 1994). Areas of Lake Superior that have been heavily stocked with hatchery-raised lake trout do show a lower level of genetic diversity and a lower frequency of rare mtDNA haplotypes than Isle Royale populations. Current research efforts are being focused on characterization of genetic diversity within and between siscowet lake trout populations to provide estimates of the levels of natural diversity in wild populations that experience little or no exploitation pressure. This data could potentially be useful for evaluating the progress and effectiveness of lake trout restoration programs. We are also using protein electrophoresis, mtDNA and nuclear DNA sequence analysis, and microsatellite DNA analyses to search for population specific genetic markers for stock identification purposes.

Genetics and the Management of Isle Royale Lake Trout

The historical morphological diversity of Isle Royale lake trout populations was lost by the extinction of several locally-adapted stocks during the height of sea lamprey predation in the mid 1960s. Several populations of the three distinct lake trout phenotypes persist in the areas around Isle Royale, and there is evidence that though historical morphological diversity was lost, genetic diversity was not. It is critical that extant populations be managed to preserve the existing genetic resources. The direct and indirect genetic effects of exploitation pressure and stocking practices should be considered in the development of a management plan. Excessive exploitation could reduce the effective population size and create a bottleneck and lower genetic diversity of the wild population. Interbreeding of genetically diverse wild populations with genetically restricted hatchery populations could reduce overall genetic diversity as locally-adapted populations become genetically homogeneous (Allendorf 1991). The potential for outbreeding depression and competition increases when hatchery fish are stocked onto populations that have evolved unique local adaptations.

Ideally, the preservation of existing diversity should be the foremost criteria in a fisheries management plan for Isle Royale lake trout because the extant populations represent a significant amount of the historical genetic diversity of the native lake trout stocks. As long as the local populations continue to thrive and sustain themselves solely through natural reproduction, every effort should be extended to protect the resource and preserve the evolutionary potential of the populations. Hybridization and genetic introgression may temporarily heighten levels of diversity in affected populations, but persistent hybrids may experience lowered fitness because of homogenization of the gene pool and lowered diversity or outbreeding depression. Preserving the natural levels of diversity is most important to recovery efforts. Frequencies of genetic characteristics can be manipulated, but once the natural diversity is lost, it is difficult, if not impossible to retrieve.

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