Review of Genetics of Lake Trout in the Great Lakes: History, Molecular Genetics, Physiology, Strain Comparisons, and Restoration Management

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ABSTRACT. This paper reviews historical differences among native lake trout (Salvelinus namaycush) populations, genetic comparisons of populations, heritability of physiological traits, performance of strains after stocking, and the role of genetics in management. Differences among lake trout were historically recognized by aboriginal people, Jesuit missionaries, and French voyageurs, and later by naturalists and biologists. Lean trout represented trout that typically spawned on shallow rocky shoals. Exceptions included river spawning populations in Lake Superior and stocks reported to spawn over beds of algae in Lakes Superior and Michigan. Siscowets had high fat content, were caught in deep water, and likely spawned year-round. Humpers resembled the siscowet but had thin ventral body walls, intermediate fat content, and small size at maturity. The siscowet form and different stocks of lean trout were reported from all the Great Lakes except Lake Ontario. Data from chromosomal banding, allozyme data, and mitochondrial DNA analysis confirmed that genetic differences occur among the three forms. Genetic data also provided evidence for distinctive populations within forms. Fat content, swimbladder gas retention, and developmental rates of eggs were different among some populations and appear to be heritable. Differences among strains after stocking have occurred in survival, dispersal from stocking location, depth distribution, and reproduction. Genetic considerations have been incorporated in species restoration plans but full use has not been made of available genetic information about lake trout. Reproductive performance of different strains should be a central focus in the evaluation of stocking programs. In Lake Superior, high priority should be given to the conservation of native stocks, the last remaining gene pools of Great Lakes lake trout. Goals for management should embrace a vision that restoration is accomplished only when some level of diversity has been re-established. Achievement of restoration should require the existence of naturally-reproducing, self-sustaining populations of different lake trout forms that use a variety of habitats.

INDEX WORDS: Siscowet, reproduction, stocking, mitochondrial DNA, genetics, lake trout, Great Lakes.

INTRODUCTION

Lake trout (Salvelinus namaycush) inhabited the Great Lakes in a rich array of stocks that used a variety of habitats from rivers to the deepest waters, and varied in shape, color, and fat content. The diversity of lake trout was recognized first by the aboriginal people and the earliest European explorers, and later by naturalists who described it as representing discrete, genetically different populations and species (Brown et al. 1981, Goodier 1981). Heavy exploitation of the stocks in the late 1800s and early 1900s caused noticeable declines in abundance that were followed by mass extinctions of the stocks after the predaceous, non-native sea lamprey (Petromyzon marinus) invaded the four upper lakes between 1920 and 1950 (e.g., Holey et al. 1995). By 1960, native lake trout were absent from Lakes Ontario, Erie, Michigan, and most of Lake Huron. Various inshore, shallow-water stocks of lake trout in Lake Superior were greatly reduced in abundance or had also become extinct. Since then, fish management agencies have sought to rehabilitate lake trout in the Great Lakes through sea lamprey control, regulation of fishing, and stocking of different genetic strains of lake trout. The rehabilitation effort has, as yet, only met with limited success (e.g., Eshenroder et al. 1995).

Phenotypic characters such as body form and fin color that helped distinguish the lake trout varieties reflected variation from both genetic and environmental sources. For some characters, genetics determines a high proportion of the phenotypic expression (e.g., the taxonomic characters used to distinguish a species). For other charac-
HISTORICAL EVIDENCE FOR STOCK DIFFERENCES

Early recorded observations of lake trout in northeastern North America often ascribed species status to lake trout of different regions, and sometimes to trout in individual lakes, based on differences in morphology and coloration presumed to reflect large genetic differences. For example, lake trout forms were described from different regions as follows: the togue (Salmo tona) occurred in the northeastern US and eastern Canada, the black lunge (Salmo conflins) and silver lunge (Salmo namaychus) were both noted from Lake Memphremagog of Vermont and Quebec and the Brompton Lakes area of southern Quebec, Salmo conflins and Salmo adirondakus were reported to occur in lakes of New York, Pennsylvania, and adjoining Canadian waters, Salmo symmetrica occurred in Lakes Winnipissiogee and Monadnock in New Hampshire, Salmo namaycush was described as the Mackinaw trout of the Great Lakes, and the fat trout caught in the deep waters of the Great Lakes was noted as Salmo siscowet (Hallock 1877, Goode 1884, Goode 1887, Scott 1875, Suckley 1874). As more biological information was gathered, observations focused on differences in spawning time that could reflect reproductive isolation among groups; these differences were usually denoted as racial distinctions rather than those of specific or subspecific status. For example, Royce (1951) describes two “races” of lake trout in the Finger Lakes of New York, one in Seneca Lake that spawns in late September and October and a second that was widespread and spawns in shallow water later in the fall about when lakes become homiothermal (fall turnover).

The Great Lakes, with a diversity of semi-isolated spawning habitats from offshore shoals to rivers, yielded a diversity of lake trout forms or varieties. Differences among lake trout from various areas of the lakes were not only recognized by naturalists (e.g., Jordan and Evermann 1911, Cook 1929, Koelz 1926) but much earlier by aboriginal people, Jesuit missionaries (Jesus Relations 1670-71 by Goodier 1981), and French voyageurs (Roosevelt 1865). Two to four general forms of lake trout were recognized from the Great Lakes based on fat content, morphology, location caught, and spawning condition and timing. Lean trout or Mackinaws, as they were sometimes called, spawned in shallow water and had less fat than other forms. In contrast, siscowets (also known as fats) were the fattest and most oily of all forms and were caught in deep offshore water, usually > 100 m. Half-breeds, noted only from Lake Superior, appeared as an intergrade between leans and siscowets but resembled siscowets morphologically and ecologically (Khan and Qadri 1970). Humpers or paperbellies, also only noted from Lake Superior, resembled the siscowet in appearance but had thin ventral body walls and small size at maturity. Other forms have been described such as the small salmon trout or bay trout that was found almost entirely in Green Bay of Lake Michigan but is now extinct.
Different varieties of each form were often recognized by commercial fishermen and naturalists. Comprehensive reviews by Goodier (1981) and Brown et al. (1981) provide indirect descriptive evidence from early naturalists and from interviews with former fishermen that support the historical occurrence of separate stocks of lake trout in Lakes Superior and Michigan. Below is a brief summary of the historical evidence for stock diversity of lean, humpers, and siscowet, and their distribution in Lakes Huron, Erie, and Ontario. Half-breed lake trout are not discussed because of a lack of specific information about them and their lack of taxonomic distinctiveness (Khan and Qadri 1970). The purpose of this section is to describe the historical evidence for genetic diversity in lake trout that existed in the Great Lakes. The populations that contained this genetic diversity are now extinct except in Lake Superior and at two locations in eastern Lake Huron.

Lean Lake Trout

The occurrence of varieties of lean trout, especially in the upper Great Lakes, was recognized by residents, early naturalists, and later by biologists (e.g., Koelz 1926). French residents from the areas around Lakes Huron and Superior identified three forms of lake trout (in addition to siscowet) known as Truite des Battures — trout of the rocky shallows, Truite des Grève — trout of the muddy shoals, and Truite du Large — trout of the deep open waters (Herbert 1851). Lean varieties in Canadian waters later were referred to based on their most distinctive feature and included names such as blacks, redfins, yellowfins, grays, salmon trout, moss trout, sand trout, and racers (Goodier 1981). Two types of lean trout were recognized by commercial fisherman along Wisconsin’s shoreline of Lake Superior, the Mackinaw (or red fin) and the bank trout (Coberly and Horrall 1980). Lean varieties of lake trout in Lake Michigan were identified by fishermen as Mackinaw, Beaver Island, redfin or reef, yellowfin, moss, and shoal trout (Brown et al. 1981). Just before their extinction in the 1950s, river spawning populations were documented in six Lake Superior rivers along the Canadian shoreline (Loftus 1957), although no mention was made of river spawning populations in the other Great Lakes. River spawning trout in Lake Superior were capable of ascending steep rapids such as in the Dog River, Ontario and were observed to return to the same river in successive spawning seasons. Areas of rocky cobble without organic materials characterize most descriptions of lake trout spawning substrate. Most unusual were the reports of some stocks of lake trout that spawned over beds of filamentous algae in Lakes Superior and Michigan. In Lake Superior, certain stocks of grays, and less frequently yellowfins, were reported to spawn over algae beds at Prince Bay, north of Caribou Island in Thunder Bay, and north of Pic Island (Goodier 1981). In Lake Michigan, moss trout were noted in Grand Traverse Bay (Organ et al. 1978). Recently, spawning by a naturalized population of Great Lakes origin on macrophyte beds (Chara delicatula) in deepwater (40-60 m) was recorded in Lake Tahoe, Nevada (Beauchamp et al. 1992).

Humpers

No mention of different varieties or stocks of humper trout in Lake Superior was found in the historical literature reviewed for this paper. This form of lake trout was also referred to by fishermen as humpies, bankers, and paperbellies. Isolated offshore reefs surrounded by water deeper than 90 m served as the fishing grounds for this lake trout (Rahrer 1965). Though apparently not exhibiting morphological differences among reefs, separate stocks probably occurred due to their isolation by deep water and distance from inshore stocks and from humper stocks on other reefs. For example, humper trout from different banks near Caribou Island in Michigan waters exhibited significantly different growth rates (Patriarca and Peck 1970). Humpers occurred on all the banks between Caribou and Michipicoten islands and were especially abundant on the northernmost bank of Superior Shoal (Goodier 1981). They were also known from the offshore waters around Isle Royale (Eschmeyer 1955). In a study of morphometric and meristic variation, humpers were clearly separated from leans and siscowets, but Khan and Qadri (1970) were hesitant to assign this form subspecific status until more was known of its biology and distribution. Humpers mature at a smaller size than is typical of the other lake trout forms (leans > 600 mm) and begin spawning in August and September. In collections from Isle Royale, humper males as small as 323 mm were mature and 100% of both sexes were mature at 485 mm (Rahrer 1965). The fat content of humpers has been reported as intermediate between that of leans and siscowet, and also distinguishes humpers from other forms (Eschmeyer and Phillips 1965).

Siscowet

The siscowet, fat lake trout most often caught in deep water, was recognized by early inhabitants of the region as being clearly different from the lean trout typically caught in shallow water. Agassiz (1850) provided the original description in the literature of the siscowet; however, Roosevelt (1865) notes that aboriginal people and French Voyageurs had always distinguished the siscowet as separate from other lake trout. In addition, Nute (1926) reports that correspondence from the American Fur Company in 1839 recognized differences between siscowet and lean trout. “Siscowet” is derived from the Ojibway word that means “cooks itself” (Goode 1887), in reference to this fish’s high fat content. The fat content of siscowet is a characteristic mentioned in virtually every reference that discusses siscowet. Siscowet trout were typically fished in water from 90 m to 300 m deep (Eddy and Surber 1943, Eschmeyer and Phillips 1965). The siscowet has been rec-
recognized taxonomically as a separate species (Agassiz 1850, Herbert 1851, Suckley 1874, Scott 1875, Hallock 1877, Garman 1884, Jordan and Evermann 1937), as a subspecies of lake trout S. n. stsciawet (Jordan and Gilbert 1882; Goode 1887; Evermann and Goldsborough 1907; Nash 1910; Jordan and Evermann 1911; Greene 1935; Hubbs and Lagler 1947, 1949), and sometimes simply as a variety of lake trout (Jordan 1882, Wright 1892, Scott and Crossman 1973). Khan and Qadri (1970) compared morphometric and meristic variation among lean, half breeds, siscowet, and humper trout and concluded that only siscowet should be considered for subspecific status separate from leans. Recently, two osteological characters, the dor­sal opercular notch and radii on the anterodorsal part of the supraethmoid, have been shown to be different between lean and siscowet trout (Burnham-Curtis and Smith 1994). As with the other forms of lake trout, different stocks or varieties of siscowet seem possible. Swee­ney (1890) mentions that two varieties of siscowet occur but possibly his second type was the humper or bank trout. Around the waters of Isle Royale in Lake Superior, black and white siscowet varieties were fished, with the black much larger than the white (Rakestraw 1968). Spawning time has been noted to be over a much broader time period than the fall-spawning leans and humpers. During the 1800s, ripe females were reported to be encountered by fishermen at all times of the year (Goode 1887, Swee­ney 1890). Ripe or spent fish were noted from the Isle Royale area for a six month period June to November (Eschmeyer 1955). Recently, a nearly-ripe male and a female with eggs running from the vent were collected in late April from the Apostle Islands area along the south shore of Lake Superior (Bronte 1993).

Distribution of Forms in the Great Lakes

Different stocks of lake trout have been reported from all the Great Lakes except Lake Ontario. The greatest vari­ety was recorded from Lake Superior where different lean and siscowet stocks plus the humper trout occurred. The variety was probably due to the diversity of habitats and Lake Superior’s large size as compared to the other lakes (see review by Goodier 1981). Similarly in Lake Michigan, a wide variety of lake trout including stocks of leans and a siscowet-like form was recognized (see re­view by Brown et al. 1981).

In Lake Huron, the occurrence of different stocks of leans as well as the siscowet is well documented. For example, two stocks of lean trout, the buckskin and race, were recognized from the waters in the vicinity of Thun­der Bay (Goode 1884). Later, the occurrences of two types were described again from the same general area, the first being the common Mackinaw trout and the sec­ond the shoal trout (U.S. Commission of Fish and Fish­eries 1900). The shoal trout was smaller and had different markings than the Mackinaw, and spawned in September over cobble, boulder, and gravel bottom in 1-3 m of water. Another type of lean trout, the black trout, was known from Yankee Reef (then called Big Reef) and was reported to spawn as late as December (Koelz 1926, Esh­enroder et al. 1995). Other varieties sought by fishermen were redfins, summer trout, and winter trout (Goodier 1981). Siscowet trout were reported to occur in Lake Huron including Georgian Bay by several authors (Her­bert 1851, Strang 1855, Smith 1894, Nash 1908, Jordan and Evermann 1937, Eshenroder et al. 1995).

In Lake Erie, different lake trout types were reported to exist in the trout habitat of the deeper eastern basin. Herbert (1851) describes his personal examination of lake trout from Lake Erie that were similar to the rocky shallows and muddy shoals trout which he described from the upper Great Lakes (see above). In addition, sis­cowet trout were reported to have occurred in Lake Erie (Nash 1908, Jordan and Evermann 1937). The occurrence of different forms of lake trout in Lake Erie seems surprising due to the small amount of lake trout habitat available relative to that in the other Great Lakes.

In Lake Ontario, no clear documentation could be found for the occurrence of different types or forms of lake trout. Only Dymond (1928) inferred that races of trout may occur in Lake Ontario based on the variation of ova counts from females of identical weights. If dif­ferent forms of lake trout occurred, their lack of docu­mentation could be due to two reasons. First, the abundance of Atlantic salmon (Salmo salar) through the early 1800s and its cultural importance may have focused the attention of natural history observations away from lake trout (see Webster 1980). Second, the extinction of various forms and varieties of lake trout may have occurred much earlier than in the upper lakes and prior to naturalist observations and the more regular reporting by agencies such as the U.S. Fish Commission. Inshore waters used by the seine fishery for lake trout and whitefish were reported to be depleted by 1860 (Koelz 1926). Thus, possibly some near-shore stocks of lake trout were already extinct by this time. By 1885, the lake trout fishery in U.S. waters was insignificant (Koelz 1926) and most of the stocks would have been extinct. For example, commercial catch of lake trout in the U.S. declined 94% between 1880 and 1892 and was presumed to reflect a collapse in the populations (Smith 1894). As a result, remaining inshore varieties of lake trout could have been lost during the 1880s. In contrast, the various forms of lake trout in the upper lakes were fished well into the 1900s, and commercial fishermen who fished then were still available for interviews and could recall the original stock diversity (Brown et al. 1981, Goodier 1981). We believe it is likely that varieties of lean trout occurred with the siscowet in Lake Ontario in view of their distribution throughout the rest of the Great Lakes.

CYTOGENETIC AND MOLECULAR GENETIC DIFFERENCES AMONG STOCKS

The relative contribution of genetic differences and environmental variation to the existence of the lake trout
morphotypes described above can not be determined based on the historical reports. Qualitative characteristics such as fin color and body shape as well as morphometric measurements and meristic counts can have important components of their expression determined by environmental variables such as water color, water temperature, and food type and abundance (e.g., Barlow 1961). Thus, such characteristics can be misleading as to the levels of genetic differences that they reflect among the varieties of lake trout. Genetic techniques such as allozyme electrophoresis yield data that reflect a more purely genetic basis for comparisons of lean, siscowet, and humper trout. Three methods, chromosomal banding, allozyme electrophoresis, and mitochondrial DNA analysis, have been applied to compare lake trout populations in Lake Superior and the hatchery stocks used to restock the Great Lakes. The data from these techniques have provided clear evidence of population differentiation among Lake Superior populations but not at the sub-specific or specific levels. Newer techniques such as ribosomal DNA (e.g., Phillips et al. 1992, Popodi et al. 1985) and microsatellite nuclear DNA analysis (e.g., Phillips and Pleyte 1991, Estoup et al. 1993), which have not yet been used for such comparisons, may provide further elucidation of the genetic relationships among various lake trout forms.

Some of the genetic techniques described below have been used to compare different strains of lake trout that have been propagated in hatcheries. However, no uniformity currently exists in the use of strain names in studies. The names, particularly for three strains, could be confused and are described below. The Superior strain refers to a widely distributed strain from a broodstock originally propagated at the Marquette State Fish Hatchery with origins from lake trout collected near Marquette, Michigan on the south shore of Lake Superior (Krueger et al. 1983). Other authors sometimes refer to the Superior strain as the Marquette strain. The Jenny strain refers to lake trout with origins from lake trout in either Jenny or Lewis lakes, Wyoming. These fish were naturalized from stockings before 1900 of trout from northern Lake Michigan and are sometimes referred to as the Wyoming or Lewis strain (Krueger et al. 1983). The Seneca strain has its origins from an early autumn spawning population in Seneca Lake, New York and is sometimes referred to as the Finger Lakes strain.

**Chromosomal Banding**

Staining of lake trout chromosomes with quinacrine hydrochloride (Q-band) and chromomycin A₂ yielded banding polymorphisms that distinguished lake trout from various Great Lakes sources. Q-band and chromomycin A₂ polymorphisms were first reported in lake trout by Phillips and Zajicek (1982) and Phillips and Ihssen (1985b). Later these polymorphisms were shown to be heritable in lake trout (Phillips and Ihssen 1986, Phillips et al. 1989b). A combination of wild and hatchery populations from the Great Lakes region (probably all were lean trout forms) was compared with both staining methods (Phillips et al. 1989b). Based on the number of chromomycin A₂ bands, three groups of trout were distinguished: first, a group from the northern shores of Lakes Superior and Huron and inland lakes north of Lake Superior; second, a group from the southern shore of Lake Superior; and third, a group composed of two samples from populations derived from stockings of Lake Michigan lake trout. This study provided evidence that genetically different populations of lake trout existed in the Great Lakes.

**Allozyme Variation**

Allelic variation at loci that encode allozymes has been used in several studies to compare wild populations in Lake Superior and the hatchery sources of fish used to restock the Great Lakes. Banding patterns on starch gels stained for specific proteins have been shown through inheritance studies of lake trout to be the expression of genes that encode the proteins (May et al. 1979, 1980; Hollister et al. 1984; Marsden et al. 1987). Based on data from an analysis of 50 loci of which six were polymorphic, few significant differences were detected among samples of lean trout from offshore areas spanning the length of Lake Superior (Caribou Island, Stannard Rock, Isle Royale, Dehring et al. 1981). Unfortunately, in this study the collections were all made in the spring, many months before spawning aggregations of lean trout develop and therefore the samples may have represented mixtures of several populations. In the same study, humpers at the three locations and siscowets at Caribou Island and Stannard Rock exhibited highly significant differences between the two forms and among humper collections from different locations (P > 0.01 level). Fixation for alternate alleles did not occur among any forms which could warrant taxonomic classifications at the species level.

In another study, lean lake trout from Lake Superior were sampled from five areas during the fall spawning season and analyzed for variation at 28 allozyme loci, 17 of which were polymorphic (Ihssen et al. 1988). Four of the five stocks had significantly different allelic frequencies at several loci. Two of the samples were not different and were of fish from spawning shoals in close proximity (~ 25 km apart). Additionally, this study compared allelic variation among collections of fish that were from naturalized populations established from stockings of trout from Lake Superior and Lake Michigan. In most cases, these transplanted populations were similar to a general grouping of Lake Superior origin samples and appeared to have retained their Great Lakes genetic identity. Lake trout from other sources (Seneca, Jenny, and Superior strains and Clearwater Lake Manitoba and Hill's Lake Ontario) also were analyzed and typically showed high levels of differentiation from the Lake Superior collections. Seven wild and two hatchery samples in this study were from the same sources as those used in the chromosomal banding study by Phillips.
et al. (1989b). The genetic relationships exhibited among these samples were similar between the two data sources.

Allozyme variation at 102 loci, 18 of which were polymorphic, were analyzed in 14 collections from the various hatchery sources of lake trout used for stocking or proposed to be stocked in Lake Ontario and in one sample each of lean and siscowet trout from the south-shore Apostle Islands region of Lake Superior (Krueger et al. 1989). Highly significant differences were observed between lean and siscowet trout from Lake Superior (P > 0.01); no fixed allelic differences were observed between the two forms. This result supported those of Dehring et al. (1981) that siscowet trout were genetically distinct from lean trout as populations but not as separate species. Allelic frequencies of the siscowet trout from Lake Superior most resembled the hatchery-origin Jenny strain fish also analyzed in this study. Historical reports about the origin of this strain suggest that siscowet lake trout from northern Lake Michigan may have been used to establish this strain in Jenny and Lewis lakes in Wyoming (Krueger et al. 1983, Smith and Snell 1891). Analysis of the other sources of lake trout used for stocking or proposed to be stocked into Lake Ontario indicated that the Seneca strain and lake trout with origins from the Adirondacks region of New York and Clearwater Lake Manitoba were considerably different from other Great Lakes lake trout—generally in agreement with the results of Ihssen et al. (1988).

Mitochondrial DNA

Mitochondrial DNA (mtDNA) restriction site polymorphisms have provided another genetic character to identify distinct populations of lake trout. Different from allozyme characters that demonstrate biparental inheritance, mtDNA haplotypes are maternally inherited. The resolution capability of mtDNA comparisons of populations appears to be enhanced by the rapid evolutionary rate of mtDNA, estimated for some vertebrates to be six to ten times the rate of the nuclear genome (Brown et al. 1979). A survey of mtDNA variation of one wild Lake Superior population and seven hatchery populations based on 18 restriction enzymes resolved 13 mitochondrial clones which were organized into three haplotype groups (Grewe and Herbert 1988). Sample sizes were typically small (< 15 trout per collection) but frequencies of haplotypes revealed a geographic distribution based on the origins of the sample: a western Great Lakes group, a central Great Lakes group, and an eastern Great Lakes group. This pattern roughly corresponded to the grouping identified by chromosomal banding and allozymes (Phillips et al. 1989b, Ihssen et al. 1988). A more intensive study of mtDNA variation was conducted that compared collections of ≥ 80 individuals per collection from each of the six lake trout strains stocked into Lake Ontario (Grewe et al. 1993). Of the strains surveyed, five had origins in the Great Lakes basin: Killala (Lake Superior drainage), Manitou (from Lake Manitou, Manitoulin Island in Lake Huron), Jenny, Seneca, and Superior. The other collection analyzed was the Clearwater strain from Clearwater Lake in northern Manitoba. Four restriction enzymes AvaI, BamHI, HinfI, and TaqI resolved seven mtDNA haplotypes. Frequencies of these haplotypes were significantly different among the six strains (P < 0.001); however, fixation for a unique haplotype did not occur in any strain. Differences between haplotype frequencies of the Killala and Superior strains permitted greater discrimination of these strains than allozyme data from Krueger et al. (1989).

Ribosomal DNA

Preliminary studies of ribosomal DNA (rDNA) variation in lake trout have not yielded genetic markers useful for comparison of populations. Variation in the chromosomal location of the nuclear organizer regions (NORs) has been observed in different populations of lake trout (Phillips et al. 1989a). NORs are specific chromosomal sites at which the rDNA is clustered in tandem arrays of repeated units. Population specific rDNA variants have been found in many organisms (e.g., Gerbi 1985). Phillips (1990) used 24 restriction enzymes on 24 lake trout from five stocks (Gull Island Shoal Lake Superior, Lake Manitou, and the Seneca, Superior, and Jenny strains) which exhibited variation in the intergenic spacer (IGS) region of the rDNA. High levels of interindividual variation were observed and was later shown to be due to variation in the number of repeating units within the IGS (Zhuo 1991). This variation has potential for use in DNA fingerprinting of lake trout for studies to determine the parental contribution of individuals to a year class such as in a hatchery. However, the high level of variation, with almost every fish being unique, makes it difficult to apply the methodology to studies of population differentiation. Variation in the sequence of the transcribed spacer region (ITS) of rDNA was investigated recently to identify potential stock specific markers (Zhuo et al. 1994). Only minimal sequence variation among individuals from five lake trout sources (Seneca, Superior, Jenny, Gull Island Shoal, and Haliburton Lakes Ontario) was found. For 12 individuals from four populations only one intraindividual polymorphism was found and it occurred in each population. No interindividual sequence variation for the first internal transcribed spacer region (ITS-1) was found among 10 individuals from five populations. The future challenge is to find variation at a level between these highly conserved sequences and the hypervariable IGS length polymorphisms that can be used to distinguish populations.

Heritability of Physiological Characteristics

Several physiological characteristics of lake trout such as fat content have been discovered to be heritable and different among populations. Genetically different lake
trout populations must exhibit a level of reproductive isolation, and therefore may also serve as repositories for specialized adaptive traits important to the survival of the populations. Genetic differences observed among populations based on allozyme or mtDNA variation can rarely be associated directly with physiological attributes essential to the survival and distribution of populations. Understanding the genetic basis for physiological characteristics can help explain the functional significance of different lake trout populations in use of available niche space for the species. The sections below review those studies that have examined the heritability of various traits in lake trout and made comparisons among populations.

Fat or Oil Content

Fat content differences between siscowet and lean lake trout forms in several of the Great Lakes were obvious to early explorers and naturalists and were thought to represent genetic differences; however, measurement of these differences have only recently occurred. Siscowet lake trout from Lake Superior have been shown to have oil content as high as 64.2% (Karrick et al. 1956, Stansby 1962). In a comparison of fillets from 23 lean and 29 siscowet trout from Lake Superior, average oil content was 9.4% for leans and 48.5% for siscowet (Thurston 1962). In a more detailed study, Eschmeyer and Phillips (1965) demonstrated that % fat (dry weight) of flesh from the mid-dorsal region in siscowets ranged from 32.5 to 88.8% and in leans from 6.6 to 52.3%. Fat content was positively correlated to total length and explained much of the individual variation in fat content. At a given length, siscowets were always fatter than lean trout. Twelve humper trout were also analyzed and were intermediate in fat content between leans and siscowets. Heritability of fat content was examined by rearing leans, siscowets, and lean x siscowet hybrids under nearly identical hatchery conditions. Siscowets always had greater fat content at a given length, lean trout were lowest, and the hybrids were usually intermediate (three fish overlapped the fat content of leans). Given these results, fat content appears to be a heritable trait distinctive for lean, siscowet, and humper lake trout in Lake Superior.

Swimbladder Gas Retention

Ability to retain gas in the swimbladder has been shown to be heritable and associated with the ability to live in deep water. As capability increases to retain gas, the ability to maintain neutral buoyancy under the high hydrostatic pressure of deep water improves. Tait (1959) determined that for seven species of salmonids, relative ability to keep the swimbladder filled was correlated with depth distribution in their normal habitat. Lake trout were found to have the best retention and brown trout (Salmo trutta) the poorest. Heritability of swimbladder gas retention was investigated by Ihssen and Tait (1974) in lake trout propagated from gametes collected from fish in Lakes Simcoe and Louisa in southern Ontario and reared under identical hatchery conditions. Gas retention was better in trout from Lake Simcoe than in those from Lake Louisa and thus their abilities to maintain depths should also be different. Crosses between the two populations were intermediate. Heritability ($h^2$) of this trait was estimated as $0.58 \pm 0.04$. The two lakes were different in their limnology—the summer thermocline was much deeper in Lake Simcoe than in Lake Louisa. The 10°C isotherms in July were at 20 m in Simcoe and 8 m in Louisa. Correspondingly, lake trout distribution in the summer was reported to be much deeper in Simcoe (25-35 m) than in Louisa (10-20 m) which corresponded to their differences in gas retention abilities. Lake Simcoe lake trout appeared better adapted for a deeper depth distribution than Lake Louisa fish.

Blue-Sac Disease

Blue-sac disease, the abnormal accumulation of bluish fluid in the yolksac of egg and sac fry stages of lake trout, has been known by fish culturists since the late 1800s (Wolf 1956). This condition has been observed in fry from the natural spawning of hatchery-origin lake trout on Stony Island Reef in Lake Ontario during the late 1980s and early 1990s (D. L. Perkins, Cornell University, personal communication 1993). The heritability of the disease was investigated in 80 experimental families of lake trout. The variability in the occurrence of the disease was partitioned as 55% due to environmental sources, and 16% due to males, 27% due to females, and 2% due to male x female interactions (Ihssen 1978). Heritability of the disease was further confirmed in the spalke hybrid (S. fontinalis x S. namaycush) and was estimated as 0.74. Symula et al. (1990) found that mortality from the disease in lake trout propagated from Seneca-strain hatchery-origin adults and captured in Lake Ontario ranged from 7 to 48%.

Eye Lens Defects

Oclusions of the eye lens, known as cataracts, have been regularly observed in hatchery lake trout and the impaired vision presumed to affect growth and survival after stocking. Causes of cataracts can be dietary deficiencies, mechanical trauma, gas supersaturation, ultraviolet light, and genotype. Four strains of yearling lake trout, the Superior, Seneca, Jenny, and “Ontario” (reared from gametes collected from hatchery-origin fish in Lake Ontario) strains, were reared under identical conditions and evaluated for the presence of cataracts before stocking (Kincaid and Elrod 1991). In two year classes examined, the Superior strain consistently had a lower frequency of cataract (6.7-7.3%) when compared to the Seneca (35-51%), Jenny (46%), and Ontario (32%). These data indicated that strains have different genetic predispositions to develop cataracts.
Early Developmental Rates

Developmental rates of fertilized eggs and fry of lake trout populations may vary to control the timing of emergence so as to correspond with the spring thermal regime for optimal survival of juveniles. Horns (1985) compared the degree days required to hatch and emergence among lake trout propagated from four populations: wild Apostle Islands Lake Superior, the Superior strain, Green Lake (hatchery population of Lake Michigan origin), and Trout Lake (wild population in a northern Wisconsin lake). Trout Lake and Apostle Island fish were significantly different from each other in hatching and emergence (P > 0.005); Trout Lake fish hatched and emerged first and Apostle Island fish hatched and emerged last. Hatching timing and emergence were not different between the two Lake Superior origin populations or between the Green Lake and Trout Lake fish. The most likely explanation for the differences observed was that developmental rates have a genetic basis.

Maturation

Timing differences in gamete ripening among hatchery lake trout strains would reduce the potential for crosses between strains stocked in the Great Lakes to occur naturally and could also affect the timing of egg deposition with respect to optimal water and substrate quality for incubation. Adults of the Seneca, Superior, and Jenny hatchery strains were held under similar light and temperature conditions for two years, and gamete ripening times and concentrations of seven hormones in plasma were compared (Foster et al. 1993). No differences among strains occurred in ovulation, spermatiation onset date, or in most hormonal levels. The lack of pronounced interstrain differences in gamete ripening dates and reproductive endocrinology suggested nothing that would provide temporal reproductive isolation of the strains. In contrast, genetic differences among lake trout stocks from the Great Lakes and Ontario inland lakes for age of maturity have been deduced from full- and half-sib matings under controlled hatchery conditions (Ihssen, P. E., unpublished data). For example, 36% of male lake trout with origins from Lake Louisa matured at age 3 whereas only 4% of trout from Lake Opeongo matured. Crosses between the two stocks were intermediate at 19%.

COMPARISON OF STRAINS AFTER STOCKING

Evaluation of the performance and behavior of hatchery-raised lake trout strains after stocking can help to identify those strains that will best achieve the goals of management. For population re-establishment to occur in the Great Lakes, stocked lake trout must first survive and grow to maturity. At maturity, hatchery-origin lake trout must locate spawning grounds, and spawn and deposit eggs in substrates that will successfully incubate eggs until they hatch and fry emerge. Effective use of available niche space for survival, growth, and reproduction will be dependent on the dispersal of trout from stocking locations and their depth distribution in the lake. Comparisons of strains in terms of performance and behavior after stocking are reviewed below.

Survival

Few studies in the Great Lakes have been conducted that compare survival and growth of lake trout strains after stocking. Valid comparisons of survival have been difficult to conduct because of confounding variables such as suspected differential vulnerability of strains to assessment gear used in the Great Lakes. In nine lakes of the Adirondack region of northeastern New York, approximately 200,000 fish each of the Seneca (from southcentral New York) and Upper Saranac Lake (from the Adirondack region) strains were stocked from 1964 to 1968 (Plisila 1977). Relative survival for all lakes combined was 15.9 to 1 in favor of the Upper Saranac Lake strain of Adirondack origin. In this case, the local native strain out performed the non-native strain. In a similar comparison in four northern Minnesota lakes, a local, native strain survived better after stocking than either a hatchery-propagated lean strain with origins in a population near Isle Royale in Lake Superior or the Superior strain (Siezenpop 1992).

Comparison of growth and survival of three lake trout strains from a single stocking in a refuge in northern Lake Michigan yielded no significant differences among strains (Rybicki 1990). From 220,000 to 240,000 yearlings each of the Superior and Jenny strains, and an outcross between females of the Superior strain and males from the Apostle Islands area of Lake Superior were stocked in 1986 and later evaluated as 4-year-olds. No significant differences were found in the relative survival rate and growth.

An important source of mortality in the Great Lakes has been sea lamprey (Petromyzon marinus) predation. Coexistence of lake trout with sea lampreys in two of the Finger Lakes of New York (Seneca and Cayuga lakes) has led to the speculation that the Seneca strain may be better adapted to a fish community that contains the sea lamprey than lake trout elsewhere (Ihssen 1984). If so, stocking of more Seneca strain could enhance survival of lake trout in the Great Lakes. Under laboratory conditions this hypothesis has not proven to be true. In aquaria, no significant difference was found in the survival of adult Superior and Seneca strains subjected to single sea lamprey attacks (Swink and Hanson 1986). However, survival of matched annual plants since 1985 of the Superior and Seneca strains in northern Lake Huron waters and at the centrally located Six Fathom Bank has been greatly different (Eshenroder et al. 1995). The Jenny strain, added later to stocking at Six Fathom Bank, was also compared. In northern waters, the Seneca strain was 43.4 times more abundant than the Superior
strain. Better survival was associated with lower sea lamprey attack rates on the Seneca strain than were observed on the Superior strain. Similarly, lake-wide recoveries of Seneca strain trout > 632 mm that had been stocked earlier on Six Fathom Bank were 4.6 times greater than the Superior strain and 3.0 times more than the Jenny strain.

**Dispersal and Depth Distribution**

Behavior of lake trout as reflected by dispersal from stocking locations and depth distribution after stocking has been shown to vary due to strain. In Lake Ontario, dispersal of the Superior, Seneca, and Clearwater strains after stocking was investigated from 1980-1985 at 16 locations for up to 26 months after stocking (Elrod 1987). Rates of dispersal for the Clearwater fish were similar to those of the Superior strain at four south-shore stocking sites; however, dispersal was less for Clearwater fish stocked at sites in the eastern basin. Dispersal of the Seneca strain (only stocked in the eastern basin) was similar to that of the Superior strain. In another study, Rybicki (1990) found that straying of the three stocked strains out of the northern Lake Michigan refuge (described above) was not different among strains (12–15%). Differences in seasonal bathymetric distribution have been shown among the Superior, Seneca, and Clearwater strains stocked in Lake Ontario (Elrod and Schneider 1987). The mean depth of capture ranged from 3.9 to 10.2 m greater for age-2 Superior strain fish than for age-2 Clearwater fish. The distribution of Seneca fish was similar to that of the Superior strain. Bathymetric distribution observed was probably related to the ability of strains to retain swimbladder gas. The inheritance of lake trout behavior has only been studied in terms of comparisons to other char species such as brook trout (e.g., Ferguson and Noakes 1982, Ferguson et al. 1983).

**Reproduction**

To estimate the reproductive success of hatchery strains requires assessment by year class of the number and proportion of young produced by each hatchery strain or combination of hatchery strains. The comparison of reproductive success among strains requires identification of the parents of naturally produced young. Young fish lack markers other than genes that can be used to identify their strain origins. Genetic markers (e.g., allozymes or mtDNA) can be used to identify the parental origins of young lake trout when baseline data on the genetic characteristics of the hatchery strains have been obtained. Mixed stock analysis of such genetic data can then provide the most probable composition of a sample of fry in terms of pure-strain and inter-strain crosses (MSA, Utter and Ryman 1993). Baseline data for the lake trout strains stocked into Lake Ontario have been developed for both allozymes (Krueger et al. 1989) and mtDNA (Grewe et al. 1993).

The first estimate of the reproductive success of hatchery strains in Lake Ontario came from a collection of 75 fry from Stony Island Reef in 1986 (Marsden et al. 1989). Lake trout fry were estimated to have been produced predominately by Seneca x Seneca strain matings (78%) and Seneca x Superior crosses (20%). Total contribution to the fry sample by the Seneca strain was estimated as 88%. These estimates were in marked contrast to the proportions stocked in the lake which were mostly Manitou, Clearwater, and Superior strains; the Seneca strain comprised only 6% of the lake trout stocked in the area of Stony Island.

In the late 1980s, two additional strains (Jenny and Killala) matured and could have contributed to the origins of naturally-produced fry in Lake Ontario. As a result, mtDNA data were used in combination with allozyme data to better distinguish the large number of potential pure strain and inter-strain crosses possible in fry collections (Grewe et al. 1994b). Parental strain origins of fry collections from Stony Island in 1988, 1989, and 1990 were on average 75% Seneca (range 67.3–86.5%), 12.9% Killala (range 7.1 to 14.9 %), and 10.8% Superior (range 3.6 to 15.9 %) based on MSA. The parental contributions of the fry did not match the strain proportions stocked in the lake. Based on stocking records, the proportion of Seneca strain that should have reproduced if all strains survived and spawned equally varied between 6% and 35%. The Seneca strain consistently contributed more to the naturally produced fry at Stony Island Reef than would have been predicted from numbers stocked.

The reproductive success of strains in Lake Ontario was investigated at four spawning sites in eastern and at four sites in western Lake Ontario. Fertilized eggs were collected from six spawning locations around the lake in the fall of 1992, reared to the fry stage, and then electrophoretically analyzed (Perkins et al. 1995). Fry were also captured from Stony Island Reef in 1991, 1992, and 1993 and similarly analyzed. These data were combined with those from eggs collected from Yorkshire Bar reported by Grewe et al. (1994b). MSA of the collections revealed that at three out of four eastern basin locations the Seneca strain contributed from 73 to 95% to the fertilized eggs or fry. At the fourth location, the Manitou (43%) and Superior/Killala (43%, baseline data for the two strains were combined) contributed the most. In the western basin at three out of four spawning areas, the Seneca and Superior/Killala strains each contributed between 33-48% to the fertilized eggs. At a fourth area, the Seneca strain was absent and most parental contributions were from the Clearwater, Manitou, and Superior/Killala strains. The prevalence of the Seneca strain at most spawning areas and the departure of strain contributions from predicted levels based on numbers stocked indicated that, on a lake-wide basis, the Seneca strain was probably better suited for reproduction in Lake Ontario than the
Superior/Killala strains, although all strains demonstrated the ability to fertilize eggs at certain locations.

**ROLE OF GENETICS IN RECENT LAKE TROUT MANAGEMENT**

Genetic considerations have been incorporated into the lake trout rehabilitation strategies of fish management plans developed in the 1980s for the Great Lakes. The use of genetics in these plans can be traced to the recognition on the Pacific West Coast that discrete spawning stocks of salmon occurred and that often they possessed special traits important for their survival (Ricker 1972). This idea became known as the stock concept. Recognition of the importance of the stock concept and its application to lake trout management in the Great Lakes was provided by Loftus (1976). He identified that the former lake trout stocks probably contained genetically-encoded traits required for survival and reproduction in the Great Lakes. Their extinction therefore was a potential obstacle to successful rehabilitation because the appropriate genetic diversity contained in these fish could not be reintroduced. In 1980, the Stock Concept International Conference examined evidence for separate stocks of Great Lakes fishes and identified potential applications of the stock concept to fish management (Billingsley 1981). The conference and its proceedings, served as a catalyst during the 1980s for the incorporation of the stock concept into Great Lakes fish management.

In Lake Ontario, lake trout management strategies were implemented to introduce a diversity of strains and to develop a "Lake Ontario strain" through collections of gametes from hatchery-origin adults that had survived to maturity in the lake (Schneider et al. 1983). The Superior, Seneca, Clearwater, Jenny, Manitou, and Killala strains were subsequently stocked and evaluated. The genetic stability of four year classes of the Seneca strain used for stocking was compared through allozyme and mtDNA analysis and found to generally show low variability (Grewe et al. 1994a). The purpose of developing the "Lake Ontario strain" was to take advantage of the forces of selection in Lake Ontario to establish a new brood stock by the use of gametes from mature lake trout that had survived for several years in the lake. The developers hoped that progeny from the brood stock would show enhanced survival, and have a reproductive advantage over other strains. Three year classes of wild fry from Stony Island Reef and six year classes of "Lake Ontario strain" developed from adults captured adjacent to the same reef were compared based on allelic frequencies of allozymes and MSA (Marsden et al. 1993). Wild fry and the "Lake Ontario strain fish" were genetically dissimilar. Survival and even aggregation adjacent to a spawning reef by strains did not necessarily indicate that they would successfully reproduce. Wild fry captured from reef areas were recommended as a better source of fish to develop the "Lake Ontario strain" than gametes of hatchery-origin adults. The Lake Erie Lake Trout Rehabilitation Plan follows strategies similar to those for the Lake Ontario plan (Lake Trout Task Group 1985).

In Lake Michigan, genetic considerations were incorporated into lake trout management plans developed for a reef in Illinois (Coberly and Horrall 1982) and for lake-wide management (Krueger et al. 1983, Lake Michigan Lake Trout Technical Committee 1985). A variety of lake trout strains was chosen for lake-wide introduction into either deep or shallow water habitats. Two strains were identified as desirable for stocking deep-water habitats, the Seneca and Green Lake strains. The Seneca strain was developed from a deep-water, early-fall spawning population from Seneca Lake (Royce 1951). The Green Lake hatchery strain, was originally derived from a population in Green Lake, Wisconsin (Hacker 1956). The Green Lake population was maintained from 1886-1944 by stocking juveniles propagated from gametes of deep-water, southern Lake Michigan lake trout (Krueger et al. 1983). Because of the extinction of lake trout in Lake Michigan, the Green Lake strain represented one of the last genetic sources of Lake Michigan origin trout. Unfortunately at the time of implementation of the Lake Michigan plan, few fish of the Green Lake strain remained as a hatchery strain. Brood-stock age fish, however, were available in southern Lake Michigan that were survivors from past plants made in middle 1970s and were identifiable by their fin-clip. Both the remnant brood stock and Green Lake strain fish in southern Lake Michigan, therefore, were used when reconstruction of the Green Lake stock was begun. Three Green Lake strain year classes were developed in the mid-1980s from feral fish captured from southern Lake Michigan and their allozyme allelic frequencies were compared to domestic progeny from the remnant brood stock (Kincaid et al. 1993). The year classes from feral parents were similar to each other but differed from the domestic year class. A modified diadel mating design was developed and implemented to produce a composite brood stock from the remnant and feral sources.

Like that for Lake Michigan, the lake-wide management plan for the rehabilitation of lake trout in Lake Huron established various zones in the lake that correspond to different habitats and rehabilitation priorities (Argyle et al. 1991). To establish populations in these zones, different strains with a variety of traits will be necessary if historic spawning sites are to be re-populated. No explicit mention was made in the plan of which strains will be used to stock different areas although, upon implementation, the Superior, Jenny, and Seneca strains were stocked (Eshenroder et al. 1995). The lake-wide Lake Huron plan identifies that studies are needed on the reproductive success. The mention of the evaluation of reproductive success, and not just the survival of strains, was unique among the Great Lakes plans. Lake Huron has two small remnant native populations, one in McGregor Bay in the North Channel and another in
Parry Sound in Georgian Bay. Though no mention was made in the lake-wide plan as to special management considerations for these native populations (Argyle et al. 1991), their conservation, rehabilitation, and potential use for reintroduction elsewhere in Lake Huron has been described in the Ontario Ministry of Natural Resource’s (1995) plan for lake trout rehabilitation of Ontario’s waters. The provincial plan also describes the proposed introduction of two Lake Superior stocks, Slate Island and Michipicoten Island, into areas of Lake Huron where native stocks do not occur.

The management plan for lake trout in Lake Superior identifies the stocking of hatchery fish propagated from wild Lake Superior strains as an important strategy to achieve rehabilitation (Busiain et al. 1986). Lake Superior is unique in that many native off-shore stocks and a few near-shore populations still exist. No management considerations were given in the plan for the management of humper or siscowet lake trout or for the importance of special management of near-shore, remnant native lean populations. Recently, management agencies have agreed on fish community objectives for the lake (Busiain 1990). Unfortunately, considering the diversity of stocks that remain, only brief mention was given to the importance of the reestablishment and conservation of native stocks.

CONCLUSIONS

Originally, the Great Lakes were the home to a wide diversity of lake trout stocks, capable of using an extensive variety of habitats. Lake trout spawned on remote offshore reefs and shoals, near-shore reefs, and tributary streams, and at other times were capable of feeding and growing in all depths of waters (> 300 m). Stock radiation of lake trout into these habitats was likely unstrained after glaciation due to the scarcity of other ecologically similar species. The diversity observed historically, and believed to have a genetic basis, was only partly confirmed by modern genetic analysis because stocks had become virtually extinct in the lower four Great Lakes and reduced in number in Lake Superior by the time these techniques were developed. Clear genetic differences were observed among the lean, siscowet, and humper forms from Lake Superior but these differences reflected the levels of differentiation observed among populations rather than among species as early naturalists thought. Distinguishing phenotypic traits of the stocks such as fat content and depth distribution were shown to have a heritable basis.

Closer attention to genetic considerations in lake trout management will accelerate progress toward population rehabilitation in the Great Lakes. Current management has initiated an important first step of employing genetic strategies in management actions, but full use of available genetic information about lake trout has not occurred. For example, the suspected poor performance of the Clearwater strain in Lake Ontario was predictable based on Ihssen and Tait’s (1974) studies more than twenty years ago on the retention of swimbladder gas and its relationship to depth distribution. The Clearwater strain originated from a shallow water population in Clearwater Lake in northern Manitoba (approximately 54°N, 101°W) where summer warming of waters does not require a deep depth distribution (July-August summer thermocline from 9 to 24 m (personal communication, Doug Leroux, Department of Natural Resources, Province of Manitoba). This strain was then introduced into Lake Ontario at the southern edge of the species distribution of lake trout (43°30’N, 78°W). The summer thermocline in the eastern basin of Lake Ontario regularly occurs at depths of 40 m. Not surprisingly, the benthothermal distribution of the Clearwater strain lake trout was shallower than other strains stocked (Elrod and Schneider 1987). Because of their shallower distribution, they probably suffered greater angling mortality because of the ease of fishing them in shallow waters. This strain has shown little reproductive potential to produce fry based on genetic analysis and MSA of naturally fertilized eggs and fry captured in Lake Ontario (Marsden et al. 1989, Grewe et al. 1994b, Perkins et al. 1995).

Choice of lake trout strains for stocking should use genetic sources from Great Lakes basin populations combined with an environmental matching approach where the original habitat of the strain to be stocked should be similar to the waters to be rehabilitated (Krueger et al. 1981, Ihssen 1984). Implementation of this approach should make use of the native lean, humper, and siscowet stocks of Lake Superior. For example, deep water habitats should be stocked with siscowet, the native deep water trout still abundant in Lake Superior. Naturalized populations that have been established by stocking of lake trout of Great Lakes origin provide other genetic sources for introduction to the Great Lakes (e.g., Jenny strain from Wyoming). Typically these populations were established from Lakes Michigan and Huron and may provide the opportunity to reintroduce lake trout of a genetic character that has become extinct from these lakes. For example, the naturalized population in Lake Tahoe that spawns on vegetation in deep water should be considered as a genetic source for reintroduction into Lakes Michigan and Huron. This population was established before 1900 through stocking of fish reared from eggs of lake trout collected from the Great Lakes. The first possible source of introduction to Lake Tahoe was a shipment of eggs to Nevada in 1885 by the United States Fish Commission; however, their distribution in Nevada was not reported (Smith 1896). These eggs were collected by the Commission from northern Lake Michigan (probably the Beaver Island area) through the port of Thompson, Michigan and from the island shoals of Thunder Bay, Lake Huron through the port of Alpena, Michigan (U.S. Commission of Fish and Fisheries 1887). The first confirmed stocking of lake trout young in Lake Tahoe occurred in 1889. Collections
of eggs in the fall of 1888 that served as the source for these fish were primarily from lake trout in northern Lake Michigan through the port of Thompson (U.S. Commission of Fish and Fisheries 1892). From these introductions in the 1880s, lake trout in Lake Tahoe were reported to be “multiplying” and weighing up to 5 kg by 1895 (Smith 1896). In 1895 and 1896, additional plants of lake trout with origins from Lakes Michigan and Huron occurred (U.S. Commission of Fish and Fisheries 1896, Smith 1896, Miller and Alcorn 1943). Since that time, the lake trout population in Lake Tahoe may have preserved some of the genetics of the original native lake trout from northern Lake Michigan and Lake Huron.

The reproductive performance of lake trout strains after stocking should be a central focus of the evaluation of stocking programs when the goal of management is population rehabilitation. Survival to maturity is an important characteristic required for reproduction but should not be viewed as equivalent to reproductive potential. A strain having modest survival after stocking relative to other strains could well contribute the most to year-class recruitment through natural reproduction. In rehabilitation programs, the foremost attribute for evaluation of strains after stocking is their contributions as parents to the next generation. Only the Lake Huron plan identified the reproduction of strains as an important aspect for evaluation (Argyle et al. 1991). The genetic analysis of naturally produced trout from the spawning of hatchery-origin adults combined with MSA (such as has occurred in Lake Ontario) provides a methodology for the reproductive evaluation of lake trout strains in the Great Lakes.

Different genetic strategies of management will need to be employed in Lake Superior than in the other Great Lakes. Though reduced in number, many native stocks remain in Lake Superior including the original lean, humpcr, and siscowet forms. High priority should be given to the conservation of these stocks, the largest remaining gene pools of Great Lakes lake trout. Unfortunately only brief mention of the importance of the genetic diversity of lake trout (or other native species) occurs in the Fish Community Objectives for Lake Superior recently established by the management agencies (Busiahn 1990). Depressed stocks should be protected from sea lamprey predation and overfishing and allowed sufficient time for recovery. Population recovery can be achieved, and has been documented for the south shore stocks of Gull Island Reef (Swanson and Wedberg 1980) and Stannard Rock (Curtis 1990). Stocking of lake trout to supplement or increase the number of fish in a native population can pose extinction risks to the native stock and risks corruption of the native gene pool if non-native sources are stocked (Evans and Wilcox 1991). Such management actions must be avoided if native stocks are to persist.

Goals and objectives for lake trout management of the Great Lakes should explicitly embrace a vision that population rehabilitation is accomplished only when a level of phenotypic diversity has been re-established. “Successful” rehabilitation should require the existence of naturally-reproducing, self-sustaining populations of different lake trout forms that use a variety of habitats. Historically, a diversity of lake trout stocks occurred in the Great Lakes; however, most attention in fish management has been given to the establishment of near-shore, shallow-water-spawning lean trout (the one exception is use in the deep waters of Lake Michigan of the Green Lake and Seneca strains as described above). Emphasis on phenotypic diversity as a strategy for management could be as simple as giving consideration to rehabilitation of both shallow-water and deep-water habitats and introducing the appropriate forms of lake trout. Establishment of near-shore lean trout stocks may be the most difficult to accomplish due to their vulnerability to fishing, sea lamprey predation, effects of exotic species, and habitat degradation. A diversified approach to lake trout management provides the opportunity for achievement of population rehabilitation in more than one habitat.

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