

Possible Impediments to Lake Trout Restoration In Lake Michigan

Prepared by

**The Lake Michigan Lake Trout Task Group
For the Lake Michigan Committee**

Great Lakes Fishery Commission

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BACKGROUND

In 1999, the Lake Michigan Committee assigned the Lake Michigan Technical Committee the task of reviewing lake trout rehabilitation efforts in Lake Michigan, as per the objectives in the 1985 lake trout restoration plan (hereafter “the 1985 Plan”)(LMLTTC 1985). This assignment was viewed as preparatory to the actual revision of the restoration plan. A Lake Trout Task Group was formed to complete this assignment. Part of that charge included identification and prioritization of possible impediments to achieving sustainable natural reproduction in Lake Michigan. The Lake Trout Task Group identified and prioritized 14 potential impediments that are thought to inhibit sustainable reproduction of lake trout in Lake Michigan.

The 14 impediments are inter-related and are grouped into three categories. The first category deals with the issue of the size of the population of lake trout lake-wide in Lake Michigan and contains four impediments: number of fish stocked, sea lamprey mortality, sport and commercial fishing, and the abundances of spawners on historically important spawning reefs.

The second category of impediments focuses on how and where lake trout aggregate for spawning. There are five impediments in this category as follows: spawning site selection, the effects of rearing practices on habitat use and site selection, imprinting, the implications of stocking yearling lake trout in nearshore high-energy zones, and the genetic diversity of stocked lake trout.

The third category of impediments relate to survival of lake trout early-life stages, and the recognition that disproportionate mortality between egg deposition and the first year of life may be a major reason for the lack of lake trout recruitment. There are five impediments: habitat degradation, contaminants, direct predation on eggs and fry by native and non-native predators, mortality from early mortality syndrome (EMS, a dietary thiamine deficiency that leads to poor survival of newly hatched lake trout), and community dominance. Community dominance may be important where top predators (i.e. lake trout) control through predation, the abundance of smaller prey fishes (i.e. sculpins, alewife), which have the potential to act as competitors and predators on juveniles of the top predator.

The report format for each of the 14 impediments provides a *Problem Statement* that hypothesizes the potential obstruction. This is followed by a discussion of the appropriate literature and of the results of recent field/assessment work. This discussion forms the basis for the final priority ranking of importance. Following the discussion, each impediment is assessed in relation to the recommendations within the 1985 Plan and to their actual implementation. This exercise measures how well the past rehabilitation effort dealt with the impediments and met the plan’s objectives. Rankings for *Biological* and *Management* constraints (Low, Medium, High) were developed by consensus of the task group. *Biological rankings* deal with the perceived importance of the impediment in inhibiting natural reproduction and sustainable recruitment whereas *Management rankings* address the prospects of remediation.

MAJOR FINDINGS

There is no conclusive evidence that any one impediment alone is preventing sustainable recruitment, but it is rather a combination of several impediments acting together that are responsible for the lack of success. The following section highlights the major findings of the impediment-analysis exercise. Each major impediment category contains up to three impediments, which were considered the most likely obstructions to lake trout restoration in Lake Michigan within that category. This synthesis of current knowledge and interpretation will be the basis for a new lake trout rehabilitation plan for Lake Michigan that will recognize technical, informational, and biological limitations but take full advantage of lessons learned from past experiences on Lake Michigan and the other Great Lakes. The following list captures the major problems with lake trout restoration and provides the framework for remediation. The new plan and its implementation should result in a higher probability of achieving measurable levels of wild recruitment in the future.

Lake-wide population too low

1. The total number of lake trout stocked is too low compared to historical recruitment and inadequate to populate available habitat in numbers to overcome behavioral and reproductive inefficiencies of the surviving adults. Annual stocking should be increased as much as possible beyond the current level of 2.4 million lake trout per year.
2. Losses to sea lamprey predation and fishing need to be minimized in order to maximize recruitment to the parental stock and increase potential egg deposition. Numbers of parasitic sea lamprey need to be reduced from current levels especially in northern Lake Michigan. Management agencies should set harvest limits commensurate with restoration goals.
3. Stocking is too low in refuge and offshore areas where the best spawning habitat and potentially the lowest fishing mortality occur. Stocking needs to be concentrated in areas with the best spawning habitat and protected from exploitation.

Spawning aggregations too diffuse and in inappropriate locations

1. Inshore, high-energy zones have and still receive stocked lake trout and result in poor survival of eggs and fry from returning adults. Stocking should be focused on offshore sites. Inshore sites should only be stocked if they were historically important, have appropriate spawning habitat, and can be protected from exploitation.
2. Genetic diversity of stocked fish is limited compared to what was present historically and may limit the potential for colonization of a variety of inshore and offshore habitats, and possibly the reestablishment of historical predator/prey relations. The stocking program needs to increase the genetic diversity within and among lake trout forms in order to enhance the potential for survival from sea lamprey predation and other mortality factors, and increase the potential for colonization of deepwater and offshore habitats.
3. The stocking program has relied almost solely on yearling fish for restoration and did not fully investigate the potential of other life-history stages. Stocking of eggs and fry should be increased to develop populations with a higher probability of homing to spawning locations and focused in areas where lake trout densities are high enough to offset losses of eggs and fry to predation.

Poor survival of early-life stages

1. EMS and predation on lake trout eggs and fry reduce the potential for recruitment, hence stocking should be concentrated where access to spawning areas is maximized and where high densities of returning adults will result in high egg deposition that can overcome survival bottlenecks. Stocking densities should emulate historical recruitment.
2. Consumption of alewives by adult lake trout reduces fry survival through EMS hence increased predation and/or fishing pressure on alewives should be considered for control in selected locations.
3. Actions articulated above to increase over all lake trout numbers will increase the presence of lake trout in the fish community and likely increase predation on certain native and possibly non-native egg and fry predators thereby decreasing losses to recruitment.

IMPEDIMENT MATRIX

Possible impediments to lake trout restoration in Lake Michigan. Priority rankings for perceived biological importance and possible remediation through management action. Developed by the Lake Trout Task Group, March 2003.

Impediment	Relation to 1985 Plan Recommendations	Relation to Plan Implementation	Result	Priority Biological	Priority Management
Lake-wide populations too low					
Number of fish stocked	6-9 million fish.	2-3.5 million fish.	Not achieved; stock sizes too low in some areas.	High	High
High lamprey predation	Not recognized as impediment.	Monitor wounding	Lamprey numbers doubled	Medium	High
Density of spawners too low	Establish refuge and rehabilitation zones.	Refuges and zones created but stocking goals not met.	Spawners abundant at a few sites, low elsewhere. Age composition young.	High	High
High exploitation	Control F, A \leq 40%.	F not controlled especially in north.	Mixed results	Medium	High
Spawning aggregations too diffuse and in inappropriate locations					
Spawning site selection	Promote trials with eggs and fry.	Astro-turf and fry stocking experiments limited	No success/ inadequate knowledge	High	Medium
Rearing practices	Promote trials with eggs and fry.	Astro-turf and fry stocking experiments limited.	No success/ inadequate knowledge.	Medium-low	High
Stocking in high-energy zones	Some nearshore stocking with offshore refuges receiving highest priority.	Many areas with good habitat not stocked, 1/3 of fish stocked in unimportant areas.	Too many fish stocked in areas with poor or little spawning habitat.	High	High
Poor imprinting and olfactory cues	Stock mostly yearlings; try eggs and fry.	Yearlings stocked; astro-turf and fry trails limited.	Stocked areas have more fish than unstocked areas.	High	Medium-low
Low genetic diversity	Specific strains slated for specific habitats; adult transfers, and gamete collections.	Inconsistent use of strains; no adult transfers and no gamete collections.	Genetic strategy inconsistent and limited.	High	High
Poor survival of early life-life stages					
Habitat degradation	Stock on good habitat; inventory habitat.	Gross surficial surveys conducted; finite spawning sites unidentified.	Mixed results with little specific knowledge of requirements.	Low	Low
Predation on eggs & fry	Not recognized as impediment.	N/A	Likely contributing; new information pending	High	High
Contaminants	Measurement of body burdens and survival of eggs and fry.	Measurements implemented.	Unlikely impediment	Low	Low
EMS	Not recognized as impediment.	N/A	Likely contributing	Medium	Medium
Community dominance	Not recognized as impediment.	Stocking rates below recommended.	Lake trout densities low. Little evidence for control of predators.	High	High

IMPEDIMENT 1 – NUMBERS OF LAKE TROUT STOCKED

- I. **Problem Statement:** The numbers of lake trout stocked into Lake Michigan are insufficient to achieve lake trout rehabilitation.
- II. **Literature/Assessments**
 - A. Stocking goals for the upper Great Lakes have been based primarily on studies conducted in Lake Superior.
 - B. In Lake Superior, the optimal stocking rate was determined to be 1-1.5 fish per acre of lake trout habitat (LSLTTC 1986). In Lake Michigan lake trout habitat has been defined as the area of water 0-40 fathoms deep (LMLTTC 1985).
 - C. Based on available habitat, numbers of lake trout required to achieve a stocking rate of 1 fish per acre (although higher in the refuges) was recommended in 1985 at 5.844 million yearling fish excluding Green Bay, and at 7.018 million fish including Green Bay (LMLTTC 1985).
 - D. The maximum production of lake trout from the federal hatcheries since 1985 has been 5.8 million, far short of the estimated numbers required for the upper Great Lakes. The Council of Lake Committees then allocated 50% of the available production to Lake Michigan and hence has received an average of 2.4 million fish or 50% of the recommended number of fish since 1974.
 - E. In 1995, the size of yearlings released into the upper Great Lakes increased from 20 fish/lb to 10-12 fish/ lb, which resulted in fewer (but larger) fish being stocked into Lake Michigan. The larger yearlings were expected to survive better than the smaller fish and compensate for the fewer numbers stocked. Results to date show that apparent survival of the larger yearlings did not increase as expected in Lake Michigan (McKee et al. 2002), but may have increased in Lake Huron (McClain et al. 2002). If survival in Lake Michigan did not improve then the numbers of fish stocked has declined further from the 1985 recommendation.
 - F. Recruitment required to support the historical fishery was estimated to be 10 million age-1 fish (Holey et. al 1995).
 - G. Lakes Superior and Ontario are the only Great Lakes that have realized consistent wild recruitment from hatchery-reared lake trout, although remnant wild fish also likely played a role in Lake Superior (Richards et al. 2004). These are the only lakes where stocking approximated the recommended numbers in their respective rehabilitation plans. A caveat here is that survival of hatchery-reared fish eventually declined in both lakes Superior and Ontario as densities increased over time, and suggests onset of density-dependent survival. In Lake Superior, densities of hatchery-reared fish were many times that of historical densities (Hansen et el.1995b), and suggest that many more hatchery-reared fish may be required to elicit wild recruitment than previously thought.

H. Recommended stocking levels have never been met in Lakes Huron and Michigan, and rehabilitation remains elusive.

I. Relation of 1985 recommendations to the impediment:

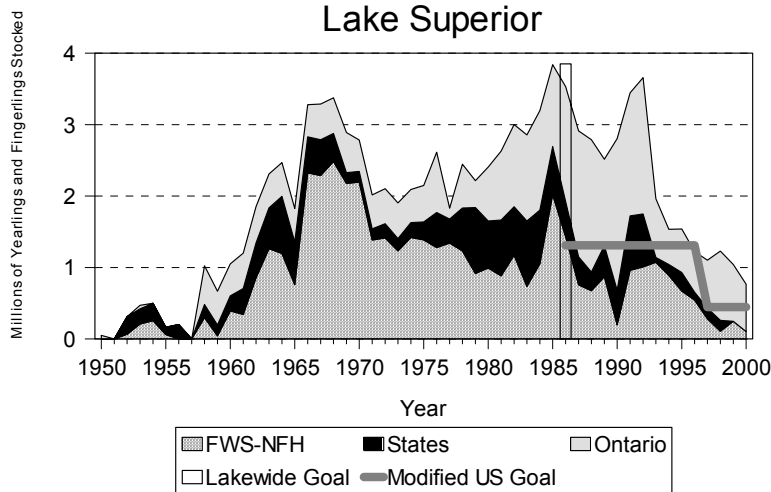
- A. The 1985 Plan recommended a stocking rate of 1-1.5 per acre, which would require 5.844 - 8.76 million lake trout to be released annually in Lake Michigan, excluding the waters of Green Bay.
- B. Areas of the lake were deferred because of excessive fishing mortality.

III. Relation of 1985 Plan Implementation and the Impediment:

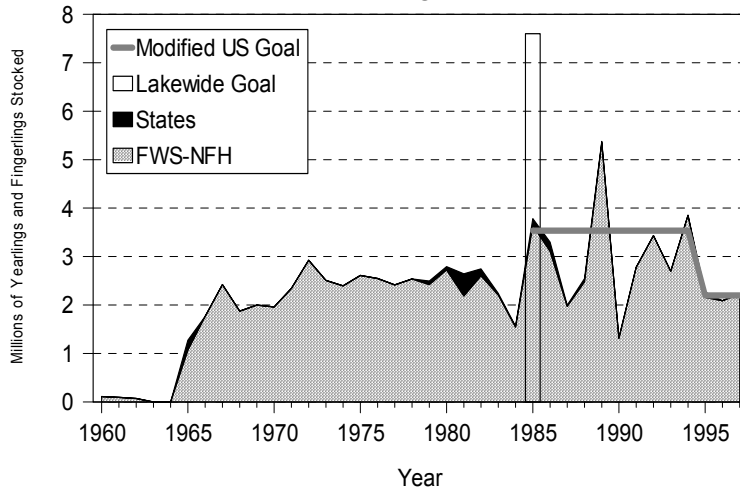
- A. Annual stocking rates were adjusted downward from 5.844 million to 3.5 million (not including Green Bay waters) to reflect the availability of lake trout from federal hatcheries.
- B. The 1995 increase in the size of yearlings stocked resulted in an additional reduction from 3.5 million to 2.1 million fish annually. If the expected increase in survival of the larger yearlings did not compensate for the reduced number of fish stocked, then less than 36% of the recommended the numbers have been stocked since 1995.

III. Conclusions - The numbers of fish currently being stocked are inadequate and likely contribute to inadequate spawner biomass in Lake Michigan. Stocking is considerably lower than recommended in the 1985 Plan and 5-fold less than the estimated recruitment of yearling lake trout before the collapse of historical populations. Increased overall stocking rates or higher density stocking in selected areas with good habitat should be pursued.

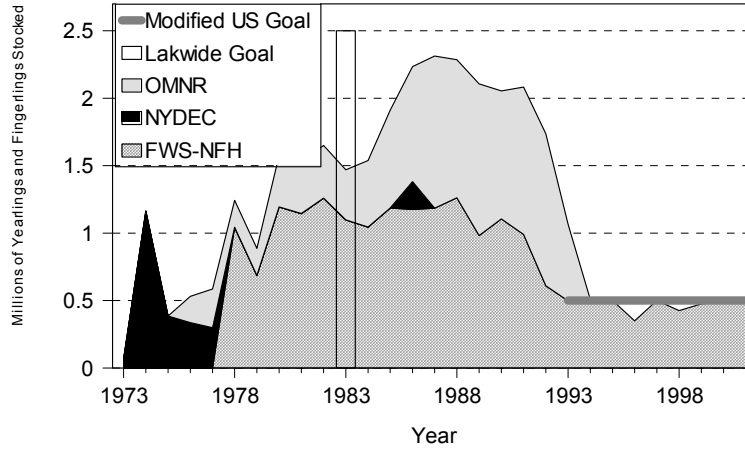
VI. Priorities- Biological : High, Management : High
Lake Superior



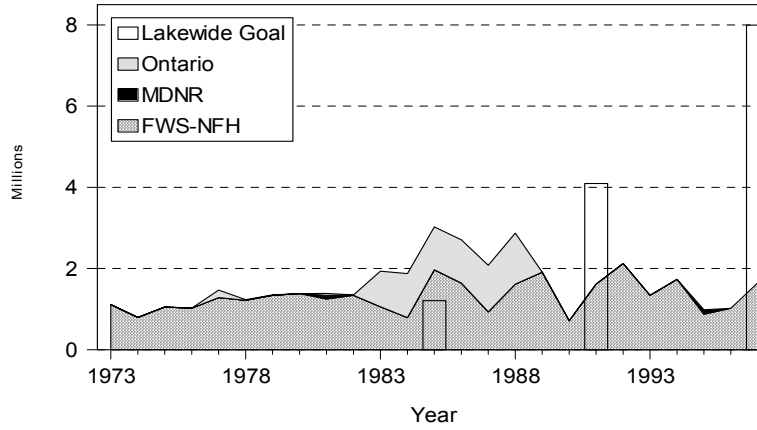
Lake Michigan



Lake Ontario



Lake Huron



IMPEDIMENT 2 – SEA LAMPREY MORTALITY

- I. **Problem Statement:** Sea lamprey-induced mortality is inhibiting lake trout rehabilitation in Lake Michigan.
- II. **Literature/Assessments**
 - A. Sea lamprey predation has been implicated in the demise of lake trout in all the Great Lakes including Lake Michigan (Hile et al. 1951, Smith and Tibbles 1980, Coble 1990).
 - B. Sea lamprey attacks on Great Lakes fishes result in some mortality (Bergstedt and Schneider 1986, Swink and Hanson 1986, Schneider et al. 1996), which depends upon the host, the host size, the size of the sea lamprey, and water temperature (Farmer et al. 1977, Swink and Hanson 1986, Kitchell 1990, Swink 1993, Swink 2003)
 - C. Sea lamprey prefer large lake trout (Farmer and Beamish 1973, Swink and Hanson 1986), which fortunately survive attacks better than smaller lake trout (Swink 1990, Kitchell 1990).
 - D. The weight of individual sea lamprey in Lake Michigan has increased along with the increase in salmonine predators. Sea lampreys weigh almost twofold more than in the 1960s (Kitchell 1990).
 - E. The faster growth of sea lampreys means the time period for mortality of small host (< 1kg) fishes has increased from one to six months in the last three decades (Kitchell 1990).
 - F. Kitchell (1990) concluded that sea lamprey-induced mortality of small host fishes <1 kg may have increased six fold in Lake Michigan during the 1970s and 1980s, and also that the effects of sea lampreys on trout and salmon have probably increased continuously and nonlinearly in Lake Michigan since the late 1960s.
 - G. Sea lamprey marking of lake trout in Lake Michigan has increased almost annually since about 1989 in response to a substantial increase in the number of sea lampreys (Fig. 1). Sea lamprey abundance has increased from an average of 50,000 spawners during 1979-1982 to an average of 90,000 spawners during 1997-2000 (Fig. 1).
 - H. Statistical relationships have now been developed that allow estimation of sea lamprey-induced mortality of lake trout based on marking data and the probability of surviving an sea lamprey attack (Sitar et al. 1999).
 - I. The number of lake trout deaths in Lake Michigan due to sea lamprey predation has been increasing in parallel with the number of sea lamprey in the lake (Fig. 2) and averaged about 60,000, or about 0.7 lake trout deaths per sea lamprey, during 1995-2000 just in Michigan waters.
 - J. Although sea lamprey-induced mortality accounts for only 5% of the total mortality of lake trout in Lake Michigan, the level of sea lamprey mortality on age 3-4 lake trout has been increasing since 1997 (Fig. 2) and will reduce adult stock size over the next few years.

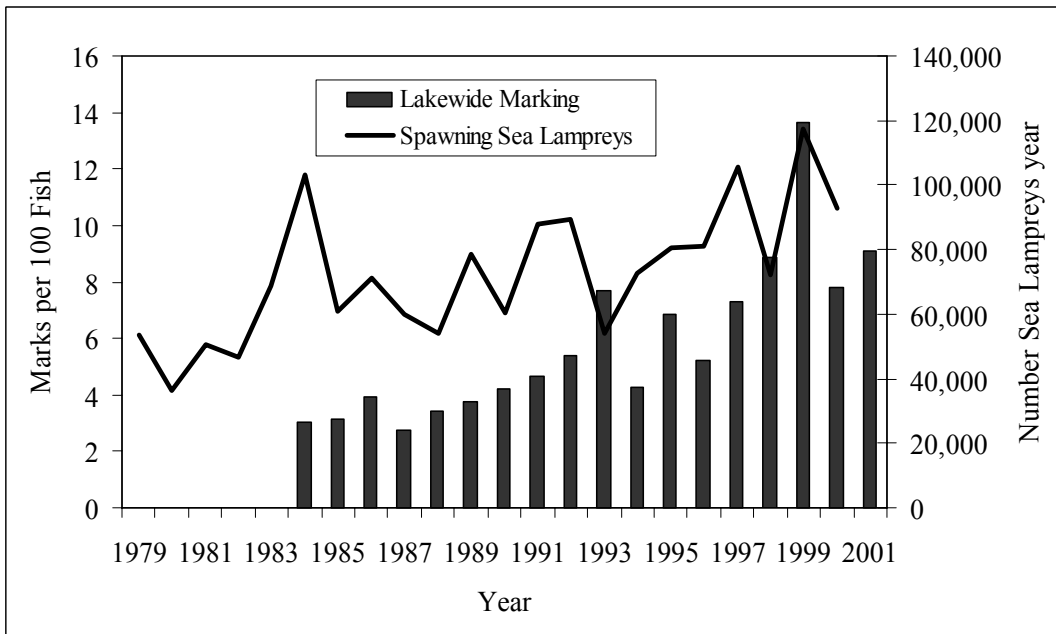


Fig. 1. Estimated number of spawning sea lampreys (line) in Lake Michigan based on their feeding year and average annual lakewide sea lamprey marking rate on lake trout (bar) during 1979-2000.

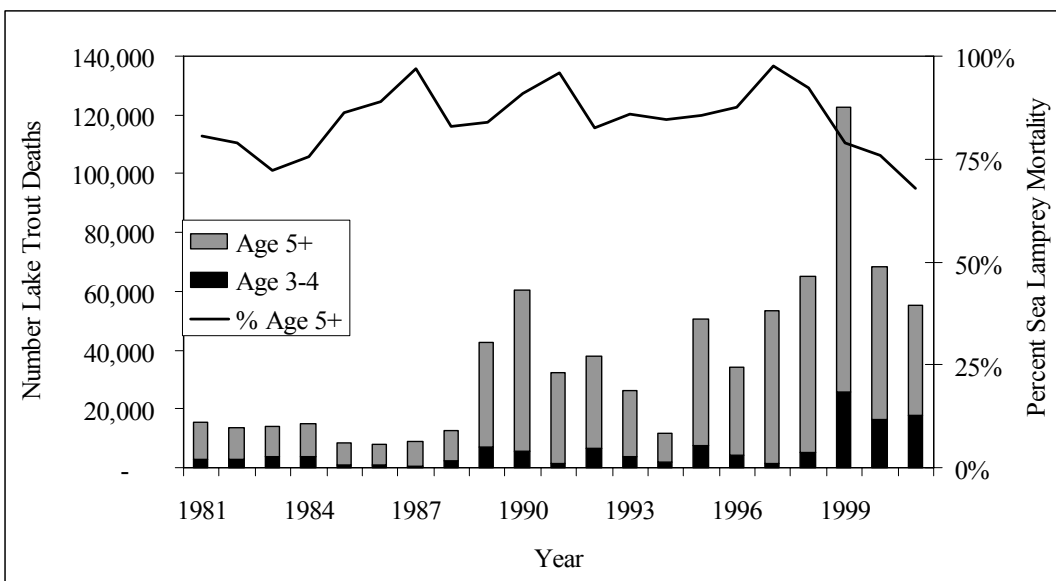


Fig. 2. Estimated number of sea lamprey-induced deaths on age 3-4 and age 5+ lake trout in Michigan waters of Lake Michigan and proportion of total deaths on age 5+ lake trout (line) during 1981-2001.

III. Relation of the 1985 Plan Recommendations to this Impediment.

- A. Sea lamprey were not specifically recognized as an impediment to lake trout rehabilitation, but the plan did recognize the need for continual monitoring of sea lamprey wounding rates on lake trout.
- B. The 1985 Plan did recognize the need for good communication between the management agencies and the Sea Lamprey Control Agents in order to suppress localized infestations of sea lamprey.

IV. Relation of the 1985 Plan implementation to this impediment.

- A. The Technical Committee charged itself to coordinate collection of marking statistics and evaluation of those statistics.
- B. The Technical Committee regularly reports marking rates to the Lake Michigan Committee, but has not specifically focused much time on sea lamprey marking statistics.

V. Conclusions - Sea lamprey abundance has increased over the last 20 years and is reducing lake trout survival. Sea lamprey populations must be reduced in order to reduce mortality. Increased chemical control and barrier construction should be implemented to achieve population reductions. Stock assessment models should be developed for Wisconsin, Illinois, and Indiana waters of Lake Michigan that will allow estimation of lake trout deaths due to sea lamprey predation (as well as to other sources of mortality). Research is needed to understand how sea lamprey production is affected by the lake sturgeon treatment protocol, by habitat restoration in tributaries, by increases in water temperatures, by changes in lampricide treatment concentrations, and by selection of streams for treatment.

VI. Priority - Biological: Medium, Management: High

IMPEDIMENT 3 - LOW SPAWNER ABUNDANCE ON HISTORICALLY IMPORTANT SPAWNING REEFS

- I. **Problem Statement:** The abundance of mature lake trout on documented historically important spawning reefs is too low for successful reproduction.

- II. **Literature/Assessments**
 - A. Most historically important spawning reefs are located in the Midlake Refuge and in northern Lake Michigan (Dawson et al. 1997).
 - B. Large populations of mature spawners are developing at two Midlake reefs, Sheboygan and East Reefs, with average CPEs of 123 fish/1000 feet and 10 year classes with a maximum age of 18 years. The majority of fish captured at these sites were stocked in the Midlake Refuge. During the 1980s, Gull Island Shoal in Lake Superior, an offshore spawning reef with a rehabilitated population (Schram et al. 1995), had spawner CPE's similar to those at the two Midlake Reefs in Lake Michigan (Bronte et al. 2002; Eshenroder and Amatangelo 2002).
 - C. Important reefs in or near the Northern Refuge have not been stocked continuously and many have not been stocked at all (Dawson et al. 1997). Furthermore, some Northern Refuge reefs that were stocked were not historically important (Dawson et al. 1997).
 - D. Spawner abundances that have resulted in natural reproduction have ranged from 17 to 135 fish/1000 feet of gill net (Selgeby et al. 1995).
 - E. In the Great Lakes, detectable but not necessarily sustainable recruitment was associated with higher densities of stocked adults on spawning reefs but in Lake Michigan even large populations of mature stocked fish typically fail to produce detectable year classes.

- III. **Relation of 1985 Plan Recommendations to Impediment**
 - A. Establish two major lake trout refuges - Northern and Midlake Refuges that have highest priority for stocking; stock with mix of selected strains.
 - B. Establish deferred and rehabilitation (40% TAM) zones.
 - C. Delay stocking in Deferred Zone.
 - D. Other small refuges are endorsed in principle.
 - E. Assessment of refuges.

- V. **Relation of 1985 Plan Implementation and the Impediment**
 - A. Two major refuges were established; reefs in each were chosen for stocking; stocking goals were established; and stocking occurred annually and included multiple strains. Stocking goals for the Northern Refuge were usually reached. However, Midlake Refuge stocking goals fell short in a number of years. Stocking goals in both refuges were modified during the mid 90s to reflect the stocking of larger yearlings.
 - B. Midlake Refuge area was increased from original size.
 - C. Majority of fish stocked for strain experiment are just starting to mature.
 - D. Annual fall assessments have been conducted in the major refuges but not at all stocked reefs in each refuge.

- E. Not all reefs chosen initially for stocking in Northern Refuge were historically the most productive.
 - F. Approximately 1/3 of annual total lakewide stocking occurs in the two refuges however, no stocking has occurred since 1985 in the deferred zone in the northern 1/3 of the lake where many historically important spawning reefs are located (Dawson et al. 1997).
- V. Conclusion** – Spawner abundance is insufficient in Lake Michigan, especially if the lower reproductive efficiency of hatchery fish is lower than that of wild fish. Spawner abundance and age composition in the Midlake Refuge should be sufficient for sustainable natural reproduction, even though stocking goals were not fully met. Historically productive spawning reefs in northern Lake Michigan have low total densities and few older spawners. These reefs need to be stocked with higher densities of yearlings or with massive amounts of eggs/fry. The Northern Refuge needs to be expanded to encompass more reefs and to provide increased protection for lake trout from fishing.
- V. Priority** – Biological: High, Management: High

IMPEDIMENT 4 – HIGH SPORT, COMMERCIAL HARVEST AND INCIDENTAL KILL

- I. **Problem Statement:** High sport and commercial harvest and incidental kill reduce spawner biomass to levels that cannot sustain reproduction.
- II. **Literature/Assessments**
 - A. Lake Michigan fish community objectives include the establishment of a diverse salmonine community capable of sustaining an annual harvest of 6 to 15 million pounds, of which 20-25% is lake trout. The ultimate goal is to establish self-sustaining lake trout populations (Eshenroder et al. 1995).
 - B. It is generally accepted that an annual mortality rate of 40% or less for age 1 and older fish is required to sustain lake trout populations (Healey 1978).
 - C. Natural reproduction in 6 areas in Lake Superior and 1 area in Lake Michigan was observed when capture rates of spawning lake trout averaged about 50 fish per 1000 foot of graded mesh gillnet (Selgeby et al. 1995).
 - D. Mortality may need to be significantly lower than 40% in Lake Michigan because 1) there are no remnant stocks in Lake Michigan and stocked fish are less reproductively efficient (Fitzsimons and O’Gorman 1996, O’ Gorman et al. 1998), and 2) egg and fry predator densities are significantly higher in Lake Michigan than in other systems (Fitzsimons et al. 2000).
 - E. Lake trout sport harvest has ranged from a high of 1.77 million pounds in 1998 to a low of 669,000 pounds in 2000, with the last ten-year average of 1.057 million pounds. The total lakewide harvest by all fisheries has ranged from 1.3 million pounds in 2001 to 2.8 million pounds in 1998 (Breidert et al. 2002).
 - F. Lake trout have comprised between 13 (in 2001) and 33% (in 1998) of total salmonine harvest and have averaged 15.5% since the mid-1980s (Breidert et al. 2002).
 - G. Lake trout populations with annual mortality rates in excess of 50% have been observed to decline (Healey 1978) and are likely unable to build up sufficient spawner biomass that would increase the potential for natural reproduction.
 - H. Estimates of annual mortality in eastern Lake Michigan ranged from 48 to 71%. Excessive mortality has been attributed to sport and commercial harvest (Rybicki 1983, 1991).
 - I. Annual mortality measured in spring 2000 and 2001 assessments ranged from 59.7% along the east shore down to 32.1% along the west shore, while it was 48.4% in the Northern Refuge and 33.6% in the Midlake Refuge. Annual mortality was below 40% in five of the seven management units in 2001 (McKee et al. 2002).
 - J. Regulations, including daily bag limits, seasonal closures and size limits have been implemented to reduce harvest by anglers in all jurisdictions. Restricted seasons exist in 2 of 4 jurisdictions and have resulted in decreased sport harvest since implementation in 1985. Minimum size limits have been effective in managing recreational catches of lake trout in Grand Traverse Bay and northern Lake Michigan.

- K. Targeted commercial harvest for lake trout ceased in all jurisdictions in the mid 1960s with the exception of 1836 treaty waters. Large mesh gillnets were banned in Michigan waters in 1970 and in Wisconsin waters south of Baileys Harbor in 1978. All state licensed commercial fishers were banned from using small mesh gillnets in Michigan in 1976. Gillnets were banned by commercial fisherman in Indiana in 1988. All commercial fishing was suspended in Indiana waters in 1997. Gear changes in the whitefish commercial fishery have resulted in lower incidental catch by commercial fishers (Holey et al. 1995). In 2000, a consent decree (United States vs State of Michigan 2000) between the State of Michigan and the tribes eliminated targeting for lake trout and converted a large portion of the gill net fishery to trap nets, hence reducing targeted and incidental mortality on lake trout.

III. Relation of 1985 Plan Recommendations to Impediment

- A. Hold total annual mortality of adult lake trout at or below 40% based on exploitation by several fisheries.
- B. Establish special zoning regulations and related restrictions on fishing for lake trout to control exploitation.

IV. Relation of 1985 Plan Implementation and the Impediment

- A. Due to uncontrollably high incidental catches of lake trout in whitefish fisheries in northern Lake Michigan and Green Bay, efforts to achieve a total annual mortality of lake trout at 40% or less were postponed in deferred rehabilitation zones until rehabilitation was progressing elsewhere.
- B. Establishment of two refuges to provide maximum protection of stocked fish. With the exception of the deferred zones, the waters in each state outside of the refuges were declared rehabilitation zones in which management efforts were directed at maintaining total annual mortality of adult lake trout at or below 40%.
- C. In 2001 results from Consent Decree between five tribes and the state of Michigan resulted in the elimination of deferred zones in northern Lake Michigan. Though presently high, annual mortality rates of 40-45% are to be achieved after 2006 when the agreement is fully implemented.

Conclusion – Increased targeted and incidental harvest of lake trout led to reduced spawner biomass, especially in northern Lake Michigan, and limited the potential for sustainable natural reproduction. Although efforts were made lakewide to reduce fishing mortality from all sources, a return to excessive harvest will limit rehabilitation efforts. Stock assessment models have been developed for Michigan waters to compartmentalize mortality and establish harvest levels commensurate with total mortality objectives, and these models need to be developed for other jurisdictions. Protection of lake trout should be continued in refuge areas and expanded, especially in the northern Lake Michigan where most of the historically important spawning areas are located.

VI. Priority – Biological: Medium, Management: High

IMPEDIMENT 5 – SPAWNING SITE SELECTION

- I. **Problem Statement:** Suitable cues may not be present for spawning site selection and reproduction by stocked lake trout.

- II. **Literature/Assessments**
 - A. Lake trout have been observed to spawn at a range of water depths. For example, wild lake trout in Algonquin Park, Ontario were observed to reproduce in water from 6 inches to 12 feet deep (Martin 1956). In Seneca Lake, New York, naturalized lake trout were observed to spawn in 100-200 feet of water (Royce 1951). Many offshore, deep sites, as well as shallow near shore locations have been identified as important historical spawning sites in Lake Michigan (Dawson et al. 1997).
 - B. Recent observations in Lake Michigan indicate that within spawning locations, the largest deposition of lake trout eggs by adult hatchery-reared fish occurs in shallowest water (1-3 meters in depth), even if “better” substrate or environmental quality in deeper water is nearby (J. Fitzsimons, personal communication).
 - C. Lake trout spawn in a variety of habitats including nearshore areas, rivers (Loftus 1958), and on deep offshore reefs (Eschmeyer 1955).
 - D. Lake trout have been observed to select new spawning sites if traditional habitat is not available however, little is known about reproductive success at these alternative sites (McAughey and Gunn 1995).
 - E. Stocked lake trout will return either to the offshore sites where stocked (Bronte et al. 2002a), or will stay or move to the near shore zone, bypassing suitable spawning habitat in the process.
 - F. There are adaptive reasons for lake trout to have strong homing instincts. For example, spawning lake trout could maximize reproductive success by synchronizing the return of adults to “proven” spawning grounds at a time when conditions are optimum for egg and fry development, while regulating the number of adults using an area thereby avoiding under or over utilization of habitat (Horrall 1981; Leggett 1977).
 - G. Biologists have a poor understanding of factors influencing spawning site fidelity for lake trout. Studies with both numbered and sonic tags in Lake Opeongo, Ontario suggested that lake trout do not home to their natal shoal (MacLean et al. 1981). In contrast, Lake Superior stream (Loftus 1958) and reef spawning (Swanson and Swedberg 1980) lake trout showed strong fidelity to spawning locations. In other studies, lake trout showed fidelity to larger spawning areas and sometimes were observed to use more than one location within in a spawning season (Martin 1960; MacLean et al. 1981; Peck 1986; Gunn 1995; Bronte et al. 2002b).
 - H. Biologists have a poor understanding of the movement and associations of lake trout while at large and not spawning. Investigators have suggested that it would be advantageous in general for migrating fish to form stock-specific schools. Schooling might influence navigational accuracy in returning to appropriate spawning locations (Larkin 1975).
 - I. Lake trout spawn in the fall when water temperatures are between 8-14°C. Environmental factors related to light levels and rate of temperature decline influence the timing of migration and duration of the

spawning period. However, the interaction among these factors is poorly understood (Gunn 1995).

- J. Lake trout spawning occurs at night (Dorr 1981), therefore specific behaviors are difficult to document and study.
- K. Male lake trout mature at younger ages than females. Males also arrive at spawning locations earlier and remain longer than females (Gunn 1995). The reasons for this behavior are poorly understood.
- L. Lake trout spawning is believed to be most successful in areas with low predator abundance or where interstitial depth is large. Researchers believe that lake trout select substrate with appropriate interstitial spaces reducing egg predation (Gunn 1995). Stream trout bury their eggs in gravel and this has been shown to reduce predation on the deposited eggs (Greeley 1932). Evidence for substrate mediated differences in egg survival or the specifics of substrate and spawning site selection by stocked lake trout relative to native trout is lacking.
- M. Cues used by fish to migrate in open water could be the orientation of the sun, polarized light, geomagnetic and geoelectric fields, temperature, water currents, oceanfronts, internal guidance, random walks, and maximization of comfort (optimization of physiological and neurological states in response to multiple stimuli) (Horral 1981; Leggett 1977).
- N. Little information exists regarding lake trout perception through vision, taste, smell hearing and lateral line sensing, all of which are likely involved in spawning activity (Gunn 1995). Foster (1985) found that spawning lake trout were attracted to chemical cues left by other trout. He further suggests that pheromones play an important role in spawning site selection by lake trout. Recent evidence from biochemical analysis has suggested that lake trout indeed use sex pheromones to locate mates (Zhang et al. 2001). In general, biologists have a poor understanding of the mechanisms used by lake trout to recognize or select spawning sites (Gunn 1995).

III. Relation of 1985 Plan Recommendations to Impediment

The 1985 plan suggested that managers and researchers conduct and/or support well-designed experiments to determine whether the planting of lake trout at different early life-stages will enhance their ability to home to spawning areas and reproduce. They suggested conducting fry planting at Horseshoe Reef in Green Bay, WI. They further suggested not stocking eggs or fry in refuge areas until methods are proven and successes of yearling stocking efforts are evaluated. The authors recommended that Lake Michigan studies coordinate with Lake Superior early life-history studies. The 1985 Plan relied primarily on bottom trawling to detect early recruitment. Spawning behaviors or other spawning site selection cues are not mentioned in the 1985 Plan.

IV. Relation of 1985 Plan Implementation and the Impediment

Egg stocking was conducted by WIDNR in 1988 for two years. Astro-turf stocking was conducted by WIDNR and USFWS from 1992-1996 on Jacksonport Deep Reef. Stocking eggs in astro-turf was conducted by MIDNR and USFWS in 1998-2000 on Big Reef in northern Lake Michigan. However, each of these efforts did not incorporate a full experimental design for evaluation of early life-

history stocking and the potential for improved recognition of appropriate spawning locations.

- V. **Conclusion** – Behavioral aspects of spawning site selection and spawning behavior by lake trout are poorly understood, and limits our remediation/management efforts. Research should focus on identifying reproductive behavior and comparative studies of wild and hatchery-reared fish.
- VI. **Priority** – Biological: High, Management: Medium

IMPEDIMENT 6 – REARING PRACTICES

I. **Problem Statement:** Rearing and stocking practices reduce the survival and reproductive success of stocked lake trout.

II. Literature/Assessments

Influences of Standard Rearing and Stocking Practices

- A. Chinook salmon of the same genetic origin from several different hatcheries in Oregon showed different survival rates to adulthood. It is believed that the quality of fish released by different facilities has profound effects on subsequent survival (Beckman et al. 1999).
- B. Wild brook trout have better survival than hatchery fish in natural lakes. Hatchery-reared brook trout were recovered only in the year after stocking, while wild fish were caught over a period of 3-4 years (Fraser 1981).
- C. Stocked brown trout were more vulnerable to angling than wild brown trout (Mezzera et al. 2001).
- D. Rearing densities of lake trout in the hatchery influences survival after stocking. Higher rearing densities resulted in lower survival after release in Lake Ontario (Elrod et al. 1989), hence lower rearing densities may be required at some hatcheries.
- E. A simulation model predicted that lake trout populations in Lake Ontario during the early 1990s had the potential to produce over 1.2 million age-1 fish annually, but this level of recruitment was never observed (Perkins et al. 1995). Natural recruitment appeared to be limited by the apparent inability of some stocked fish to locate or recognize spawning habitat (among other factors).
- F. Inappropriate light and feeding conditions in hatcheries have been shown to induce cataracts in hatchery-reared lake trout (Steucke et al. 1968), which may affect post-release survival.

Revised Rearing Practices

- G. Steelhead raised in tanks with high habitat complexity had better competitive strategies than did those raised in standard rearing environments (Berejikian et al. 2000).
- H. Hatchery-reared brook trout trained to recognize predators gained survival benefits when tested in staged encounters with predators (Mirza et al. 2000).

Revised Stocking Practices

- I. Lake trout stocked offshore experienced reduced predation and enhanced first-year survival compared to those stocked nearshore (Elrod 1997).

- J. In Minnesota waters of Lake Superior, local stocks were used for rehabilitating lake trout populations and for re-establishing extinct populations. Non-native or hatchery-reared stocks may be less able to cope with potential predators or competitors, and may exhibit lower survival (Siesennop 1992).

III. Relation of 1985 Plan Recommendations to Impediment

To reduce the influences of rearing practices on young lake trout, the 1985 Plan suggested well-designed experiments to determine whether planting lake trout at earlier life-stages might enhance their ability to home to spawning areas and reproduce. The 1985 Plan suggested fry planting at Horseshoe Reef in Green Bay, WI, and further suggested not stocking eggs or fry in refuges until these methods are proven and successes of yearling stocking efforts are evaluated. The 1985 Plan recommended that Lake Michigan studies coordinate with Lake Superior early life-history studies. Evaluations of specific influences of current rearing practices are not discussed in the 1985 Plan.

IV. Relation of 1985 Plan Implementation and the Impediment

Stocking fertilized eggs in astro-turf incubators was conducted by WIDNR and USFWS during 1988-1996 on Jacksonport Deep Reef, and MIDNR and USFWS during 1998-2000 on Big Reef in northern Lake Michigan. Evaluation at Jacksonport Deep Reef suggested that few of these fish returned (USFWS; unpublished data) in contrast to the apparent success of this technique in Lake Superior (Bronte et al. 2002b).

- V. **Conclusion** – Increased stocking of early life stages (eggs and fry) should be pursued with field controls to re-establish spawning aggregations and compared to yearling controls to determine efficacy. Deepwater forms of lake trout should be introduced to encourage the use of deepwater spawning habitat.

- VI. **Priority** – Biological: Medium-low, Management: High

IMPEDIMENT 7- NEARSHORE STOCKING IN HIGH ENERGY ZONE

- I. **Problem Statement:** Lake trout have been stocked in nearshore locations in Lake Michigan that have poor spawning habitat compared to offshore locations.
- II. **Literature/Assessments**
 - A. In many inland lakes, lake trout have been documented to spawn on nearshore habitat (Gunn 1995).
 - B. In Lake Superior, stocking nearshore areas in Michigan and Minnesota waters where suitable spawning substrate exists has resulted in successful rehabilitation (Hansen et al. 1995a; Wilberg et al. 2003).
 - C. Nearshore spawning habitat that is suitable in inland lakes may not be so in Lake Michigan due to high wave energy and sedimentation (Eshenroder et al 1995a, 1995b). Conversely, spawning areas less than 10-m deep can provide spawning habitat for hatchery-reared fish in the Great Lakes provided that they are protected (e.g. lee side of islands, peninsulas) and ideally have comparatively strong currents that sweep areas clean in autumn. Successful spawning by hatchery trout in such areas has been observed in Lake Ontario (Marsden and Krueger 1991). Spawning habitats such as these likely occur in Lake Michigan around areas such as northern Door County Peninsula, the Beaver Islands Complex, and Manitou Islands. As spawning areas increase in their exposure to physical forces of wind and ice, water depth likely must also increase to provide protection from these forces and thus provide a suitable incubation environment.
 - D. In Lake Michigan, the abundance of potential egg and fry predators is higher in the nearshore zone. More aggressive exotic species (e.g. goby, rusty crayfish) are also more prevalent in the nearshore zone (Fitzsimons et al.; personnel communication 2000).
 - E. Reefs exposed to long fetch and prevailing winds may receive too much wave energy to protect eggs, and eggs that are well protected may suffer from high sedimentation (Sly and Schneider 1984; Marsden and Krueger 1991).
 - F. In southern Lake Michigan, sites where lake trout eggs were found were less than 12 m deep and within 4 km of shore (Marsden 1994).
 - G. Clay Banks Refuge, established in 1985, was stocked at twice the recommended rate for three consecutive years and a large spawner population developed. No reproduction has been detected probably due to marginal habitat in the high-energy zone; ripe female lake trout were found by WIDNR in less than 5 feet of water very near the beach, hence refuge status was removed 1995.
 - H. Suitable spawning habitat in Lake Michigan probably occurs in narrow habitat envelopes at offshore reef sites and north along extensive rocky littoral stretches with meager fines, i.e. Midlake reefs, Door County, Northern Refuge reefs, and UP shore (Eshenroder et al. 1995b).
 - I. Based on the protection afforded lake trout populations in refuge areas, and the locations of historical catches during the spawning period (Dawson et al. 1997), rehabilitation efforts should continue to emphasize the two refuges as well as at sites identified with high historical catches during the spawning period.

- J. The few areas in Lake Michigan where some successful natural reproduction has been documented occurred mostly in nearshore waters and most were associated with manmade structures with clean substrate (Holey et al. 1995; B. Briedert; personal communication).

III. Relation of 1985 Plan Recommendations to Impediment

- A. Stocking goals by rehabilitation zones and stocking methods recommended that much of the stocking occur in nearshore waters throughout Lake Michigan.
- B. Deferred Area (northern Lake Michigan) should not be stocked.
- C. Create offshore reef refuges and stock at highest priority.

IV. Relation of 1985 Plan Implementation and the Impediment

- A. Stocking goals were not routinely met. Since 1985 lake trout stocking has increased in Secondary Zones averaging about 33% of total annual stocking in the last decade, whereas only 4.6% of the historical commercial catch came from these areas (Dawson et al. 1997). Stocking occurred in nearshore areas with less suitable spawning habitat.
- B. Many historically important offshore sites in or near the Northern Refuge have not been stocked and no historically important sites (Dawson et al. 1997) in the Deferred Zone have been stocked.

V. **Conclusion** – Lake trout should be stocked at historically important offshore spawning sites especially in the northern third of Lake Michigan. Most nearshore habitats are not the best spawning locations for lake trout reproduction and should be de-emphasized as stocking sites, but can be considered if landscape features afford adequate protection for good habitat. Stocking should be shifted offshore.

VI. Priority – Biological: High, Management: High

Definition of nearshore vs. offshore - We chose to adopt the definition created by Dawson et al. 1997; "A site is classified as onshore {nearshore} if it was connected to the mainland by depths less than 40 m on at least three sides (270°) or offshore if it was separated from the mainland by depths greater than 40 m on at least three sides." We define the high-energy zone in nearshore waters as that area in which wave action is of sufficient strength, especially during fall storms, to scour the bottom and create conditions that cause mechanical damage to incubating eggs.

IMPEDIMENT 8 - POOR IMPRINTING OR USE OF OLFACTORY CUES BY STOCKED YEARLINGS

I. Problem Statement: Failure of stock yearling lake trout to imprint to natal areas or sense olfactory cues have impaired adults from finding and selecting spawning substrate or mates.

II. Literature/Assessments

- A. Stocked yearling lake trout appear to prefer near shore areas rather than offshore reefs and this may be related to light and depth conditions during rearing in the hatchery raceways (Foster 1984).
- B. In Lake Superior stocking of inexperienced hatchery fish in the near-shore area has been successful because suitable habitat is found inshore along much of the Michigan and Minnesota shoreline (Hansen et al. 1995a) and may also be due to the presence of residual wild lake trout imprinted to those areas.
- C. It is thought that imprinting to spawning substrate occurs at an early life stage. Hatchery reared fish are still in the hatchery when imprinting is thought to occur rather than on natal reefs in the lake (Horrall 1981; Foster 1984; Binkowski 1984).
- D. Fish stocked as yearlings likely have less reliable cues that can guide them to good spawning substrate when mature so they behave essentially as strays or colonists. Colonizing strategies in lake trout may have been shaped by ancestral adaptations appropriate for relatively small inland lakes, where most of the spawning habitat is associated with shorelines. The largest aggregations of stocked lake trout on historically important offshore reefs in the Great Lakes are found on structures separated from the mainland by large expanses of deep water, which suggests that stocking locality affects subsequent movement and selection of spawning habitat. (Eshenroder et al. 1995a; Eshenroder et al. 1995b).
- E. Recent assessment of reefs during fall indicate that lake trout in spawning condition were most abundant on sites that had a long history of stocking (Bronte et al. 2002a).
- F. Yearlings stocked on Midlake Reefs have returned in large and increasing numbers as mature fish and have deposited eggs (Holey et al. 1995, McKee et al. 2002, Bronte et al. 2002a, J. Janssen personal communication).
- G. Hatchery-reared fish stocked as yearlings at offshore reefs were captured during the spawning period at near-shore reefs in northeastern Lake Michigan, potentially contributing to the near-shore spawning population (Little Traverse Bay 13.3%, Bay Harbor 12.5%, and Fisherman's Island 22.4%; Michigan Department of Natural Resources Assessment Data, Charlevoix, MI).
- H. Out of 260 lake trout that were floy-tagged at three near-shore spawning sites in northern Lake Michigan from 1999-2001, a total of 5.76% were recaptured. From the recaptures, 53.3% were caught at the same spawning site during the spawning period. Also, 26.7% of the recaptures were at one of the three spawning sites (but not the original tagging location). The remaining 20% of recaptures were caught at various

locations in Lake Michigan (e.g.-Grand Traverse Bay, Ludington, and Milwaukee; Randy Claramunt; personal communication).

- I. Few lake trout shoreline stocked as yearlings near Eagle Island Shoal (Apostle Islands, western Lake Superior) used this offshore area for spawning. They did however congregate on the shoreline at Squaw Point near the stocking site, which was located less than three miles away from Eagle Island Shoal (Bronte 1987; Krueger et al. 1986).
- J. Hatchery-reared lake trout, when mature, tended to return to areas where they were originally stocked, which suggests they do remember where they lived as juveniles (Elrod et al. 1996).
- K. Some laboratory evidence suggests that lake trout may use pheromones to locate spawning substrate but a passive or active search for a particular smell is unlikely to provide a full answer as to how mature fish find spawning substrate (Gunn 1995).
- L. Van Tassels Point near Bayfield (Apostle Islands) had no native lake trout and little habitat but attracted an aggregation of fish, perhaps because the outfall from the Bayfield State Fish hatchery where lake trout are reared is about 0.4 mile away (Krueger et al. 1986).
- M. Cat Island Shoal (Apostle Islands region) always had more native lake trout than hatchery-reared fish even though Devils Island Shoal and Rocky Island Reef were closer to shoreline stocking sites (pheromones?) (Krueger et al. 1986).
- N. Electro-olfactogram recording demonstrated that bile acids released by lake trout were detectable by their olfactory system at nanomolar concentrations, which is well below the levels of bile acids released into the water. The exquisite olfactory sensitivity of lake trout to water-borne bile acids released by their conspecifics is consistent with a role for these compounds as important chemical signals (Zhang et al. 2001).
- O. Long term exposure to low levels of toxicants found in the lake may disable the sense of smell, as has been found in other salmonines, thus impair all smell related mechanisms for search of spawning substrate.
- P. Likely there are other cues than early imprinting, such as innate recognition of site characteristics (i.e. substrate size) involved in finding suitable substrate (Gunn 1995).
- Q. Lake trout have an affinity for spawning on clean or new substrate (including manmade structures) (Marsden et al. 1995) and the only documented sites of natural reproduction in Lake Michigan have been manmade structures (Holey et al. 1995).
- R. Experiments involving stocking early life stages on reefs in Green Bay and Lake Michigan have so far yielded disappointing results (Eshenroder et al. 1999), in contrast to the apparent success on Devils Island Shoal in Lake Superior (Bronte et al. 2002b).

III. Relation of 1985 Plan Recommendations to Impediment

- A. Use yearlings as life stage for majority of stocking.
- B. Lake trout fry planting on Horseshoe Reef.
- C. Plant unmarked eggs/fry outside refuges until use of yearlings is discontinued.

IV. Relation of 1985 Plan Implementation and the Impediment

- A. Large populations of mature lake trout originating from yearling stocking aggregate at a variety of spawning reefs of differing quality but have not produced sustainable (replacement) levels of reproduction.
- B. Since 1997 approximately 90 - 99% of mature fish captured on Midlake Refuge reefs during fall spawner assessments were fish originally stocked there; in assessments conducted at nearshore sites off Milwaukee approximate 15-20% of the lake trout captured were originally stocked on Midlake Refuge reefs (WIDNR assessment data).
- C. Less than 10% of fish captured in fall assessments in the Midlake Refuge were originally stocked at nearshore locations and have moved to (colonized) Midlake Refuge reefs.
- D. Mature fish stocked as yearlings are attracted to clean rock substrate, especially new manmade structures near shore; the majority of offshore reefs with little or no stocking history seemed to attract few if any mature fish (Bronte et al. 2002a).
- E. Very limited egg/fry stocking experiments in Green Bay and Lake Michigan have had disappointing results so far.

V. Conclusion – Imprinting is important for homing. Lake trout, stocked as yearlings are unable to imprint to specific locations, as do wild fish. This lack of homing by hatchery fish probably decreases their reproductive effectiveness. However, some stocked lake trout do return to the same stocking site for spawning so stocking should occur on or near high priority spawning reefs. when mature. More experiments with egg/fry stage stocking should be undertaken. Research should focus on understanding the mechanism(s) mature lake trout use to locate spawning habitat. This research should examine the roles of imprinting, olfactory homing, pheromones, life stages stocked, and hatchery conditioning.

VI. Priority – Biological: High, Management: Medium-low

IMPEDIMENT 9 – LOW GENETIC DIVERSITY

- I. **Problem Statement:** The low genetic diversity of lake trout stocked into Lake Michigan is limiting their potential to fully colonize the variety of inshore and offshore habitats suitable for the species and to access food resources typical of large lakes.
- II. **Literature/Assessments**
 - A. Lake Michigan has a variety of lake trout habitats. Near shore habitats represent the smallest portion of the historically important spawning habitat (Dawson et al. 1997).
 - B. Native lake trout in Lake Michigan expressed a great amount of phenotypic diversity that provided the ability to occupy the full range of habitats and to be trophically diverse (Brown et al. 1981).
 - C. Phenotypic diversity has a genetic basis and includes traits such as retention of fat reserves, emergence timing, and swim bladder gas retention (Eschmeyer and Phillips 1965; Horns 1985; Ihssen and Tait 1974). Some of these traits when expressed under wild conditions can translate into characteristics such as depth distribution, diet, timing of spawning, and selection of incubation environments.
 - D. The genetic diversity represented by the lake trout stocked over the past three decades represents only a limited portion of the phenotypic diversity available within the Great Lakes basin and therefore only a small suite of the adaptive gene complexes available in lake trout have been reintroduced to the lake (Krueger et al. 1983; Krueger and Ihssen 1995; Page 2001). The Superior or Marquette strain originating from the Apostle Islands area of Lake Superior has been the primary strain introduced into Lake Michigan. This strain, though having high allelic diversity based on microsatellite loci, showed the lowest or moderate values of most measures of genetic diversity among six hatchery broodstocks surveyed by Page (2001) while Lewis Lake and Seneca Lake showed the largest values for genetic diversity and divergence. This same study showed that among 12 collections of wild lake trout from Lake Superior a significant portion of total variation in allele frequency was partitioned among the lean, humper (banker), and siscowet morphotypes. Lean populations from Lake Superior represented a small proportion of overall available genetic diversity (Page 2001).
 - E. The Marquette, Lewis Lake, Gull Island Shoal, and Isle Royale strains of lake trout stocked in the past were best adapted for life in the shallow-water zones of Lake Michigan. The Green Lake and Seneca strains are two possible exceptions to this generalization. The Green Lake strain unfortunately has several problems within its pedigree (see Kincaid et al. 1993; Eshenroder et al. 1999). The Seneca strain originates from gamete collections made in early October from Seneca Lake, New York, at depths of approximately 30m. This strain when stocked into Lake Ontario was reported to have spawned in < 10 m during the 1980s and 1990s (Marsden et al. 1989; Grewe et al. 1994). Whether this strain also spawned in deep waters in Lake Ontario is unknown.
 - F. Because the full range of genetic diversity has not been utilized, many adaptations have not been introduced and the innate ability of stocked

lake trout to colonize suitable habitats and to trophically diversify is compromised (Krueger et al. 1995).

III. Relation of the 1985 Plan Recommendations to this Impediment

The genetic strategy for the use of lake trout strains in Lake Michigan is described in Krueger et al. 1983 (cited in the 1985 Plan). The Superior (Marquette), Superior (Marquette) x Gull Island Shoal, and Lewis Lake strains were recommended for shallow-water stocking. Seneca Lake, and Green Lake strains were recommended deep-water stocking. In addition, the development of a new broodstock was recommended from Gull Island Shoal, Lake Superior. In the late 1990s, gamete collections were recommended to begin from near-shore shallow waters and from the Midlake Refuge so that shallow- and deep-water broodstocks could be propagated directly from Lake Michigan and benefit from the natural selective forces in the lake. Last, adult transfers were recommended from Isle Royale, Caribou Island, Michipicoten Island, and Gull Island shoal to sites in Lake Michigan.

IV. Relation of the 1985 Plan Implementation and the Impediment

Implementation of the 1985 Plan was characterized by variation in the strains stocked from year to year, planting some of the strains recommended in the two habitats, and stocking shallow-water strains into deep water habitats and deep-water strains into shallow water habitats. Stocking was not proportionately balanced among strains and in some years only one strain was stocked. In the shallow-water spawning habitat of the Northern Refuge the Superior (Marquette), Lewis Lake, Seneca, Isle Royale, and Superior (Marquette) x Gull Island shoal hybrid were stocked sporadically (Holey et al. 1995). In the deep-water spawning habitat of the Midlake Refuge, the Superior (Marquette), Superior (Marquette) x Gull Island Shoal, Seneca, Lewis Lake, and Green Lake strains of lake trout were stocked (Holey et al. 1995). No adult transfers from Lake Superior or gamete collections from Lake Michigan occurred.

V. Conclusion -The inability to implement a consistent stocking strategy in nearshore and offshore waters prevented the comparison of strains in terms of re-colonization capabilities (e.g., survival, return to stocking site, amount of straying). A commitment should be made to consistently propagate and stock strains that are expected to be suitable for colonizing nearshore and offshore habitats, and to commit to their assessment in terms of survival and reproduction. A variety of lake trout types should be introduced to a variety of habitats.

V. Priority – Biological: High, Management: High

IMPEDIMENT 10 – HABITAT DEGRADATION

- I. **Problem Statement:** Traditional spawning reefs have been degraded to the point where they will not support reproduction.
- II. **Literature/Assessments**
 - A. Historically in Lake Michigan, offshore lake trout spawning habitat appeared to be more productive than nearshore habitat (Dawson et al. 1997).
 - B. Substrate evaluation at over 31 lake trout spawning sites around the Great Lakes revealed that all but two sites were likely to support production of viable fry from egg deposition in shallow water (Edsall and Kennedy 1995). The best spawning and fry habitat in the lower Great Lakes seems to be at deeper offshore sites.
 - C. In Lake Michigan, Marsden et al. (1995) observed that lake trout spawned on new substrate, and this has also been observed elsewhere in the Great Lakes (Schreiner et al. 1995).
 - D. Artificial or manmade structures have been shown to attract lake trout in each of the Great Lakes (Fitzsimons 1996).
 - E. Substrate size and location influence spawning site selection and influence the potential for egg survival (Marsden et al. 1995).
 - F. Optimum lake trout spawning habitat consists of piles of cobble or rubble with interstitial depths of 20-30 cm (Wagner 1982; Peck 1986; Nester and Poe 1987; Marsden et al. 1988; and Marsden and Krueger 1991).
 - G. Historical lake trout spawning sites have been identified based on interviews with fisherman and data from catch reports (Smith 1968; Coberly and Horrall 1980; Goodyear et al. 1982; Dawson et al. 1997) but these anecdotal reports do not guarantee the presence of suitable substrate.
 - H. Commercial catch reports in the period leading up to the decline in lake trout populations, indicate that nearly half of the entire lake trout catch came from the northeast section of Lake Michigan. Results would suggest that a high proportion of spawning reefs are located in northern Lake Michigan (Eshenroder et al. 1995b; Holey et al. 1995; Dawson et al. 1997).
 - I. Wide-scale habitat degradation from physical or chemical sources is not evident, but colonization of zebra mussels on spawning reefs may affect egg deposition and incubation by reducing interstitial depth (Eshenroder et al. 1999). Further, although no direct impacts were noted in laboratory experiments, lake trout deposited fewer eggs on zebra mussel infested shoals in southern Lake Michigan, and damaged eggs were observed (Marsden and Chotkowski 2001).
 - J. Lake trout spawning habitat has been evaluated at a variety of locations throughout Lake Michigan (e.g. Clay Banks, Richards, Boulder, Jacksonport Deep, Julian's, and Wilmette Reef) primarily using side-scan sonar and ROVs (Holm et al. 1987; Edsall et al. 1989; Edsall et al. 1992a,b; Edsall et al. 1995; Edsall and Kennedy 1995). Better methods are needed to classify/quantify reef structures, substrate size and quality, water quality and physical forces on spawning habitats (Marsden et al. 1995; Eshenroder et al. 1995a). Further understanding of microhabitat use within a reef structure is also of critical importance.

- K. Clay Banks Reef in western Lake Michigan had rocky substrates suitable for spawning and fry production and there is no indication of substrate degradation by eutrophication (Edsall et al. 1992a; 1995b).

III. Relation of 1985 Plan Recommendations to Impediment

The 1985 Plan suggests that managers establish stocking strategies to colonize spawners on best “known” habitat. Bathymetric mapping is suggested as a means of identifying potential lake trout spawning habitat.

VII. Relation of 1985 Plan Implementation and the Impediment

Side scan sonar was used at many sites in Lake Michigan to identify potential spawning locations. However, only a fraction of the potential spawning habitat was identified, and no attempt was made to determine finite spawning locations within reef structures or to link results to adult lake trout abundance or stocking strategies.

- VIII. Conclusion** - Whether spawning habitat has been degraded is unknown but except for encrustation by zebra mussels, there is no reason to believe that offshore habitat has been degraded since the loss of native populations. Without a clear understanding of critical lake trout habitat characteristics, it will be difficult to evaluate and improve the survival of lake trout in early life stages. Continued and enhanced inventorying of surficial characteristics of historical lake trout spawning and nursery sites is recommended. Priority emphasis should be placed on understanding how depth, fetch, currents, and interstitial depth make rocky deposits suitable for lake trout spawning.

- IX. Priority** – Biological: Low, Management: Low

IMPEDIMENT 11 - CONTAMINANTS

- I. **Problem Statement:** Environmental contaminants limit the successful reproduction of lake trout in Lake Michigan through reduced hatching rates and swim-up survival.
- II. **Literature/Assessments**
 - A. Lake trout are sensitive to PCB toxicity, and studies have linked lake trout reproductive failure in Lake Michigan with PCB exposure (Wilford et al. 1981, Mac et al. 1993).
 - B. Mortality of Lake Michigan eggs were higher than for eggs from lakes Superior and Huron when reared under identical conditions and eggs from all sources had poorest survival when reared in Lake Michigan water (Mac et al. 1985).
 - C. A significant correlation was found between egg mortality and PCB concentrations in eggs but not for swim-up fry (Mac et al. 1993).
 - D. Early life survival of feral Lake Michigan lake trout eggs and fry reared in the lab has been poorest at the swim-up stage, not the egg hatching stage (Holey et al. 1995).
 - E. Critical review of contaminant effects on early life stage mortality showed that contaminant levels required to induce mortality are higher than what is measured from Great Lakes lake trout and that swim-up mortality has never been correlated with contaminant levels (Fitzsimons 1995).
 - F. No correlation was found between hatching or swim-up survival and PCB concentrations for eggs collected from 73 Lake Michigan lake trout captured during 1996-98 (Stratus Consulting 1999). Swim-up mortality was present and was correlated with egg thiamine concentrations.
 - G. Projections of historical egg PCB levels indicate that the percent of egg samples in 1975 that would have exceeded the LD50 ranged from 20-40%, but that by 1980, less than 1% of Lake Michigan lake trout eggs were high enough to cause mortality (Stratus Consulting 1999).
- III. **Relation of 1985 Plan Recommendations to Impediment**
 - A. Support continued testing of lake trout for chemical contaminants suspected of adversely affecting hatchability of eggs and/or survival of fry.
 - B. Develop and institute a program for periodically testing lake trout eggs and fry from south, central, and northern regions of the lake for hatchability and survival of fry.
- IV. **Relation of 1985 Plan Implementation and the Impediment**
 - A. Efforts of the Great Lakes Science Center, the Wisconsin Department of Natural Resources and the U.S. Fish and Wildlife Service have resulted in measuring lake trout egg survival annually from 1980 to present, primarily from Clay Banks Reef, Wisconsin waters, Lake Michigan.
 - B. Studies comparing egg contaminants and thiamine concentrations to egg and fry survival were conducted from 1996-1998 at the Clay Banks Reef .

- V. Conclusion** - Reproductive failure of Lake Michigan lake trout cannot be attributed to post-1980 egg concentrations of commonly tested chemical contaminants like PCBs. Prior to 1980, contaminant burdens in lake trout eggs from Lake Michigan were likely high enough to result in decreased egg survival. Decreased survival at the swim-up stage, described as Early Mortality Syndrome (EMS), continues to impair reproduction, is attributed to low concentrations of thiamine in eggs, and does not correlate with concentrations of PCBs in eggs.
- VI. Priority** — Biological: Low, Management: Low

IMPEDIMENT 12 – PREDATION OF EGGS AND FRY

- I. **Problem statement:** Predation on lake trout early life stages by epibenthic and interstitial egg and fry predators inhibits successful natural reproduction.
- II. **Literature/Assessments**
 - A. A thiamine deficiency in adult lake trout has been associated with early mortality syndrome (EMS; Fitzsimons et al. 1998, 1999, Brown et al. 1998; Ji et al. 1998). EMS averages 30% in Lake Michigan lake trout and is not sufficient to completely block reproduction. However, low thiamine levels in young fish may influence vulnerability to predation.
 - B. It has been suggested that although toxins are not likely responsible for direct mortality on lake trout in Lake Michigan (Fitzsimons 1995; Stratus Consulting 1999), there may be indirect influences increasing the vulnerability of lake trout fry to predation.
 - C. Houde (1987) evaluated recruitment variability on a variety of fish species, and observed that predation was more important than starvation as a regulator of recruitment in the larval stage. Also, fish with large-yolk-sac embryos are less vulnerable to starvation.
 - D. Field observations in several locations indicate that lake trout fry predators (i.e. alewife) may have the potential to create a second predation based recruitment barrier in specific locations (Krueger 1995; Johnson and Van Amberg 1995). In contrast, cursory modeling efforts indicate that fry predation probably has a relatively small effect on lake trout recruitment (Savino et al. 1999). Further, preliminary observations from near-shore zones in northern Lake Michigan indicate little spatial and temporal overlap between emerging lake trout fry and alewife (Fitzsimons et al. 2000; personal communication).
 - E. Lake trout sac fry tend to move out of the substrate at night before filling the swimbladder. Thus, they may be more vulnerable to predation by fishes that feed at night near the bottom because of poor swimming capability (Baird and Krueger 2000).
 - F. Recent modeling work suggests that there are three potential groups of egg and fry predators (Savino et al. 1999); epibenthic egg predators that consume eggs on the substrate surface during spawning, interstitial egg predators that can move in rock substrate and consume incubating eggs, and fry predators that consume pre-emergent and emergent fry in the spring.
 - G. The importance of fry predation depends very much on the spatial-temporal overlap of lake trout fry and their predators, most notably alewives (Krueger et al. 1995a). As many as 18 individual fry were found in the stomach of an alewife captured at a spawning reef in Lake Ontario during emergence, although most alewives appeared not to have eaten fry (J. Fitzsimons, unpublished data). Detection of fry in alewife gut

contents is difficult because fry are not identifiable approximately 3 hours after being consumed (Krueger et al. 1995b). Current research efforts in northern Lake Michigan aim to identify spatial and temporal overlap of alewives with newly emerged lake trout fry (Fitzsimons et al. 2000).

- H. In 1985, it was generally believed from modeling efforts and the literature regarding self-sustaining lake trout populations in Lake Superior that mortality rates on lake trout populations needed to be below 40%. When egg and fry predators are considered, it is very likely that this rate will vary significantly among systems and probably should be lower for Lake Michigan (Fitzsimons et al. 2000).
- I. The qualities of bottom substrate influence the vulnerability of lake trout eggs and fry to predation. For example, Biga et al. 1998 used mixtures of rubble and gravel and found that substrate size can minimize predation pressure on eggs by excluding larger mottled sculpins from interstitial spaces.
- J. Recently introduced exotic species (i.e. zebra mussels, round goby, rusty crayfish) need to be evaluated and integrated into current predation models. Exotic predators like the rusty crayfish and round goby are likely to increase predation rates on eggs and fry as they tend to tolerate higher densities in a given area and are more aggressive than native species (Chotkowski and Marsden 1999). In laboratory studies, the hatching success of lake trout eggs on substrate with and without zebra mussels were similar, however in southern Lake Michigan, lake trout were attracted to spawn on newly constructed artificial reefs, and the presence of zebra mussels reduced egg deposition and increased damage to eggs (Marsden and Chotkowski 2001). Zebra mussels may also influence vulnerability to predation by occluding interstitial spaces. Marsden (1996) identified common carp as a predator on lake trout eggs where their distributions overlap.
- K. Based on laboratory studies, slimy sculpin do not alter their feeding patterns in the presence crayfish. However, the native crayfish (*Orconectes virilis*) was influenced by the presence of sculpins and available refugia and had significantly lower predation rates in the presence of sculpins (Miller et al. 1992).
- L. Stauffer and Wagner (1979) observed lower predation rates on natural verses artificially deposited lake trout eggs.

III. Relation of 1985 Plan Recommendations to Impediment

No emphasis was placed on egg and fry predators in the 1985 Plan however, the authors made an indirect reference (see Appendix) by encouraging studies that evaluate early life history bottlenecks. Specific studies were to be conducted in the Northern Refuge as a first priority after bottom-trawling efforts have failed to detect naturally produced lake trout from increased experimental plants.

IV. Relation of 1985 Plan Implementation and the Impediment

Studies have evaluated egg and fry predators in southern Lake Michigan (Marsden 1996; Marsden and Janssen 1997; Chotkowski and Marsden 1999). More recent work in northern Lake Michigan will compare predation rates among systems (Huron, Ontario, Champlain) and among onshore and offshore sites in northern Lake Michigan.

V. Conclusion – Recent studies indicate that one reason for the lack of lake trout recruitment is excessive mortality between egg deposition and the first year of life. Predation is likely occurring but at unknown levels. Decreased predation on eggs and fry can be accomplished by reestablishing high densities of lake trout that can reduce predation by reef predators such as alewife and sculpins. Higher stocking rates are needed to reestablish the ecological dominance of lake trout as well as increase the potential for sustainable reproduction.

VI. Priority – Biological: High, Management: High

IMPEDIMENT 13 – EARLY MORTALITY SYNDROME (EMS)

I. **Problem Statement:** The lack of the dietary vitamin thiamine leads to excessive mortality (Early Mortality Syndrome) in newly hatched lake trout and additional negative effects of low thiamine levels may also affect survival past the larval stage.

II. Literature/Assessments

- A. EMS occurred in the fry from eggs of 48% of feral female lake trout from Lake Ontario (Brown et al. 1998).
- B. Thiamine is an essential vitamin and it must come from the diet (Halver 1989).
- C. EMS typically occurs when lake trout egg total thiamine levels drop below 1.0 nmol/g (Brown et al. 1998). EMS has been observed at thiamine levels as high as 4 nmol/g (D. Honeyfield, unpublished data).
- D. Predator avoidance was negatively correlated to egg thiamine in Finger Lakes lake trout (J. Fitzsimmons, unpublished data).
- E. Lake trout fry with low thiamine (<2 nmol/g) showed reduced foraging on zooplankton compared to fry with higher levels (> 4nmol/g)(J. Fitzsimmons, unpublished data).
- F. Adult mortality from thiamine deficiency may also be occurring (D. Honeyfield, unpublished data).
- G. Thiamine levels in all Great Lakes forage fish and food webs that have been sampled are greater than the recommended dietary intake of 3.3 nmol/g (Fitzsimons et. al. 1999).
Non-indigenous forage such as rainbow smelt and alewife contain significantly higher levels of thiaminase, the thiamine-destroying enzyme, than native forage like bloaters and sculpins. Thiaminase activity in forage fish 1) varied by species (alewife 6.6 nmol/g/min; rainbow smelt 2.6 nmol/g/min; bloater 0 nmol/g/min), location (6-7 fold range), and season (spring >fall> summer), and was negatively correlated with whole body lipid in fish populations in the Finger Lakes, New York. (J. Fitzsimons; unpublished data.)

Thiminase was 3-7 times greater in viscera than for the whole body or carcass (in rainbow smelt and alewife; Zajicek unpublished data).

Alewife Organ	Thiaminase,nmol/g/min	% of body Wt
Spleen	49.758	0.13
Intestine	29.351	4.69
Kidney	19.913	0.86
Gill	11.414	2.76
Liver	2.233	1.22
Heart	1.892	
Ovaries	0.623	
Brain	0.425	
Muscle, skinless	0.104	56

- H. Thiamine concentrations were one-ninth to one seventeenth in eggs of lake trout that feed on alewife and rainbow smelt compared to eggs of lake trout that lacked these species in their diet (Fitzsimons et al. 1999). In 1998, 19 of 69 lots of lake trout fry showed signs of EMS in females collected from Lake Michigan and survival was less than 5% for 9 of these lots and ranged from 15.6 to 87.2% for the remaining 10 lots. First signs of EMS appeared two weeks after normal fry were transferred to glass tanks but sometimes did not develop until 4-5 weeks after transfer. All fry died over a 14 to 28 day period after showing signs of EMS. Fry survival to 75 days post-hatch was 98 to 100% for those lots that did not show EMS (C. Edsall, personal communication).
- I. It is currently believed that thiaminase is produced by bacteria (*Paenibacillus thiaminolyticus* and other *Paenibacillaceae* closely related to *P. thiaminolyticus*) isolated from alewife viscera and is one potential source of thiaminase in these fish (Honeyfield et al., 2001).
- J. Predator avoidance was negatively correlated to egg thiamine for the Finger Lakes lake trout (Fitzsimmons et al., unpublished data).
- K. Lake trout fry with low thiamine (<2 nmol/g) showed reduced foraging on zooplankton compared to fry with high levels (>4 nmol/g) (Fitzsimmons et al., unpublished data).

III. Relation of 1985 Plan Recommendations to Impediment

Not identified as an impediment in 1985.

IV. Conclusion – As long as Lake Michigan lake trout continue to rely on rainbow smelt and alewife we can expect that approximately 25% of their progeny will exhibit EMS. The indirect (chronic) effects of thiamine deficiencies on foraging efficiency and predator avoidance broaden the potential for even lower survival. EMS alone is not the sole reason for the lack of successful reproduction by lake trout, but contributes to the lack of sustainable reproduction.

VI. Priority – Biological: Medium, Management: Medium

IMPEDIMENT 14 - COMMUNITY DOMINANCE

I. Problem Statement: Low population densities of lake trout have allowed native and non-native- lake trout egg and/or fry predators to become abundant enough to suppress reproduction.

II. Literature/Assessments

- A. The northward distribution of lake trout in North America (Scott and Crossman 1973) and the existence of Alaskan haplotypes in Lake Superior (Wilson and Hebert 1996) suggest that the species is an early colonizer of deglaciated lakes.
- B. As an early colonizer and top predator, lake trout are viewed as an ecologically dominant species in oligotrophic lakes where under natural conditions this species suppresses other fish that have potential to suppress its reproduction. Walters and Kitchell (2001) call this type of suppression cultivation/depensation and believe that it is common in freshwater communities.
- C. Lake trout may have expressed dominance historically in Lake Michigan (and in the other deep Great Lakes).
- D. Recruitment of hatchery-reared lake trout is low in relation to historical levels for wild fish (Eck and Brown 1985; Holey et al. 1995).
- E. Eshenroder and Amatangelo (2002) showed that lake trout reproduction virtually ceased in northern Lake Michigan at a time (1944) when wild lake trout were likely more plentiful than hatchery-reared trout are now.
- F. The regional population density of lake trout may be an important determinant in the survivorship of their eggs and fry.
- G. The presence of many exotic species (both predator and prey) in the Lake Michigan ecosystem may make it difficult for lake trout to control recruitment of egg and fry predators. Hence, the role lake trout would play, if dominant, is less predictable.

III. Relation of the 1985 Plan recommendations to this impediment.

- A. Stocking rates recommended in the 1985 Plan for rehabilitation zones were based on availability but were not to exceed one fish/acre, two-thirds of the rate used successfully in U.S. waters of Lake Superior. Refuge stocking rates were based on an interagency agreement that allocated an increase in capacity (completion of phase II) from the Iron River NFH.
- B. The concept of community dominance was not considered in the planning exercise. Although the refuge stocking rates, in particular, were viewed as being high in comparison to contemporary rates, they were likely low in comparison to historical levels of natural recruitment.

IV. Relation of the 1985 Plan implementation to this impediment.

- A. Numbers of lake trout stocked have typically remained below the target level.
- B. Even if target numbers were reached, densities of lake trout may be too low for the species to achieve dominance.

V. Conclusion - To test the dominance hypothesis, near-historical population levels of lake trout need to be determined (i.e. Wilberg et al. 2003) and created in a region that contains an abundance of spawning habitat used by hatchery-reared lake trout. The Midlake Refuge is likely nearest this condition now and contains nearly all potentially important native egg and fry predators, although the abundance of exotic egg and fry predators (i.e., alewife and rainbow smelt) is uncertain. Prey species in the region to be tested need to be tracked to determine if high densities of lake trout suppress their abundance.

VI. Priority – Biological: High, Management: High

Literature Cited

- Baird, O.E. and Krueger, C.C. 2000. Behavior of lake trout sac fry: vertical movement at different developmental stages. *Journal of Great Lakes Research* 26: 141-151.
- Beckman, B.R., Dickhoff, W.W., Zaugg, W.S. Sharpe, C., Hirtzel, S., Schrock, R., Larsen, D.A., Ewing, R.D., Palmisano, A., Schreck, C.B. and Mahnken, C.V.W. 1999. Growth, smoltification, and smolt-to-adult return of spring chinook salmon from hatcheries on the Deschutes River, Oregon. *Transactions of the American Fisheries Society* 128: 1125-1150.
- Berejikian, B.A., Tezak, E.P., Flagg, T.A., LaRae, A.L., Kummerow, E., and Mahnken, C.V.W. 2000. Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 628-636
- Bergstedt, R. A. and Schneider, C. P. 1988. Assessment of sea lamprey (*Petromyzon marinus*) by recovery of dead lake trout (*Salvelinus namaycush*) from Lake Ontario, 1982-85. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1406-1410.
- Biga, H., Janssen, J. and Marsden, J.E. 1998. Effect of substrate size on lake trout egg predation by mottled sculpin. *Journal of Great Lakes Research* 24: 464-473.
- Binkowski, F.P. 1984. Stocking practices, p. 10-21. In R.L. Eshenroder, T.P. Poe, and C.H. Olver [ed.]. *Strategies for rehabilitation of lake trout in the Great Lakes: proceedings of a conference on lake trout research, August 1983*. Great Lakes Fishery Commission Technical Report 40.
- Breidert, B.R., Wright, K., Palla, J.S., Clapp, D., Toneys, M., Hess, R., Schneeberger, P., and DeSorcie, T. 2002. Harvest of fishes from Lake Michigan, 2001. *Lake Michigan Committee 2002 Annual Meeting, Duluth, Minnesota, March, 2002*.
- Bronte, C.R. 1987. Assessment of lake trout spawning activity at selected sites in the Apostle Islands. Red Cliff Fisheries Department, Assessment Report 87-2, Bayfield, Wisconsin.
- Bronte, C., Holey, M., Breidert, B., Claramunt, R., Ebener, M., Fleischer, G., Hess, R., Jonas, J., Martel, A., Toneys, M., McKee, P., and Olsen, E. 2002a. Evaluation of current stocking strategies to recolonize lake trout spawning reefs in Lake Michigan. *Lake Michigan Committee 2202 Annual Meeting – March 21-22, Great Lakes Fishery Commission, Ann Arbor, Michigan*.
- Bronte, C.R., Schram, S.T., Selgeby, J.H., and Swanson, B. L. 2002b. Reestablishing a spawning lake trout population in Lake Superior with fertilized eggs in artificial turf incubators. *North American Journal of Fisheries Management* 22:796-805.
- Brown, S.B. and Honeyfield, D.C. 1999. Research task report on Early Mortality Syndrome Workshop, Ann Arbor MI., May 17-18. Board of Technical Experts Briefing Book, October 1999, Great Lakes Fishery Commission. p 191-220.

- Brown, S.B., Fitzsimons, J.D., Palace, V.P. and Vandenbyllaardt, L. 1998. Thiamine and early mortality syndrome in lake trout. Pages 18-25 in *Early Life Stage Mortality Syndrome in Fishes of the Great Lakes and the Baltic Sea*. American Fisheries Society Symposium 21, Bethesda, MD.
- Brown, E.H., Jr., Eck, G.W., Foster, N.R. Horrall, R.M. and Coberly, C. E. 1981. Historical evidence for discrete stocks of lake trout (*Salvelinus namaycush*) in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences*. 38:1747-1758.
- Chotkowski, M.A. and Marsden, J. E. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. *Journal of Great Lakes Research* 25: 26-35.
- Coberly, C.E. and Horrall, R.M. 1980. Fish spawning grounds in Wisconsin waters of the Great Lakes. Report WIS-SG-80-235. University of Wisconsin Sea Grant Institute, Madison, WI.
- Coble, D.W., Bruesewitz R.E., Fratt, T.W., and Scheirer, J.W. 1990. Lake trout, sea lampreys, and overfishing in the upper Great Lakes: a review and reanalysis. *Transactions of the American Fisheries Society* 119:985-995.
- Dawson, K.A., Eshenroder, R.L. Holey, M. E., and Ward, C. 1997. Quantification of historic lake trout (*Salvelinus namaycush*) spawning aggregations in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2290-2303.
- Dorr, J.A., III, O' Conner, D.V., Foster, N.R., and Jude, D.J. 1981. Substrate conditions and abundance of lake trout eggs on a traditional spawning area in southeastern Lake Michigan. *North American Journal of Fisheries Management* 1:165-172.
- Eck, G.W. and Brown, Jr, E.H. 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s. *Canadian Journal of Fisheries and Aquatic Sciences* 42(3): 449-454.
- Edsall, T.A., Brown, C.L., Kennedy, G.W. and French III, J. R. 1992a. Surficial substrates and bathymetry of five historical lake trout spawning reefs in near-shore waters of the Great Lakes. *Great Lakes Fishery Commission Technical Report* 58.
- Edsall, T.A. and Kennedy, G.W. 1995. Availability of lake trout reproductive habitat in the Great Lakes. *Journal of Great Lakes Research* 21: 418-432.
- Edsall, T.A., Holey, M.E., Manny, B.A., and Kennedy, G.W. 1995. An evaluation of lake trout reproductive habitat on Clay Banks Reef, northwestern Lake Michigan. *Journal of Great Lakes Research* 21: 418-432.

- Edsall, T.A., Holey, M.E., Manny, B.A., and Kennedy, G.W. 1992b. Lake trout (*Salvelinus namaycush*) spawning habitat on Clay Banks Reef, northwestern Lake Michigan. Research completion report. Great Lakes Fishery Commission.
- Edsall, T.A., Poe, T.P., Nester, R.T., and Brown, C.L. 1989. Side-scan sonar mapping of lake trout spawning habitat in northern Lake Michigan. North American Journal of Fisheries Management 9: 269-279.
- Elliott, R. F. 2003. Estimated recruitment of hatchery-reared lake trout into sport and commercial fisheries by management unit in Lake Michigan. U.S. Fish and Wildlife Service, Green Bay Fishery Resources Office, Station Report 02-1. New Franken, WI.
- Elrod, J.H. 1997. Survival of hatchery-reared lake trout stocked near shore and off shore in Lake Ontario. North American Journal of Fisheries Management 17: 779-783.
- Elrod, J.H., O' Gorman, R., Schneider, C.P., and Schaner, T., 1996. Geographical distributions of lake trout strains stocked in Lake Ontario. Journal of Great Lakes Research 22(4): 871-883.
- Elrod, J. H., Ostergaard, D. E., and Schneider, C. P. 1989. Effect of rearing density on post stocking survival of lake trout in Lake Ontario. The Progressive Fish-Culturist 51: 189-193.
- Eschmeyer, P.H. 1955. The reproduction of lake trout in southern Lake Superior. Transactions of the American Fisheries Society 84: 47-74.
- Eschmeyer, P.H. and Phillips, Jr., A.M. 1965. Fat content of the flesh of siscowets and lake trout from Lake Superior. Transactions of the American Fisheries Society. 94: 62-74.
- Eshenroder, R.L. and Amatangelo, K.L. 2002. Changes in catch per unit effort of spawning lake trout in Lake Michigan during the 1900s with emphasis on the population collapse of the 1940s. Great Lakes Fishery Commission Technical Report 65.
- Eshenroder, R.L., Bronte, C.R., and Peck, J.W. 1995a. Comparison of lake trout-egg survival at inshore and offshore and shallow-water and deepwater sites in Lake Superior. Journal of Great Lakes Research 21 (Supplement 1): 313-322.
- Eshenroder, R.L., Crossman, E.J., Meffe, G.K., Olver, C.H., and Pister, E.P. 1995b. Lake trout rehabilitation in the Great Lakes: an evolutionary, ecological, and ethical perspective. Journal of Great Lakes Research 21 (Supplement 1): 518-529.
- Eshenroder, R.L., Holey, M.E., Gorenflo, T.K., and Clark, Jr., R.D. 1995. Fish-community objectives for Lake Michigan. Great Lakes Fishery Commission Special Publication 95-3. 56 p.

- Eshenroder, R.L., Payne, R.N., Johnson, J.E., Bowen II, C., and Ebener, M.P. 1995c. Progress toward lake trout rehabilitation in Lake Huron. *Journal of Great Lakes Research* 21 (Supplement 1): 108-127.
- Eshenroder, R.L., Peck, J.W., and Olver, C.H. 1999. Research priorities for lake trout rehabilitation in the Great Lakes: a 15-year retrospective. Great Lakes Fishery Commission Technical Report 64.
- Eshenroder, R.L., Poe, T. P., and Olver, C.H. 1984. Strategies for rehabilitation of lake trout in the Great Lakes: Proceedings of a conference on lake trout research, August 1983. Great Lakes Fishery Commission Technical Report 40.
- Evans, D.O., Casselman, J.M., and Willox, C.C. 1991a. Effects of exploitation, loss of nursery habitat, and stocking on the dynamics and productivity of lake trout populations in Ontario lakes, pp. 1-193. Ontario Ministry of Natural Resources, Ontario, Canada.
- Evans, D.O., Brisbane, J., Casselman, J.M., Coleman, K.E., Lewis, C.A., Sly, P.G., Wales, D.L., and Willox, C.C. 1991b. Anthropogenic stressors and diagnosis of their effects on lake trout populations in Ontario lakes, pp. 1-115. Ontario Ministry of Natural Resources, Ontario, Canada.
- Farmer, G.J., Beamish, F.W.H., and Lett, P.F. 1977. Influence of water temperature on the growth rate of the landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality. *Journal of the Fisheries Research Board of Canada* 34: 1373-1378.
- Fitzsimons, J.D. 1995. A critical review of the effects of contaminants on early life stage (ELS) mortality of lake trout in the Great Lakes. *Journal of Great Lakes Research* 21 (Supplement 1): 267-276.
- Fitzsimons, J.D., Brown, S.B., Honeyfield, D.C. and Hnath, J.G. 1999. A review of early mortality syndrome in Great Lakes salmonines and its relationship with thiamine. *Ambio* 28: 9-15.
- Fitzsimons, J.D., Brown, S.B., and Vandenbyllaardt, L. 1998. Thiamine levels in food chains of the Great Lakes. Pages 90-98 in G. McDonald, J. D. Fitzsimons and D. C. Honeyfield, editors. *Early Life Stage Mortality Syndrome in Fishes of the Great Lakes and Baltic Sea*. American Fisheries Society Symposium 21, Bethesda, Maryland.
- Fitzsimons, J.D. and O' Gorman, R. 1996. Fecundity of hatchery lake trout in Lake Ontario. *Journal of Great Lakes Research* 22: 304-309.
- Houde, E.D. 1987. Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* 2: 17-29.
- Foster, N.R. 1984. Physiology and behaviour, p. 22-27. In R.L. Eshenroder, T.P. Poe, and C.H. Olver [ed.]. *Strategies for rehabilitation of lake trout in the Great Lakes: proceedings of a conference on lake trout research, August 1983*. Great Lakes Fishery Commission Technical Report 40.

- Foster, N.R. 1985. Lake trout reproductive behavior: influence of chemosensory cues from young-of-the-year. *Transactions of the American Fisheries Society* 114: 794-803.
- Fraser, J.M. 1981. Comparative survival and growth of planted wild, hybrid, and domestic strains of brook trout (*Salvelinus fontinalis*) in Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1672-1684.
- Goodyear, C.D., Edsall, T.A., Ormsby-Dempsey, D.M., Moss, G.D., and Polanski P.E. 1982. Burbot and lake trout distributions. Pages 163-166 and 91-110 in *Atlas of the spawning and nursery areas of Great Lakes Fishes Volume IV Lake Michigan*. U.S. Fish and Wildlife Service, Ann Arbor, MI.
- Greeley, J.R. 1932. The spawning habits of brook, brown and rainbow trout, and the problem of egg predators. *Transactions of the American Fisheries Society* 62: 239-248.
- Gunn, J.M. 1995. Spawning behavior of lake trout: effects on colonization ability. *Journal of Great Lakes Research* 21 (Supplement 1): 323-329.
- Halver, J.E. 1989. The vitamins. Pages 37-43 in *Fish nutrition*, second edition. Academic Press, Toronto.
- Hansen, M.J., Peck, J.W., Schorfhaar, R.G., Selgeby, J.H., Schreiner, D.R., Schram, S. T., Swanson, B.L., MacCallum, W.R., Burnham-Curtis, M.K., Curtis, G.L., Heinrich, J.W. and Young, R. J. 1995a. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959-1993. *Journal of Great Lakes Research* 21 (Supplement 1):152-175.
- Hansen, M.J., Schorfhaar, R.G., Peck, J.W., Selgeby, J.H. and Taylor, W.W. 1995b. Abundance indices for determining the status of lake trout restoration in Lake Superior. *North American Journal of Fisheries Management* 15:830-837.
- Healey, M. C. 1978. The dynamics of exploited lake trout populations and implications for management. *Am. J. Wildlife Manage.* 42:307-328.
- Hile, R., Eschmeyer, P.H., and Lunger, G.F. 1951. Decline of the lake trout fishery in Lake Michigan. U.S. Fish and Wildlife Service Fisheries Bulletin 52: 77-95.
- Holey, M.E., Rybicki, R.W., Eck, G.W., Brown, E.H., Jr., Marsden, J.E., Lavis, D.S., Toneys, M.L., Trudeau, T.N., and Horrall, R.M.. 1995. Progress toward lake trout restoration in Lake Michigan. *Journal of Great Lakes Research* 21 (Supplement 1): 128-151.
- Holm, N.P., Norby, R.D., Smith, L.R., and Collinson, C. 1987. The role of Silurian bedrock reefs in the Lake Michigan lake trout fishery. Final Federal Aid Report No. F-54-R, University of Illinois.

- Horns, W. H. 1985. Difference in early development among lake trout (*Salvelinus namaycush*) populations. Canadian Journal of Fisheries and Aquatic Sciences 42:737-743.
- Horrall, R. M. 1981. Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. Canadian Journal of Fisheries and Aquatic Sciences 38: 1481-1496.
- Ihssen, P. E., and Tait, J.S. 1974. Genetic differences in retention of swimbladder gas between two populations of lake trout (*Salvelinus namaycush*). Journal of the Fisheries Research Board of Canada 31:1351-1354.
- Janssen, J. 2002. Early-life history studies, southern Lake Michigan. *A video presentation Lake Michigan Committee 2002 Annual Meeting* – March 21-22, 2002. Great Lakes Fishery Commission, Ann Arbor, Michigan.
- Ji, Y. W., Warthesen, J.J. and Adelman, I.R. 1998. Thiamine nutrition, synthesis, and retention in relation to lake trout reproduction in the Great Lakes. Pages 99-111 in G. McDonald, J. D. Fitzsimons and D. C. Honeyfield, editors. *Early Life Stage Mortality Syndrome in Fishes of the Great Lakes and Baltic Sea*. American Fisheries Society Symposium 21, Bethesda, Maryland.
- Jones, M. L., Eck, G.W., Evans, D.O., Fabrizio, M.C., Hoff, M.H., Hudson P.L., Janssen, J., Jude, D., O' Gorman, R., and Savino, J.F. 1995. Limitations to lake trout (*Salvelinus namaycush*) rehabilitation in the Great Lakes imposed by biotic interactions occurring in early life stages. Journal of Great Lakes Research 21(Supplement 1): 505-517.
- Kapuscinski, A.R., and Jacobson, L.D. 1987. Genetic guidelines for fisheries management. Minnesota Sea Grant Publication 17, University of Minnesota, St. Paul.
- Kincaid, H.L. 1977. Rotational line crossing: an approach to the reduction of inbreeding accumulation in trout brood stocks. The Progressive Fish Culturist 39:179-181.
- Kincaid, H.L. 1995. An evaluation of inbreeding and effective population size in salmonid broodstocks in federal and state hatcheries. *In Uses and effects of cultured fishes in aquatic systems*. American Fisheries Society Symposium 15:193-204.
- Kincaid, H.L., Krueger, C.C. and May, B. 1993. Preservation of genetic variation in the Green Lake strain lake trout derived from remnant domestic and feral populations North American Journal of Fisheries Management 13:318-325.
- Kitchell, J.F. 1990. The scope for mortality caused by sea lamprey. Transactions of the American Fisheries Society 119: 642-648.
- Krueger, C.C., Horrall, R.M., and Gruenthal, H. 1983. Strategy for the use of lake trout strains in Lake Michigan. Wisconsin Department of Natural Resources Administrative Report 17, Madison.

- Krueger, C.C., and Ihssen, P. E. 1995b. Review of genetics of lake trout in the Great Lakes: history, molecular genetics, physiology, strain comparisons, and restoration management. *Journal of Great Lakes Research* 21 (Supple. 1):348-363.
- Krueger, C.C., Jones, M.L., and Taylor, W.W. 1995a. Restoration of lake trout in the Great Lakes: challenges and strategies for future management. *Journal of Great Lakes Research* 21(Supplement 1): 547-558.
- Krueger, C.C., Perkins, D.L., Mills, E.L., and Marsden, J.E. 1995c. Predation by alewives on lake trout fry in Lake Ontario: role of an exotic species in preventing restoration of a native species. *Journal of Great Lakes Research* 21 (Supplement 1): 458-469.
- Krueger, C.C., Swanson, B.L., and Selgeby, J.H. 1986. Evaluation of hatchery-reared lake trout for reestablishment of populations in the Apostle Islands region of Lake Superior, 1960-84. Pages 93-107 in R.H. Stroud (ed). *Fish culture in fisheries management*. American Fisheries Society, Bethesda, Maryland.
- Larkin, P.A. 1975. Some major problems for further study on Pacific salmon. *International North Pacific Fishery Commission Bulletin* 32:3-9.
- Leggett, W.C. 1977. The ecology of fish migrations. *The Annual Review of Ecology and Systematics* 8:285-308.
- LMLTTC (Lake Michigan Lake Trout Technical Committee). 1985. A draft lakewide plan for lake trout restoration in Lake Michigan. In *Minutes Lake Michigan Committee (1985 annual minutes)*, Ann Arbor, MI, Great Lakes Fishery Commission, March 19, 1985.
- Loftus, K.H. 1958. Studies on river-spawning populations of lake trout in eastern Lake Superior. *Transactions of the American Fisheries Society* 87: 259-277.
- LSLTTC (Lake Superior Lake Trout Technical Committee). 1986 A lake trout restoration plan for Lake Superior. In *Minutes of the Lake Superior Committee (1986 annual minutes)*, Ann Arbor, MI, Great Lakes Fishery Commission, March 20, 1986.
- Mac, M.J., Edsall, C.C., and Seelye, J.G. 1985. Survival of lake trout eggs and fry reared in water from the upper Great Lakes. *Journal of Great Lakes Research* 11(4): 520-529.
- Mac, M.J., Schwartz, T.R., Edsall, C.C., and Frank, A.M. 1993. Polychlorinated biphenyls in Great Lakes lake trout and their eggs: Relations to survival and congener composition 1979-1988. *Journal of Great Lakes Research* 19(4): 752-765.
- McDonald, G., Fitzsimons, J.D., and Honeyfield, D.C. [eds]. 1998. *Early Life Stage Mortality Syndrome in Fishes of the Great Lakes and Baltic Sea*. American Fisheries Society Symposium 21, Bethesda, Maryland.

- MacLean, J.A., Evans, D.O., Martin, N.V., and DesJardine, R.L. 1981. Survival, growth, spawning distribution, and movements of introduced and native lake trout (*Salvelinus namaycush*) in two inland Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1685-1700.
- Marsden, J.E. 1994. Spawning by stocked lake trout on shallow, near-shore reefs in southwestern Lake Michigan. *Journal of Great Lakes Research* 20: 377-384.
- Marsden, J.E. 1996. Common carp diet includes zebra mussels and lake trout eggs. *Journal of Freshwater Ecology* 12: 491-492.
- Marsden, J.E., Casselman, J.M., Edsall, T.A., Elliott, R.F., Fitzsimmons, J.D., Horns, W.H., Manny, B.A., McAughey, S.C., Sly, P.G., and Swanson, B.L. 1995. Lake trout spawning habitat in the Great Lakes-a review of current knowledge. *Journal of Great Lakes Research*. 21 (Supplement 1): 487-497.
- Marsden, J.E. and Chotkowski, M.A. 2001. Lake trout spawning on artificial reefs and the effect of zebra mussels: fatal attraction? *Journal of Great Lakes Research* 27: 33-43.
- Marsden, J.E. and Janssen, J. 1997. Evidence of lake trout spawning on a deep reef in Lake Michigan using an ROV-based egg collector. *Journal of Great Lakes Research* 23: 450-457.
- Marsden, J.E. and Krueger, C.C. 1991. Spawning by hatchery-origin lake trout (*Salvelinus namaycush*) in Lake Ontario: data from egg collections, substrate analysis, and diver observations. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2377-2384.
- Marsden, J.E., Krueger, C.C., and May, B. 1989. Identification of parental origin as of naturally produced lake trout in Lake Ontario: application of mixed-stock analysis to a second generation. *North American Journal of Fisheries Management* 9: 257-268.
- Marsden, J.E., Krueger, C.C., and C.P. Schneider. 1988. Evidence of natural reproduction by stocked lake trout in Lake Ontario. *Journal of Great Lakes Research* 14:3-8.
- Marsden, J.E., Perkins, D.L., and Krueger, C.C. 1995. Recognition of spawning areas by lake trout: Deposition and survival of eggs on small, man-made rock piles. *Journal of Great Lakes Research* 21 (Supplement 1): 330-336.
- Martin, N.V. 1956. Reproduction of lake trout in Algonquin Park, Ontario. *Transactions of the American Fisheries Society* 86: 231-244.
- Martin, N.V. 1960. Homing behavior in spawning lake trout. *The Canadian Fish Culturist* 26: 3-6.
- McAughey, S.C., and Gunn, J. M. 1995. The behavioral response of lake trout to a loss of traditional spawning sites. *Journal of Great Lakes Research* 21 (Supplement 1): 375-383.

- McKee, P., Toney, M., Jonas, J., Hess, R., Claramunt, R., Madenjian, C., DeSorcie, T., Olsen, E., Martell, A., Breidert, B., Holey, M., and Bronte, C. 2002. *Status of Lake Trout Rehabilitation in Lake Michigan*. Lake Michigan Committee 2002 Annual Meeting, Duluth, Minnesota, March 2002.
- Mezger, M., and Largiader, C.R. 2001. Evidence for selective angling of introduced trout and their hybrids in a stocked brown trout population. *Journal of Fish Biology* 59: 287-301.
- Miller, J.E., Savino, J.F. and Neely, R.K. 1992. Competition for food between crayfish (*Orconectes virilis*) and slimy sculpin (*Cottus cognatus*). *Journal of Freshwater Ecology* 7: 127-136.
- Mirza, R.S., and Chivers, D.P. 2000. Predator-recognition training enhances survival of brook trout: evidence from laboratory and field-enclosure studies. *Canadian Journal of Zoology* 78: 2198-2208.
- Moore, S.A. and Bronte, C.R. 2001. Delineation of sympatric morphotypes of lake trout in Lake Superior. *Transactions of the American Fisheries Society* 130: 1233-1240.
- Nester, R.T., and Poe T.P. 1987. Visual observations of historical lake trout spawning grounds in western Lake Huron. *North American Journal of Fisheries Management* 7: 418-424.
- O' Gorman, R., Elrod, J.H., and Schneider, C.P. 1998. Reproductive potential and fecundity of lake trout strains in southern and eastern waters of Lake Ontario, 1977-1994. *Journal of Great Lakes Research* 24: 131-144.
- Page, K.S. 2001. Genetic diversity and interrelationships of wild and hatchery lake trout in the upper Great Lakes: inferences for broodstock management and development of restoration strategies. M. S. thesis. Michigan State University, East Lansing.
- Peck, J.W. 1986. Dynamics of reproduction by hatchery lake trout on a man-made spawning reef. *Journal of Great Lakes Research* 12 4: 293-303.
- Perkins, D.L., and Krueger, C.C. 1995. Dynamics of reproduction by hatchery-origin lake trout (*Salvelinus namaycush*) at Stony Island Reef, Lake Ontario. *Journal of Great Lakes Research* 21(Supplement 1): 400-417.
- Richards, J.M., Hansen M.J., Bronte, C.R., and Sitar, S.P. 2004. Recruitment dynamics of the 1971-1991 year classes of lake trout in Michigan waters of Lake Superior. *North American Journal of Fisheries Management* (in press).
- Royce, W.F. 1951. Breeding habits of lake trout in New York. *U.S. Fish and Wildlife Service Fishery Bulletin* 52:59-76.

- Rybicki, R.W. 1983. Lake trout populations in Michigan waters of Lake Michigan. 1977-1982. Lansing, MI. Michigan Department of Natural Resources, Fisheries Research Report No. 1914.
- Rybicki, R.W. 1991. Growth, mortality, recruitment and management of lake trout in eastern Lake Michigan. Ann Arbor, MI. Michigan Department of Natural Resources, Fisheries Research Report No. 1979.
- Savino, J.F., Hudson, P.L., Fabrizio, M.C. and Bowen, C.A. 1999. Predation on lake trout eggs and fry: a modeling approach. *Journal of Great Lakes Research* 25: 36-44.
- Schneider, C.P., Owens, R.W., Bergstedt, R.A., and O’Gorman, R. 1996. Predation by sea lamprey (*Petromyzon marinus*) on lake trout (*Salvelinus namaycush*) in southern Lake Ontario, 1982-1992. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1921-1932.
- Schram, S.T., Selgeby, J.H., Bronte, C.R., and Swanson, B.L. 1995. Population recovery and natural recruitment of lake trout at Gull Island Shoal, Lake Superior, 1964-92. *Journal of Great Lakes Research* 21 (Supplement 1):225-232.
- Schreiner, D.R., Bronte, C.R., Payne, N.R., Fitzsimons, J.W., and Casselman, J.M. 1995. Use of egg traps to investigate lake trout spawning in the Great Lakes. *Journal of Great Lakes Research* 21(Supplement 1): 433-444.
- Scott, W.B., and Crossman, E.J. 1973. *Freshwater fishes of Canada*. Bulletin Fishery Research Board of Canada. No. 184.
- Selgeby, J.H., Bronte, C.R., Brown Jr., E.H., Hansen, M.J., Holey, M.E., VanAmberg, J.P., Muth, K.M., Makauskas, D.B., McKee, P., Anderson, D.M., Ferreri, C.P., Schram, S.T. 1995. Lake trout restoration in the Great Lakes stock-size criteria for natural reproduction. *Journal of Great Lakes Research* 21(Supplement 1): 498-504.
- Siesennop, G.D. 1992. Survival, growth, sexual maturation, and angler harvest of three lake trout strains in four northeastern Minnesota lakes. Minnesota Department of Natural Resources, Grand Marais, Minnesota.
- Sitar, S.P., Bence, J.R., Johnson, J.E., Ebener, M.P., and Taylor, W.W. 1999. Lake trout mortality and abundance in southern Lake Huron. *North American Journal of Fisheries Management* 19: 881-900.
- Sly, J.H. and Schneider, C.P. 1984. The significance of seasonal changes on a modern cobble-gravel beach used by spawning lake trout, Lake Ontario. *Journal of Great Lakes Research* 10: 78-84.
- Smith, S.H. 1968. Species succession and fishery exploitation in the Great Lakes. *Journal of the Fisheries Research Board of Canada* 25: 667-693.

- Smith, B.R. and Tibbles, J.J. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936-78. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 1780-1801.
- Spangler, G.R., Robson, D.S., and Regier, H.A. 1980. Estimates of lamprey-induced mortality in whitefish, *Coregonus clupeaformis*. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 2146-2150.
- Stauffer, T.M., and Wagner, W.C. 1979. Fish predation on lake trout eggs and fry in the Great Lakes, 1973-1978 Fisheries Research Report No. 1864, Michigan Department of Natural Resources, Fisheries Division.
- Steucke, E.W., Jr., Allison, L.H., Piper, R.G., Robertson, R., and Bowen, J.T. 1968. Effects of light and diet on the incidence of cataract in hatchery-reared lake trout. *The Progressive Fish Culturist* 30: 220-226.
- Stratus Consulting. 1999. Reproductive injuries to lake trout. (Chapter 7) In *Injuries to fishery resources, Lower Fox River/Green Bay Natural Resource Damage Assessment*. Final report to U.S. Fish and Wildlife Service, U.S. Department of Interior, Department Of Justice.
- Swanson, B.L., and Swedberg, D.V. 1980. Decline and recovery of Lake Superior Gull Island Reef lake trout (*Salvelinus namaycush*) population and the role of sea lamprey (*Petromyzon marinus*) predation. *Canadian Journal of Fisheries and Aquatic Sciences* 37:2074-2080.
- Swink, W.D. 1993. Effect of water temperature on sea lamprey growth and lake trout survival. *Transactions of the American Fisheries Society* 122: 1161-1166
- Swink, W.D. 2003. Host selection and lethality of attacks by sea lampreys (*Petromyzon marinus*) in laboratory studies. *Journal of Great Lakes Research* (In press).
- Swink, W.D., and Hanson, L.H. 1986. Survival from sea lamprey (*Petromyzon marinus*) predation by two strains of lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences* 43: 2528-2531.
- United States vs State of Michigan. 2000. Consent Decree, August 8, 2000. U.S. District Court, Western District of Michigan, Southern Division. Case No. 2:73 CV 26.
- Wagner, W.C. 1982. Lake trout spawning habitat in the Great Lakes. Fisheries Research Report No. 1904, Michigan Department of Natural Resources, Fisheries Division.
- Walters, C., and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 39-50.
- Wilberg, M.J., Hansen M.J., and Bronte, C.R. 2003. Historic and modern abundances of wild lean lake trout in Michigan waters of Lake Superior: implications for restoration goals. *North American Journal of Fisheries Management* 23:100-108.

- Willford, W.A., and eight co-authors. 1981. Introduction and summary. In *Chlorinated Hydrocarbons as a Factor in the reproduction and Survival of Lake Trout (Salvelinus namaycush) in Lake Michigan. Technical Paper No. 105*, U.S. Fish and Wildlife Service, ed. Washington, DC: U.S Government Printing Office. pp 1-7.
- Wilson, C.C., and Hebert, P.D.N. 1996. Phylogeographic origins of lake trout (*Salvelinus namaycush*) in eastern North America. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 2764-2775.
- Zhang, C., Brown, S.B., and Hara, T.J. 2001. Biochemical and physiological evidence that bile acids produced and released by lake char (*Salvelinus namaycush*) function as chemical signals. *Journal of Comparative Physiology and Biology* 171: 161-171.

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