RESEARCH PRIORITIES FOR LAKE TROUT REHABILITATION IN THE GREAT LAKES: A 15-YEAR RETROSPECTIVE

Great Lakes Fishery Commission

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ABSTRACT. We review research relating to the rehabilitation of lake trout in the Great Lakes published since 1984 (when a previous assessment was made) and recommend priorities for the future. First-order research priorities (those issues that have potential to completely block recruitment from hatchery-origin spawners), and second-order priorities (those issues relating to enhancement of recruitment from hatchery or wild spawners) are identified for seven subject areas: population dynamics, stocking practices, genetics, behavior, fish health, spawning habitat, and biotic interactions. Recommendations for first-order research fall into five larger problem areas: early-life bottlenecks, imprecise homing, low genetic diversity, thiamine deficiency, and spawning habitat classification. Among these five areas, two (resolution of early-life bottlenecks and low genetic diversity) are viewed as most important because they emerge repeatedly in the analysis and have potential to provide larger insights.

INTRODUCTION

Reestablishment of self-sustaining populations of lake trout *(Salvelinus namaycush)* over their former range is arguably the most profound ecological challenge in the Great Lakes. Lake trout were the dominant top predator in all of the lakes except Lake Erie. Even in Lake Erie, they were important in the eastern basin (Smith 1968b; Christie 1974). Although self-sustaining populations have been reestablished in much of Lake Superior (Hansen et al. 1995a), populations in the other lakes are maintained by stocking. In these lakes, the functional role of lake trout as top predator has been replaced, in part, by introduced Pacific salmon (Oncorhynchus spp.). Contemporary communities of mostly stocked salmon and trout in Lakes Michigan, Huron, and Ontario are capable of exerting predatory pressure-especially on the introduced and prolific alewife *(Alosa pseudoharengus)* (Rand et al. 1995). Salmon, however, are pelagic obligates in the Great Lakes (Eshenroder et al. 1995b; Eshenroder and Bumham-Curtis 1999). Their contribution to community structure is limited in lakes with deep hypolimnia.

Salmon-alewife communities are prone to collapse (Kocik and Jones 1999). Management of these communities is under considerable political pressure to implement unsustainable practices-for example, over-stocking (Gale 1987; Eshenroder 1989; Eshenroder et al. 1995b; Stewart et al. 1999). Without self-sustaining populations of lake trout, the lakes will likely face more perturbation. Weak regulation of food webs by stocked trout and salmon will likely lead to more fishery upheavals that, in turn, encourage demands for even more-risky solutions.

Rehabilitation of lake trout is an important fishery goal for every lake. If an effective approach for rehabilitating lake trout was widely recognized, reestablishment would not be the profound problem that it is today. In terms of its history, spatial scale, cost, and institutional complexity, the attempt to rehabilitate lake trout in the Great Lakes is surely the largest recovery program ever for a single species. Although more could have been done, substantial efforts were made in pursuit of rehabilitation goals. We believe that the most immediate problem is scientific. Biologists have not reached a consensus on the cause of reproductive failures, even in the following situations where spawning lake trout were abundant regionally:

- Lake Superior, Wisconsin inshore (Krueger et al. 1986)
- Lake Michigan, Claybanks (Holey et al. 1995)
- Lake Huron, southern main basin (Eshenroder et al. 1995c)
- Lake Ontario (O'Gorman et al. 1998)

Proven strategies for rehabilitating lake trout are needed. Eshenroder et al. (1984), responding to evidence that existing rehabilitation strategies were problematical, attempted to establish a consensus on research needs 15 yrs ago. This effort, the Conference on Lake Trout Research (CLAR), brought together 43 experts who developed research priorities in seven disciplines. Much has been learned about lake trout in the Great Lakes since CLAR, and an especially rich repository for this knowledge was presented or referenced in RESTORE (Selgeby et al. 1995b). This symposium, a product of the Great Lakes Fishery Commission's (GLFC) Board of Technical Experts (BOTE), provided a spectrum of research ideas; however, a synthesis was not provided. Recognizing this shortfall, BOTE sought a research synthesis within its Lake Trout Research Coordination Task. This paper responds to BOTE's request for an up-to-date synthesis of priorities for research on lake trout rehabilitation.

Our objectives here are to revisit and update the research priorities identified in CLAR. We

- Review the state of knowledge at the time of CLAR
- Identify major findings published subsequently
- Note unresolved, continuing issues
- Discuss new, emerging issues
- Make recommendations for research priorities

Seven subject areas (population dynamics, stocking practices, genetics, behavior, fish health, spawning habitat, and biotic interactions) parallel those in CLAR (Eshenroder et al. 1984). However, we separate species (here called biotic) interactions from population dynamics, consider physiology within other subjects, omit socioeconomics, and address contaminants within a new subject area of fish health. In a further departure from CLAR, we classify priorities in each subject area as either first- or second-order research-a scheme used only in the CLAR overview. First-order research pertains to issues that we suspect have the potential to completely block recruitment from hatchery-origin parents. Second-order research pertains to enhancement of recruitment from hatchery or wild parents.

As in CLAR, we provide an overview with recommendations for what we believe is the highest priority research. These recommendations cross subject areas.

REHABILITATION THEN AND NOW

The environment for lake trout rehabilitation has changed appreciably since CLAR was held in 1983. Then, only offshore populations of lake trout in Lake Superior had rebounded. Now most inshore populations in Lake Superior have recovered to a level where stocking has become unnecessary and eliminated (Hansen et al. 1995b). In the other lakes, sustainable reproduction is not evident. One exception is in eastern Georgian Bay where a residual wild population persists in Parry Sound (B. Henderson, Ontario Ministry of Natural Resources, 1450 Seventh Ave. East, Owen Sound, Ontario, CANADA, N4K 2Z1, personal communication). Although progress in rehabilitation lags behind expectations in most of the Great Lakes, strategies are now more experimental than they were in the early 1980s. Refuges have been established to control the effect of fishing and to provide areas for stocking experiments with alternative genotypes. Stocked populations, however, are small in comparison to native populations; use of available genetic diversity remains limited (Krueger and Ihssen 1995); and some of the best spawning grounds are not stocked because of fishery conflicts (Eshenroder et al. 1995c; Dawson et al. 1997).

New realities regarding altered fish communities have important implications for rehabilitating lake trout. Burbot *(Lota lota),* a deepwater native predator, were at low numbers in each of the lakes when lake trout planting efforts began. Burbot have since proliferated in Lakes Michigan (Fratt et al. 1997) and Huron (McLain et al. 1995) and are beginning to recover in Lakes Erie and Ontario. Although co-evolved with lake trout, burbot, once well reestablished, may impede rehabilitation by preying on recently planted lake trout. Invasive faunas are more of a concern now than in the early 1980s. Thought to be under control, the sea lamprey *(Petromyzon mavinus)* population in Lake Huron surged in the mid-1980s in response to a partial recovery of the bloater *(Coregonus hoyi)* (Eshenroder et al. 1995c). The inshore community in the Great Lakes has recently been enriched by the round goby *(Neogobius melanostomus)* (Jude et al. 1992), ruffe *(Gymnocephalus cernuus)* (Pratt et al. 1992) threespine stickleback *(Gasterosteus aculeatus)* (Stedman and Bowen 1985), and zebra mussel *(Dreissena polymorpha)* (Marsden et al. 1995a). All four species have the potential to interfere with lake trout reproduction.

Additional realities involve new perceptions of old problems. Contaminants in the Great Lakes are at lower concentrations now than in the early 1980s (Stow et al. 1995). Therefore, the associated threat to lake trout reproduction appears less ominous (Fitzsimons 1995a; Zint et al. 1995; Guiney et al. 1996). In contrast, early mortality syndrome (EMS)-a lethal thiamine deficiency-has apparently interfered with salmonid reproduction, at least since the 1960s (Honeyfield et al. 1998). However, the problem (a parental diet of alewives) was only recently recognized (McDonald et al. 1998). Also, the role of the alewife as a potentially important predator on lake trout fry was demonstrated only recently (Krueger et al. 1995b). Previously, alewives were not thought to be an important source of lake trout mortality because both species coexisted in Lake Ontario for nearly a century (Christie 1973).

Prospects for achieving lake trout rehabilitation throughout the Great Lakes remain challenging. Although substantial scientific progress has been achieved, new problems have emerged and old problems have taken on new dimensions. If lake trout had not played such a major role historically and if an ecological replacement was evident, support for rehabilitation would be less. The lack of a suitable replacement species places a premium on finding solutions for reestablishing lake trout.

Although much has changed since CLAR was held in 1983, the need to refocus priorities to guide lake trout research remains critical.

POPULATION DYNAMICS

Life-table models are as important now for assessing the rehabilitation of lake trout as they were in the early 1980s when Hatch (1984) identified data gaps that limited predictive capability. Hatch sought knowledge of population size-particularly for planted adult fish-and needed estimates of mortality from the time of planting through the subsequent juvenile period when fish were not fully vulnerable to assessment nets. Total adult mortality then was estimated from catch curves, and a method was sought for partitioning total mortality into its natural, fishing, and sea lamprey-induced components. These data were needed to estimate regional or lakewide population sizes and responses of populations to fishing and sea lampreys. Hatch (1984) feared that too few stocked lake trout were surviving to a reproductive age.

Quantitative population models envisioned by Hatch (1984) have evolved now to include bioenergetics, but these approaches are typically applied at large spatial scales (Negus 1995). Simple models of catch per effort are still needed for tracking regional, more-localized trends in population abundance (see the lake case-history papers in RESTORE). Despite the recent emphasis on qualitative data, survival estimates for juvenile lake trout remain important because recruitment of hatchery fish has slowed considerably in several lakes (Hansen et al. 1994; Elrod et al. 1993; Fabrizio et al. 1997). Better estimates of sea lamprey-induced mortality are also available from field (Schneider et al. 1996) and laboratory studies (Swink 1990). Moreover, since the early 1980s, the widespread recovery of wild lake trout in Lake Superior (Hansen et al. 1995a) provides a model for the other lakes.

Notwithstanding these accomplishments, why sustainable reproduction is lacking in areas where native lake trout populations were formerly abundant and where stocked lake trout became abundant is not resolved. Variations in stocking density or in regional population size have not been predictors of recruitment in other than Lake Superior because wild-fish abundance has rarely exceeded threshold levels of detection. In contrast, variation in numbers of mature hatchery lake trout on spawning reefs is large compared with variation in stocking rates. Selgeby et al. (1995a) showed that detectable-but not necessarily sustainable - recruitment was associated with higher densities of spawning adults on reefs. This finding and the prolonged failure of even the larger populations of stocked lake trout to reproduce on a sustainable basis indicate that research is needed most, not at the regional level, but on spawning reefs where the reproductive bottleneck(s) is likely occurring. Estimates of survival for all ontological life stages between egg and alevin - for example, those reported by Perkins and Krueger (1995) - are needed. Survival estimates from self-sustaining wild populations in Lake Superior (Bronte et al. 1995b; Schram et al. 1995) can be used to assess the ecological significance of survival estimates for stocked populations.

Historical benchmarks can be used to assess the status of lake trout rehabilitation (Hansen et al. 1995b), but more-refined stock-recruitment relations will be needed to account for changes in growth, maturity, and fecundity. When relationships among these key life-history variables are understood for reference populations, rehabilitation status may be inferred for other populations. Stock-recruitment relationships are also needed to determine when populations are fully rehabilitated (Bronte et al. 1995a). Although considerable progress has been made for estimating the lethality of sea lamprey attacks for lean lake trout (Swink and Hanson 1986; Swink 1990), similar estimates are needed for siscowet (fat) lake trout to correctly estimate mortality and determine the population abundance for this dominant form of lake trout in Lake Superior.

First-Order Research

Identify reproductive bottlenecks on spawning reefs.

Second-Order Research

Establish stock-recruitment relationships for wild populations of lean and siscowet lake trout and estimate the lethality of sea lamprey attacks on siscowets.

STOCKING PRACTICES

Rearing lake trout in hatcheries and stocking at fingerling and yearling life stages were thought to contribute, in part, to their failure to develop self-sustaining populations in the Great Lakes (Horrall 1981; Foster 1984). In Lake Superior, ‘hatchery lake trout dominated inshore populations and were found on historic inshore spawning reefs. However, they were not as abundant on historic offshore reefs (Peck 1979; Krueger et al. 1986). Hatchery lake trout appeared to have a greater affinity for shallow water than the former native populations. Foster (1984) suspected that hatchery rearing exposed lake trout to abnormally high light levels, which could condition the lake trout to spawn at inappropriate times. Foster (1984) and Binkowski (1984) believed that imprinting occurred mainly during the fry life stage. In addition, stocking fingerling and yearling stages that were less likely to imprint was responsible for the lack of homing to offshore stocking sites. Hatcheries now shade raceways to reduce light intensity, and more stocking is done on offshore historic spawning reefs. Thus far, these practices have not resulted in the establishment of self-sustaining populations; however, assessments are incomplete.

If rearing and stocking practices negatively affect the performance of hatchery lake trout, partial compensation might be achieved by increasing stocking density. Binkowski (1984), reflecting widespread concerns during the early 1980s, urged experimentation with stocking densities well above conventional levels. In Lake Superior, the highest stocking densities were all lower than those subsequently recommended by the Lake Superior Technical Committee by percentages ranging from 48% in Ontario waters to 7% in Minnesota waters (Hansen et al. 1995a). Density of hatchery-origin adults in Lake Superior decreased in the 1970s and 1980s as hatchery production was diverted to the other Great Lakes and as survival of stocked fish decreased (Peck and Schorfhaar 1991; Hansen et al. 1994). Despite lower-than-desired stocking levels, abundance of adult hatchery-reared fish in Michigan and Wisconsin waters of Lake Superior during the late 1960s to early 1980s exceeded the average abundance of native stocks from 1929 to 1943 (Pycha and King 1975; Hansen et al. 1995b). Analysis of hatchery and wild adult lake trout abundance and subsequent recruitment of wild lake trout indicated that hatchery-reared lake trout contributed the most to recruitment and restoration of lake trout populations in inshore waters of Michigan and Minnesota (Hansen et al. 1995a, 1997). In Lake Michigan, however, stocking the Clay Banks Refuge at twice the conventional rate did not result in recruitment of wild lake trout (Holey et al. 1995; Fabrizio et al. 1997).

Stocking early life-history stages with greater potential to imprint to stocking sites was recommended to speed colonization of spawning habitat (Binkowski 1984; Eshenroder et al. 1984). Fry stocking on offshore Lake Huron reefs (Bergstedt et al. 1990) and on inshore reefs in Green Bay, Lake Michigan, was not successful. Early returns of juveniles from eggs stocked in artificial-turf incubators on Jacksonport Deep Reef, Lake Michigan, have not been encouraging (Holey et al. 1995). Stocking eggs in artificial-turf incubators in Lake Superior appears to be more promising (S. Schram, Wisconsin Department of Natural Resources, 141 S. 3rd Street, Bayfield, WI, 54814, personal communication). The experiment in stocking eggs in artificial turf has been continued in Lake Michigan, and a parallel study has been initiated in Lake Huron.

Decreased returns from stocked lake trout in Lakes Superior, Michigan, and Ontario have recently led to a reappraisal of optimum stocking size. Yearlings had previously been stocked in the spring at a size of 23-27 g based on studies by Pycha and King (1967). The study was done during a period when the abundance of potential predators and competitors was relatively low. Hatcheries can now produce spring yearlings twice as large as those recommended by Pycha and King. These larger yearlings have been stocked in the upper Great Lakes, and preliminary results from Lake Superior indicate that they are surviving better than comparably stocked 23-27-g yearlings (D. Schreiner, Minnesota Department of Natural Resources, 5351 North Shore Dr., Duluth, MN 55804, personal communication). Elrod et al. (1993), however, found that larger yearlings (40.0-54.5 g) did not always survive better than smaller yearlings (22.6-40.0 g) in Lake Ontario

Improved rearing and stocking practices have the potential to produce more adult lake trout capable of producing more offspring. Lake trout are top predators that shape their environment by suppressing potential competitors/predators. This community perspective suggests that larger populations of lake trout overall are desirable, especially in view of species changes in the Great Lakes (Eshenroder et al. 1995b). A reverse in the recent declines in hatchery lake trout survival and/or only modest improvements in survival may not result in long-sought surges in the recruitment of wild fish. Except in Lake Superior, high-density populations were not self-sustaining. A biotic change, however, could conceivably eliminate a bottleneck and allow sustainable reproduction.

We especially endorse research on stocking practices that represent a major departure from conventional approaches. This caveat suggests a priority for deployment of ontologically different life stages. A balanced effort devoted to both eggs and fry is suggested--eggs because of uncertainty about when imprinting occurs and fry because of logistical ease. We also encourage continued experimentation with the conventional practice of stocking juveniles (fingerlings and yearlings).

Variables of concern are:

- Size at stocking
- Condition
- Depth of water stocked
- Depth of release
- Density of stocked fish (numbers released at a specific site)

Experiments should control for a single variable so that hatchery history and handling before release are as similar as possible. Size-at-stocking experiments also need to account for the effect of growth rate in the hatchery on longevity. We are concerned that size and age at stocking may interact and that size is not the only variable in size-at-stocking experiments.

First-Order Research

Evaluate reproductive performance of stocked early-life stages.

Second-Order Research

Assess effects of growth, size, and method of release on reproductive performance of lake trout stocked as fingerlings and yearlings.

GENETICS

Technological advances made in molecular genetics since the early 1980s are likely unmatched by any of the other areas of inquiry discussed in this paper. This science was just emerging in the early 1980s (Ihssen et al. 1981), and it was not clear then how much genetic variation was in lake trout from the Great Lakes or how much of the phenotypic variation among these populations was heritable (Ihssen 1984). Native lake trout from the Great Lakes were known to be much more morphologically diverse than lake trout from inland lakes (Behnke 1980). However, it was not until the late 1980s that the greater morphological diversity in the Great Lakes was linked to greater genetic diversity (Ihssen et al. 1988). Ihssen et al. (1988) and Krueger et al. (1989) reported that 14% to 21% of the variation among lake trout populations was due to differences among stocks, and most of this variation occurred in the Great Lakes. Of the three recognized forms of the lake trout, two (humpers and siscowets) are endemic to the Great Lakes. Phenotypic differences among and within forms were subsequently shown to have a genetic basis (Krueger and Ihssen 1995). These differences include traits important for recolonization of the Great Lakes:

- Reproductive performance
- Maturation rate
- Rate of early development
- Home range
- Depth distribution
- Fat content and swim-bladder gas retention (traits associated with depth distribution)

- Interactions with sea lampreys
- Disease resistance

Advances in lake trout genetics have not been fully applied in rehabilitation efforts (Bumham-Curtis et al. 1995; Krueger et al. 1995a; Perkins et al. 1995). Particularly evident is the near absence of efforts to reintroduce deepwater forms of lake trout - humpers and siscowets. Lake trout resembling siscowets occurred in Lakes Michigan and Huron, but humpers were not reported outside of Lake Superior (Krueger and Ihssen 1995). Humpers are readily distinguished by their small size and may have been overlooked in the other lakes, where, based on laboratory and hatchery records, they likely would have been larger. A 1916 letter from a Lake Huron fisherman, now archived with the Michigan Department of Natural Resources, refers to a deepwater lake trout with “flesh made up of thinner layers,” a characteristic of deepwater trout (Bumham-Curtis and Smith 1994). Deepwater lake trout in the upper lakes could have spread from one source, especially during high lake levels, or could have evolved independently and converged because of common selection pressures. Regardless of origin, Lake Superior deepwater genotypes have the potential to restore phenotypic and genetic diversity missing from the other lakes. Humpers and siscowets have higher mtDNA diversity than shallow-water Lake Superior strains (M. Bumham-Curtis, Great Lakes Science Center, 1451 Green Rd., Ann Arbor, MI 48105, personal communication).

Traits associated with endemic (deepwater) forms of lake trout are only poorly understood but may be especially valuable for rehabilitation. The shallow-water strains currently stocked have limited potential to inhabit depths beyond 85 m (Eck and Wells 1983; Elrod et al. 1996a). Approximately 50% of the volume of Lakes Michigan, Huron, and Ontario is associated with greater depths (Christie and Regier 1988). Endemic forms, having evolved in deep water, may select spawning habitat not used or only marginally used by shallow-water lake trout. Hacker (1956) observed that lake trout spawned from deepwater Lake Michigan parents and stocked in Green Lake, Wisconsin, remained in deep water for spawning. This characteristic may have been lost in the second and later generations of the Green Lake strain because of outbreeding with inshore strains (Coberly and Horrall 1982). Because the Green Lake strain is the only deepwater strain used in the rehabilitation program, an unambiguous assessment of the potential role for deepwater lake trout is lacking.

The effort to reintroduce lake trout in the Great Lakes has employed little of the available genetic diversity. Bumham-Curtis et al. (1995), Eshenroder et al. (1995b), and Krueger and Ihssen (1995) recommended using more of the available diversity. Their admonition pertained to shallow-water strains that appear promising (for example, the Parry Sound strain) but applies especially to deepwater morphotypes ignored for reintroduction. Bowles (1995), referring to salmon restoration on the West Coast, stated that selective recovery efforts do not promote sustainability. We agree.

First-Order Research

Reintroduce the full range of Great Lakes phenotypes and assess their reproductive performance.

Second-Order Research

1. Delineate heritable traits associated with habitat use and successful reproduction.

2. Develop more genetic markers for identifying parental origin.

3. Archive tissues (scale samples) from extinct populations to facilitate selection of brood stocks that are closest to ancestral genotypes.

BEHAVIOR

Researchers in the early 1980s believed hatchery rearing resulted in behavioralanomalies in lake trout that were potentially serious obstacles to their reestablishment in the Great Lakes (Foster 1984). These researchers recognized that physiochemical differences between hatchery and natural environments had the potential to affect behavior. However, their major concern reflected a recognition that lake trout likely imprinted and homed to natal reefs, and hatchery rearing would uncouple this process. Olfactory cues (pheromones) were suspected of being important in imprinting and homing in part because of evidence for this mechanism in Arctic char *(Salvelinus alpinus)* (Selset and Doving 1980). Interest in pheromones was stimulated in part because of the potential to mimic them in the lakes. Researchers were also aware that an array of behavioral differences among lake trout genotypes represented adaptations to ancestral environments that would affect their performance in the Great Lakes (Ihssen 1984).

Exactly how lake trout select spawning sites in the Great Lakes remains conjectural. Lake trout in Lake Superior are more apt to spawn each year on the same reef than on reefs not previously used (Krueger et al. 1986; Peck 1986), but no one has shown that they return exactly to where they originated. Homing is assumed to occur (Eshenroder et al. 1995b). Hatchery fish, not imprinted to specific spawning locations in the Great Lakes, respond to other environmental cues such as depth, substrate composition, and slope (Marsden 1994; Marsden et al. 1995b) when selecting spawning habitat. Elrod et al. (1996b) showed that mature hatchery-origin lake trout in Lake Ontario tended to return to the region where they were planted, which suggests they recognized where they lived as juveniles. This recognition may be part of a mechanism that allows lake trout to return to the area they inhabited as young juveniles, which would be near the area where their parents spawned. Despite such behaviors, spawning aggregations of hatchery lake trout have been observed frequently on habitats in Lake Michigan apparently not used for spawning by native lake trout (Dawson et al. 1997).

Matched plantings of various lake trout genotypes have provided important insights on behavioral differences among strains (Krueger and Ihssen 1995). Differences in depth preferences (Elrod et al. 1996a) and resistance to sea lamprey predation (Eshenroder et al. 1995c; Schneider et al. 1996) have important implications for performance of lake trout in the Great Lakes. In addition, significant differences in fry production among strains (Grewe et al. 1994; Perkins et al. 1995) may have a behavioral basis. An important insight from strain-stocking experiments conducted at remote locations was that lake trout of all strains were more likely to aggregate for spawning on deep reefs if the reefs were separated from the mainland by wide expanses of deep water (Eshenroder et al. 1995c). This finding implies that searching by hatchery-origin lake trout for shallow spawning sites is affected by experience. More information on performance differences among strains will be available in the near future when the stocking experiments begun in the mid-1980s are completed.

Two major questions about behavior emerge.

- Can spawning on appropriate substrates be encouraged by stocking early-life stages?

- Will deepwater lake trout select deepwater habitats for spawning?

Spawning lake trout were scarce on some historically important spawning sites (Peck 1979; Krueger et al. 1986; Eshenroder et al. 1995c) and the intent of deploying early-life stages is to find a better way to reestablish self-sustaining populations. Deepwater lake trout may similarly provide a method of repopulating spawning habitats not used or marginally used by shallow-water strains. If hatchery-reared deepwater lake trout remain in deep water for spawning, they would provide a valuable rehabilitation tool. Eshenroder et al. (1995b) hypothesized that the shallow-water form of lake trout, when stocked, expresses behaviors adaptive for colonists, i.e., they spawn in shallow water where the probability of locating suitable substrates in inland lakes is highest. For instance, Fitzsimons (1994a) stated that 95% of spawning shoals in inland lakes were within 10 m of the shore. This trait in shallow-water forms of lake trout may account for many of the observations of spawning aggregations of stocked lake trout on inappropriate, inshore substrates.

Effect of genotype on habitat selection and identification of homing mechanisms are also important behavioral issues. Elrod et al. (1996b) did not find differences in geographical distribution among strains in Lake Ontario, but he did report differences in depth distribution. Evaluating a full array of genotypes would likely reveal even more differences in habitat use and diet. Homing mechanisms in lake trout are likely complex and may involve

- Imprinting to pheromones (Foster 1984)

- Recall of geographical location (Elrod et al. 1996b)

- Attraction to conspecifics (Krueger et al. 1986)

- Habitat recognition (Marsden et al. 1995b; McAughey and Gunn 1995)

Sorting the component mechanisms out may be difficult, but if resolved may allow for artificial imprinting.

First-Order Research

1. Assess the potential of reestablishing spawning aggregations by stocking eggs and/or fry.

2. Determine the effect of hatchery rearing on spawning-habitat selection in deepwater lake trout.

Second-Order Research

Determine the effect of genotype on spawning-habitat selection and identify homing mechanisms.

FISH HEALTH

Contaminants such as PCBs, DDT, DDE, dioxin, and toxaphene have long been suspected of affecting reproduction of lake trout and other salmonines in the Great Lakes (Berlin et al. 1981; Mac et al. 1981, 1985; Willford et al. 1981). Willford (1984) expressed the generally accepted view during the early 1980s that contaminants impeded lake trout rehabilitation in at least some areas of the Great Lakes. By the early 1980s, researchers had focused on lake trout early-life stages rather than on adults. Although these researchers recognized a need to account for the effects of multiple contaminants and to establish threshold levels, these tasks remained for the future.

More recently, Walker and Peterson (1991) and Smith et al. (1994) applied the concept of toxic equivalents based on toxicity relative to 2,3,7,8-substituted polychlorinated dioxins (TCDDs) for the major contaminants and their congeners. Walker et al. (1994) defined threshold levels for lake trout eggs and fry. However, a consensus on whether ambient levels of contaminants in the past exceeded threshold levels has not emerged. Cook et al. (1994) concluded that dioxin levels in Lake Ontario lake trout from the 1940s to the late 1970s probably resulted in 100% sac fry mortality, but a full exposition of his methods has not been published. Mac et al. (1993) reported a weak relationship between blue sac mortality, an indicator of contaminant effects, and concentrations of PCBs. However, Fitzsimons (1995a) thought that the concentrations of PCBs in Mac et al. (1993) were too low to induce blue sac mortality. Fitzsimons reviewed laboratory and field studies and concluded that concentrations of the major contaminants like DDT, PCBs, PCDDs, and PCDFs in lake trout eggs have been too low to result in significant blue sac and swim-up mortality in contemporary populations.

The perceived diminishment in recent years of the threat of contaminants to lake trout has been accompanied, unfortunately, by three new lake trout health concerns:

- Epizootic epitheliotropic disease (EED)
- Bacterial kidney disease (BKD)
- Early mortality syndrome (EMS)

The viral pathogen associated with EED caused extensive mortalities of yearling and younger lake trout in state and federal hatcheries during the 1980s (McAllister and Herman 1989). A strategy of complete destruction of hatchery brood stocks and chlorine disinfection was apparently successful because no subsequent outbreaks have been reported.

In the Great Lakes, BKD is classified as a restricted disease (Hnath 1993). Detection in a hatchery prevents transfers of positive fish to hatcheries negative for the pathogen. Although lake trout show resistance to the causative pathogen (Starliper et al. 1997), BKD-induced epizootics among chinook salmon *(O. tshawytscha)* in Lake Michigan (Holey et al. 1998) were associated with an unexpectedly high proportion of positives among tested lake trout (Jory Jonas, Charlevoix Fisheries Station, 96 Grant St., Charlevoix, MI 49720, personal communication). No BKD-symptomatic lake trout have been reported in the Great Lakes, but field testing has been limited.

EMS describes an otherwise unexplained mortality of the swim-up fry of lake trout and other Great Lakes salmonines. The characteristics of EMS are loss of equilibrium, aberrant swimming, lethargy, and eventually death. Fitzsimons (1995a) was the first to link EMS with a deficiency of thiamine in lake trout. This deficiency apparently results not from a scarcity of thiamine in lake trout diets in Lake Ontario and Lake Michigan (Fitzsimons and Brown 1998), where EMS has been most prevalent, but from a diet of alewives 'that contain high levels of the thiamine-degrading enzyme, thiaminase (Honeyfield et al. 1998; Ji and Adelman 1998). The incidence of EMS in lake trout averaged 27% during 1988-97 in Lake Ontario and 31% during 1975-89 in Lake Michigan (Fitzsimons et al. 1999). Questions remain whether thiamine deficiency masks the effect of some other factor(s) and whether EMS interacts with contaminants (Brown et al. 1998). Variations in the prevalence of EMS in lake trout also remain to be explained as do the chronic effects of EMS. Of the fish health issues addressed, EMS clearly poses the best-documented threat to lake trout rehabilitation, especially in Lakes Michigan and Ontario. One goal for the rehabilitation program should be to virtually eliminate thiamine deficiency in lake trout.

First-Order Research

Develop a predictive model for thiamine/thiaminase transfer between forage fishes and lake trout.

Second-Order Research

1. Determine interactions between contaminants and diseases of lake trout.

2. Determine chronic effects of EMS.

3. Determine modes by which lake trout become infected with BKD after stocking.

SPAWNING HABITAT

The consensus of fishery biologists in the early 1980s - that most of the Great Lakes have sufficient spawning and nursery habitat for lake trout restoration-has not changed. The major habitat problem still appears to be the use of inappropriate spawning habitat by hatchery lake trout (Dorr et al. 1981; Marsden et al. 1995b, Dawson et al. 1997). Historic spawning reefs in the upper lakes have been identified from fisherman interviews (Smith 1968a; Coberly and Horrall 1980; Goodyear et al. 1982), but these accounts may exaggerate availability (Fitzsimons 1995b). In Lakes Michigan and Huron, much of the historic spawning habitat (as determined from actual catch records) is located in northern waters (Dawson et al. 1997; Eshenroder et al. 1995c) and is underutilized by hatchery-reared lake trout. It is either distant from the shore habitats preferred by the strains of lake trout currently being stocked or is inshore but not stocked because of excessive fishing mortality or inadequate hatchery capacity (Eshenroder et al. 1995c; Holey et al. 1995). Together, these factors reflect a mismatch in many areas of the two lakes between available spawners and spawning habitat.

Wide-scale physical and chemical degradation of historic spawning areas, even in Lakes Erie and Ontario and the southern parts of Lakes Michigan and Huron, is not evident. Some habitat was excavated from Lake Ontario (Sly 1991). Studies during the 1980s indicated that successful reproduction could or did occur in Lakes Ontario and Huron (Marsden 1988; Manny et al. 1995). Sly (1988) and Casselman (1995) reported that oxygen levels remained near saturation on lake trout spawning reefs in Lake Ontario despite extensive organic sedimentation. Elrod et al. (1995) suggested that organic sedimentation in Lake Ontario would be even less of a problem in the future because of phosphorus reduction programs. Zebra mussel encrustation of lake trout spawning reefs may affect lake trout egg deposition and incubation by reducing interstitial depth.

Although most of the historic lake trout spawning reefs are not believed to have been substantially degraded, an inability to clearly separate unsuitable from suitable spawning habitat prevents a field quantification of lake trout reproduction. Numerous studies have described lake trout spawning substrate, but even substrate size classification has not been standard among these studies (Marsden et al. 1995a). Since the early 1980s research has indicated that the relationship between lake fetch, water depth, and interstitial depth is critical for understanding lake trout reproductive habitat in the Great Lakes (Sly and Schneider 1984; Fitzsimons 1994b, 1995b; Eshenroder et al. 1995a; Manny et al. 1995). These three factors define a spawning-habitat envelope that needs to be better described to facilitate identification of reproductive bottlenecks. Without a working definition of spawning habitat:

- Quantification of lake trout reproductive dynamics is elusive

- Determination of overuse or underuse of spawning habitat is problematical

- Selection of the best locations for egg/fry stocking is subjective

We suggest first a synthesis of published and unpublished data followed by field studies to till in the gaps. In the field studies, artificial reefs can provide better control of variables-for example, substrate particle size and interstitial depth. Technologies are now available to remotely classify and quantify habitat (Edsall et al. 1997), but even better methods are needed (Marsden et al. 1995a).

First-Order Research

Determine how fetch, water depth, and interstitial depth interact to limit survival of lake trout embryos.

Second-Order Research

Develop more-efficient methods for assessing lake trout spawning habitat.

BIOTIC INTERACTIONS

During the early 1980s data were beginning to suggest that species other than the sea lamprey could pose a threat to lake trout rehabilitation. Hatch (1984) was aware that populations of rainbow smelt *(Osmerus mordax)* in Lake Superior and alewives in Lake

Michigan were declining and that both species were extensively consumed by lake trout and introduced salmonines. He suspected that competition for food between adult lake trout and adult introduced salmonines could result in reduced population fecundity for lake trout.

The potential for detrimental biotic interactions took on a new dimension when Krueger et al. (1995b) reported that alewives readily consumed emergent lake trout fry. Savino and Henry (1991) had previously suggested that overly abundant native fishes had the potential to become major predators on lake trout early-life stages. More introductions of littoral fishes (for example, round goby and ruffe) (Jude et al. 1992; Pratt et al. 1992) will. likely increase predation on lake trout early-life stages.

Are the newer concerns regarding predation or the older concerns regarding competition among lake trout and other species still justified? Jones et al. (1995) and Savino et al. (1999) showed with models that egg and fry predators could nearly eliminate lake trout early-life stages. Confirmation of these models with field studies is lacking. More research has been done on the competition issue. Eby et al. (1995) reported that lake trout consumption of prey fishes in Lakes Superior, Michigan, and Ontario did not decline with reductions in prey density. This finding suggests that lake trout were little affected by competition with other salmonines. Negus (1995), however, thought that reduced prey-fish availability in Minnesota waters of Lake Superior could lead to slower growth of lake trout. Biotic interactions involving adult lake trout are well studied compared to interactions involving early-life stages (Stewart and Ibarra 1991; Jones et al. 1993; Rand et al. 1994; Mason et al. 1995). The lack of resolution on competition after so much research tends to downplay its significance as a major factor responsible for recruitment failure of lake trout.

Three observations indicate a potential for a recruitment bottleneck early in the lake trout life cycle:

- The negative relationship between species richness and successful introductions of lake trout in inland lakes (Evans and Olver 1995)

- The drastic alteration of the original Great Lakes fish community

- The vulnerability of lake trout eggs and/or fry to a variety of predators: alewife, round goby (Savino and Henry 1991; Chotkowski and Marsden 1999), sculpins *(Cottus* spp.) (Biga et al. 1998), and crayfish *(Orconectes* spp.) (Horns and Magnuson 1981)

Competition between adult lake trout and other adult salmonines may ultimately limit lake trout carrying capacity (Negus 1995; Elrod et al. 1996a). However, this issue will not be a priority for research until lake trout are self-sustaining outside of Lake Superior. In the Population Dynamics section, we discussed research needs associated with improved estimation of sea lamprey-induced mortality on lake trout. The focus here is on research that minimizes the interaction between the two species. Especially encouraging has been the finding that at least one strain of lake trout shows resistance to sea lamprey predation (Eshenroder et al. 1995a; Schneider et al. 1996). Increased resistance at the population and community levels is clearly the most-benign form of pest management.

First-Order Research

Assess the effects of altered fish communities on survival of lake trout eggs and fry. Opportunities should be sought to piggyback this research onto research about reproductive dynamics.

Second-Order Research

Assess food competition between lake trout and other salmonines, and develop lake trout brood stocks that are more resistant to sea lamprey predation.

OVERVIEW

Even though the biology of lake trout in the Great Lakes is much better understood now than when CLAR was held in 1983, the causes of widespread reproductive failures remain an enigma. As we have shown, possible solutions -to the enigma are numerous, but here we need to identify those most plausible. We believe that the most plausible solutions will link disciplines and offer more than an incremental addition to existing knowledge. One danger here is a profusion of isolated ideas. Recognizing this problem, we employ Loftus and Regier's (1972) analysis-of-variance organizing concept used to organize the Salmonid Communities in Oligotrophic Lakes Symposium. The lake case histories (observations) are arrayed against system stresses (treatments). Here we use lake trout phenotypes as observations and our hypothesized impediments to rehabilitation as treatments. This approach recognizes Krueger and Ihssen's (1995) idea that lake trout rehabilitation will not be accomplished until phenotypic diversity is restored. It also recognizes that the traits shown to be heritable in lake trout have implications for reproductive performance. Our phenotype-by-impediment construct assumes that the severity of an impediment will vary with lake trout phenotype. Both shallow-water and deepwater phenotypes need to be deployed concurrently to maximize life-history contrasts and the potential for positive results. If phenotypes are tested sequentially, the interaction between phenotype and impediment can be obscured by system changes (temporal bias). Although multiple phenotypes add experimental complexity, we believe that reproductive success, the ultimate dependent variable, will still be very discernible.

Five general problem areas emerge from our recommendations for first-order research, but only early-life bottlenecks and low genetic diversity stand out as being multidisciplinary (identified more than once) and as having potential to yield the largest insights. The other three problem areas-imprecise homing, thiamine deficiency, and classification of spawning habitat-are important, but their resolution is not likely to fully explain the widespread reproductive failures. For example, considerable progress in rehabilitation has been achieved in large areas of Lake Superior without resolution of homing mechanisms or spawning-habitat classification, and thiamine deficiency does not account for reproductive failure in Lake Huron. Lake Superior, moreover, differs from the other lakes in having a less-enriched fauna (with less potential to bottleneck reproduction) and a more-diverse lake trout gene pool.

Early-life bottlenecks can be divided into two subproblems with possible genetic interactions.

- Excessive mortality occurring between egg deposition and the late-alevin life stage

- Insufficient egg deposition on appropriate spawning habitats

The second impediment may aggravate the first. Higher egg densities on spawning reefs may overcome losses to predators (Savino et al. 1999). Both impediments affect shallow-water lake trout, but their effects on deepwater lake trout may be less severe.

- If excessive mortality is caused by a predator, the predator may be less abundant where deepwater lake trout spawn.

- Stocked deepwater lake trout may not be as prone as shallow-water lake trout to aggregate for spawning on unstable substrates in high-energy zones along beaches (Eshenroder et al. 1995a).

With diversity better established, variations in reproductive. success among life-history types can lead to an improved understanding of impediments and of appropriate management responses.

We recommend deployment of early-life stages as a way to imprint lake trout naturally, but deployment also offers possibilities for more-controlled research on:

- The dynamics of reproduction

- Interactions between lake trout eggs and fry and their predators/competitors

- Sublethal effects of EMS

- Suitability of spawning habitat

Stocking early-life stages on specially designed artificial reefs can provide even more control for these important studies.

Rehabilitation is inhibited by more than one impediment and solutions will at best be partial. The challenge is enormous. Ultimately, the lake trout themselves need to become part of the solution by occupying more of the available habitat, proliferating at least gradually, and structuring these systems more to their advantage (Eshenroder et al. 1995b). Our recommended research may not clearly reveal the causes of the widespread reproductive failures. Because of this possibility, opportunities for lake trout to successfully reproduce should be maximized by maintaining large, genetically diverse populations that occupy more of each lake. For example, Ward et al. (2000) reported that the area of Lake Michigan inhabited by juvenile lake trout declined from about 55% in the early 1930s to only about 20% in the 1970s. Our strategy of employing deepwater genotypes is one solution to this problem of range contraction. Large, diverse populations also increase the prospects that lake trout can respond to fortuitous environmental changes in a way that furthers our understanding.

Our purpose is to identify those priorities that appear to have the most potential to explain why recruitment of wild lake trout has been unsatisfactory except in Lake Superior. We gave special attention to only two impediments and caution about diminishing the importance of other priorities identified earlier. Our choices are opinions based on fragmentary insights. At the minimum, we want to stimulate critical thinking and introspection. Long-standing strategies aimed at reestablishing self-sustaining lake trout populations in the Great Lakes need frequent reassessment. Our examination sought early input from virtually all lake trout researchers and provided them with an opportunity to critique our output. We are much indebted for their contribution, and hope that this collaboration channeled our conclusions towards what time will reveal as the right choices.

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