Research priorities for lake trout restoration in Lake Ontario, 2022

Prepared by the Lake Ontario Technical Committee: Lake Trout Working Group

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Contributing Agencies

New York State Department of Environmental Conservation - *Cape Vincent Fisheries Station*

U.S Geological Survey - *Lake Ontario Biological Station*

U.S Fish and Wildlife Service - *Lower Great Lakes Fish and Wildlife Conservation Office*

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OVERVIEW

Restoration of a wild-produced lake trout population in Lake Ontario has not yet been accomplished; however, several benchmarks and management objectives have been met. Early management strategies focused on reducing predation on lake trout by sea lamprey and increasing the genetic diversity and size of the adult spawning population of lake trout. Given contemporary population estimates of stocked lake trout and the current state of the Lake Ontario ecosystem, the Lake Ontario Technical Committee (LOTC) Lake Trout Working Group reviewed the impediments to lake trout restoration and the research priorities identified in the previous management plan, *A Management Strategy for the Restoration of Lake Trout in Lake Ontario, 2014 Updat*e (Lantry et al., 2014). The Working Group identified current research needs and has made recommendations for an updated set of research priorities. Through a collaborative process involving the New York State Department of Environmental Conservation (NYSDEC), U.S Fish and Wildlife Service (USFWS), U.S. Geological Survey (USGS), Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (NDMNRF), and New York Sea Grant (NYSG), the Working Group identified research priorities, objectives, and recommendations to stimulate progress towards lake trout restoration in Lake Ontario. The Working Group overwhelmingly agreed that factors affecting early-life survival are currently limiting natural production. Additionally, four research priorities were identified as 1) Identify and evaluate lake trout spawning locations; 2) adopt standardized methods to collect early life stages of lake trout and record environmental variables at spawning locations; 3) identify relative impact of different impediments on early life survival with use of time series and cross gradient experiments; and 4) continue assessment of lake trout population dynamics. This review of restoration impediments and research priorities should be used to amend the most recent 2014 management strategy for lake trout restoration and guide future research priorities.

I. BACKGROUND/RATIONALE

Lake trout were extirpated from Lake Ontario in the 1950s due in part to overfishing, predation by parasitic sea lamprey *Petromyzon marinus*, thiamine deficiency and habitat degradation (Brown et al., 2005; Krueger et al., 1995a; Muir et al., 2012; Riley et al., 2011; Sullivan et al., 2021). Through extensive stocking and sea lamprey control efforts by Canada and the United States, a population of mainly hatchery-produced lake trout currently exists. A series of strategic plans (named after the year they were adopted - 1983,1990, and 1998 plans) guided management of lake trout (Schneider et al., 1983, 1990, 1998). These strategic plans focused on the continued suppression of sea lamprey, while increasing the size and genetic diversity of the spawning stock of lake trout. In 2014, the most recent management strategy was adopted in Lake Ontario. The 2014 management strategy called for increased stocking densities and optimization of stocking practices to build and maintain sufficient adult stock populations to facilitate natural reproduction (Lantry et al., 2014). The 2014 management strategy also identified the necessity of a stable forage base and supported the reintroduction of native forage species. Impediments to lake trout restoration and recommended action items were also detailed in the 2014 management strategy (Lantry et al., 2014).

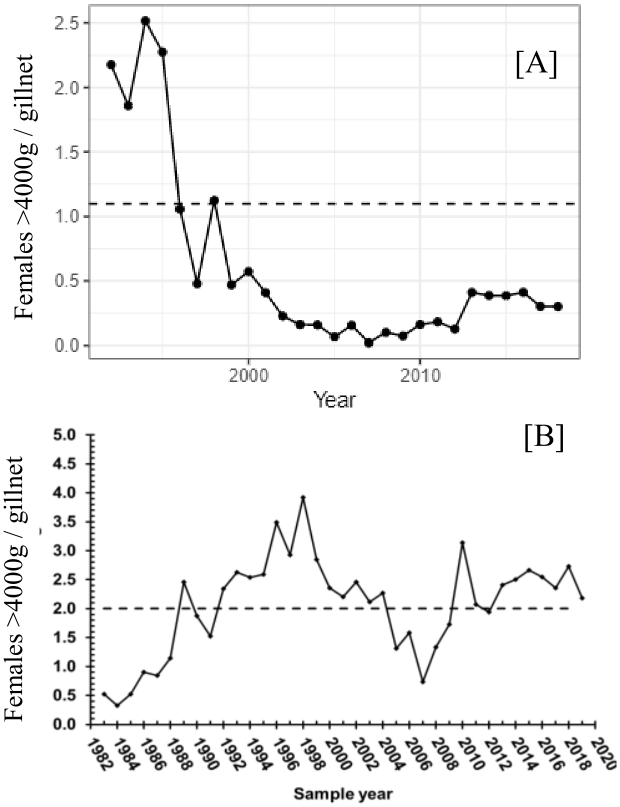

Figure 1. CPUE of adult female lake trout (> 4,000g/gillnet) on the north shore [A] and south shore [B] of Lake Ontario (Holden, 2019; Lantry et al., 2020). Dashed line represents the target CPUE of female/gillnet set by Schneider et al., 1983 and Lantry et al., 2014.Adult female lake trout targets differ in the U.S. and Canadian waters due to different gill net surveys sampling.

Since the implementation of the 2014 management strategy, hatchery-reared adult spawning stock abundances have met or exceeded restoration targets (CPUE = 2.0 females >4000g per gillnet) in U.S waters but have been consistently below targets in Canadian waters of Lake Ontario (CPUE = 1.1 females >4000 g; Figure 1; Holden, 2019; Lantry et al., 2020). Increases in abundance of adult lake trout in Lake Ontario have been due to stocking and reduction of sea lamprey predation (Lantry et al., 2014; Muir et al., 2012; Schneider, 1983). Sea lamprey wounding is currently below target levels in Lake Ontario (< 2 A1 wounds/100 lake trout; Figure 2); however, continuation of sea lamprey suppression is important for maintaining the adult lake trout population in Lake Ontario and likely needs to be implemented indefinitely (Holden, 2019; Lantry et al., 2020). Although lake trout spawning stock size has been above targets in U.S waters and sea lamprey predation has decreased, natural recruitment is still minimal and accounts for less than 10% (1998 plan-benchmark) of the lake trout stock (Lantry et al., 2020). With the adult spawning stock above target levels in the U.S., failure of natural production is likely driven by factors other than the size of the spawning population, most likely factors affecting survival of wild lake trout at early life stages (e.g., egg, free embryo, and post embryo; Marsden et al., 2021). The Lake Ontario Technical Committee (LOTC) Lake Trout Working Group, hereafter "the Working Group", recognizes the importance of continued stocking and sea lamprey control to maintain spawner stock size but does not believe these two factors (adult population size and sea lamprey predation) are impeding natural recruitment of lake trout in contemporary Lake Ontario. Considering this opinion, the Working Group focused on identifying current impediments and updating research priorities to best fit lake trout restoration goals. Specifically, the objectives of the Working Group were to; 1) review the current strategic plan and management objectives, 2) update the list of impediments to lake trout restoration, and 3) identify research needs and make recommendations for an updated set of research priorities.

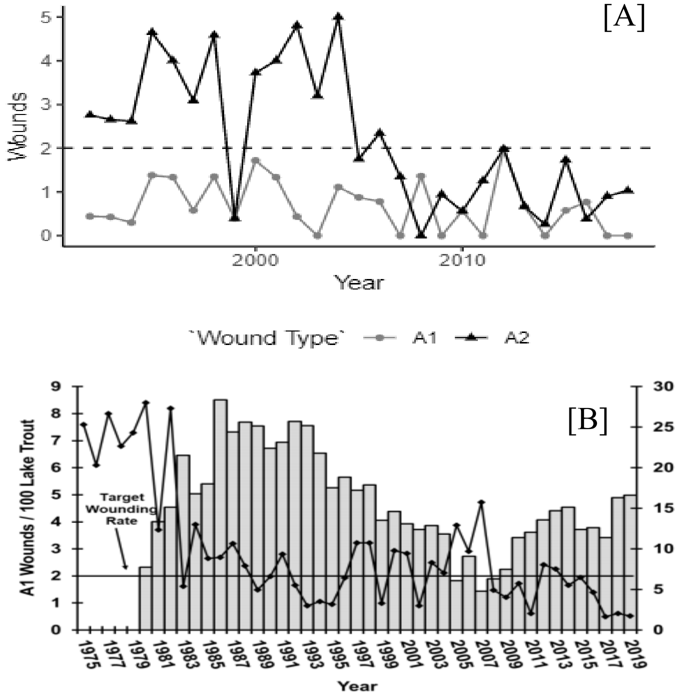

Figure 2. Wounding rate of Lake Ontario Lake trout on the north shore [A] and south shore [B]. Target wounding rate (2 wounds/100 lake trout) is represented by horizontal line (Holden, 2019, Lantry et al., 2020).

II. THE IMPEDIMENT TO LAKE TROUT RESTORATION

The 2014 management strategy for lake trout restoration identified nine impediments to lake trout restoration (Lantry et al., 2014). As our understanding of lake trout biology and behavior broadens, and the Lake Ontario ecosystem changes, these impediments require reevaluation. Herein, we present updated impediments to lake trout restoration in contemporary Lake Ontario based on multiple literature reviews that included the previous management strategies and current peer-reviewed journal articles.

Failure of early life survival –

- Lake trout restoration in Lake Ontario has focused on the mature, adult life stage of lake trout for the past 50 years (Lantry et al., 2014; Schneider et al., 1983, 1990, 1998). Given the consistent catch of hatchery-reared mature female spawners over the past 10 years (exceeding restoration goals in NY; Lantry et al., 2020), failure of survival at an earlier life stage is likely the largest impediment to lake trout restoration in contemporary Lake Ontario (Figure 3). However, although lake trout eggs have been sampled at multiple sites in Lake Ontario (Fitzsimons, 1995a), free embryo and post-embryo (formally referred to as fry; See terminology corrections in Marsden et al. 2021) production has been studied at very few sites (e.g., Marsden et al., 1988) and survey methods have not been standardized. Several methods to collect eggs and post-embryo have been used experimentally in Lake Ontario (e.g., Furgal, 2019), and egg bags have been used to collect standardized density data for eggs (e.g., Marsden and Krueger 1991, Marsden et al. 2016); however, they are challenging to use for assessment surveys because they require scuba divers. Sampling of lake trout eggs and post-embryo stages occurs at times of the year when storm and wave action, cold temperatures, and ice formation hinder researchers' ability to access areas where eggs and post-embryo stages are found. The severe weather conditions during sampling are an obstacle in collection of these life stages and new collection methods and standardized practices are likely necessary to accomplish large-scale surveys. The driving mechanism for failure of early life stages is not well understood and warrants further research. Factors such as degradation of spawning habitat, insufficient thiamine concentrations in eggs and post-embryo stages, predation on eggs and post-embryo, and a lack of resources (e.g., sufficient forage) for post-embryo life stages all likely play a role in impeding successful recruitment.

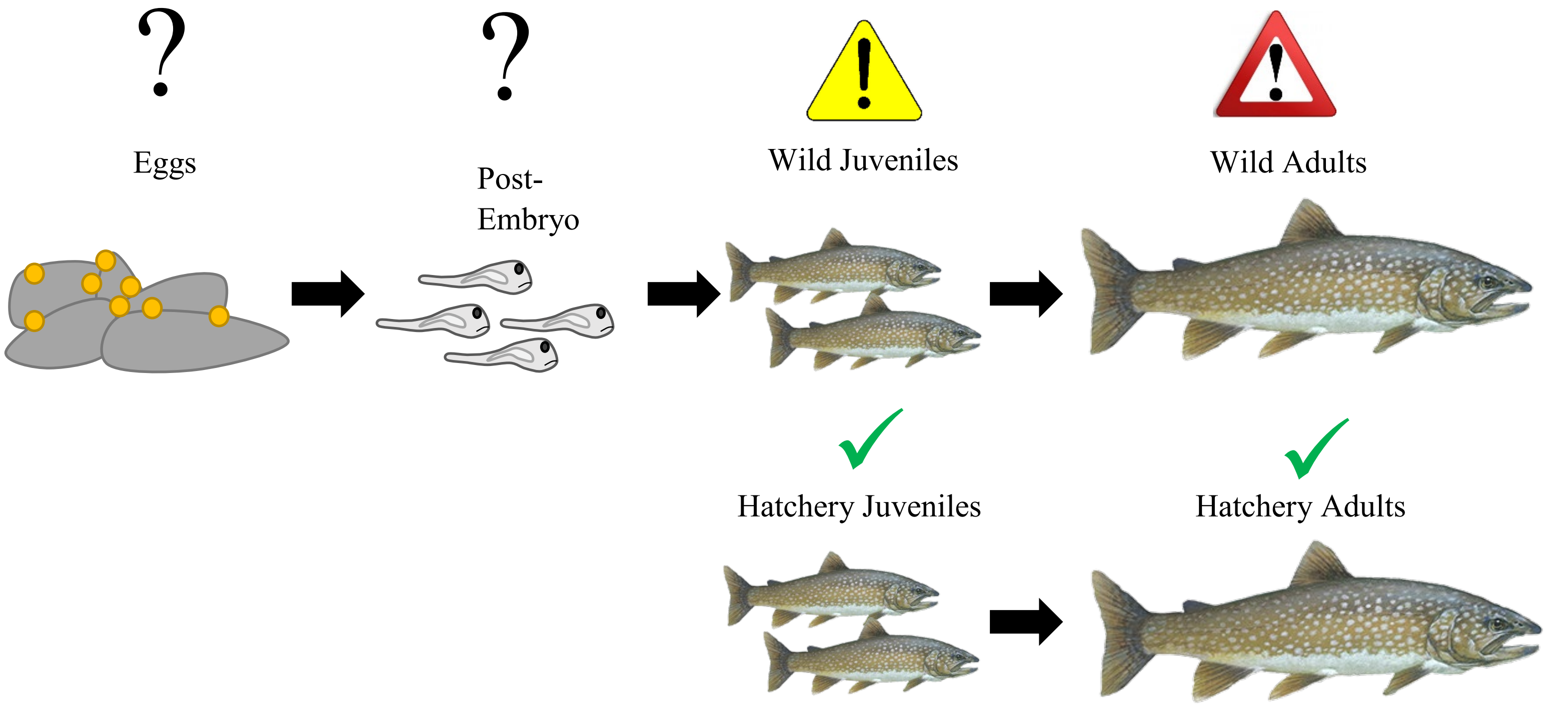

Figure 3. Conceptual model of our understanding of the state of lake trout life stages in contemporary Lake Ontario given wild and hatchery-reared individuals that are collected in annual surveys. Symbols represent life stages that are collected in current surveys with green check marks representing high frequency, yellow triangle representing low frequency, red triangle representing rare or not detectable, and question mark representing a life stage that is not targeted in annual surveys.

Mechanisms for failure of early life stages

Degradation of spawning and egg incubation habitat –

Lake trout typically spawn on rocky shoals and shallow reefs in water depths of less than 15m (Marsden et al., 1995; Riley et al., 2019). Piled cobbles and rubble create interstitial spaces used for incubation and protection of eggs from strong currents and predators as they incubate for 5-6 months (Binder et al., 2021; Riley et al., 2019). However, changes to the Great Lakes watershed (e.g., deforestation, agricultural and urban sprawl) have caused an increase in sediment input and continued resuspension of these sediments causes infilling of interstices in Lake Ontario (Figure 4; Furgal, 2019; Krueger et al., 1995a; Muir et al., 2012). In areas where high wind/wave action reaches bottom substrates (i.e., < 5 m), interstices flush naturally; however, these areas may not always be suitable for successful lake trout egg incubation due to strong currents which damage or remove eggs from interstitial spaces (Fitzsimons and Marsden, 2014; Riley et al., 2019; Roseman et al., 2001). Similarly, invasive species such as dreissenid mussels also degrade nearshore spawning habitat, acting in a similar way as sediments by blocking interstices but also by reducing the quality of water near eggs incubating in interstices (Marsden and Chotkowski, 2001). Consistent near-shore ice coverage may protect incubating eggs in shallow-nearshore rocky spawning habitats from late fall and winter from storm-driven currents, granted, a certain amount of currents are necessary to keep substrates free of silt (Fitzsimons and Marsden, 2014). Climate change has created inconsistent ice coverage with an overall shortening of winter conditions, forming ice later in the year and for shorter durations in contemporary Lake Ontario, potentially leaving eggs susceptible to mortality and removal from spawning habitats (Brown et al., 2021). Areas of spawning habitat that are in deeper water (i.e., > 5 m) and protected from strong wind driven currents, may be degraded by sediments that can lower survival for incubating eggs (Gatch et al., 2020, Weidel et al., in prep). In other Great Lakes, spawning habitat remediation and enhancement have been successful in increasing the quality of spawning habitat and increasing egg deposition by lake trout and other lithophilic spawners, suggesting habitat enhancement may be a viable tool in Lake Ontario to increase lake trout egg deposition on quality bottom substrates (Fitzsimons, 1996; Marsden et al., 2016; McLean et al., 2015). Spawning habitat remediation is typically achieved though augmentation of spawning materials, but recent studies have found cleaning of degraded substrates to be effective in

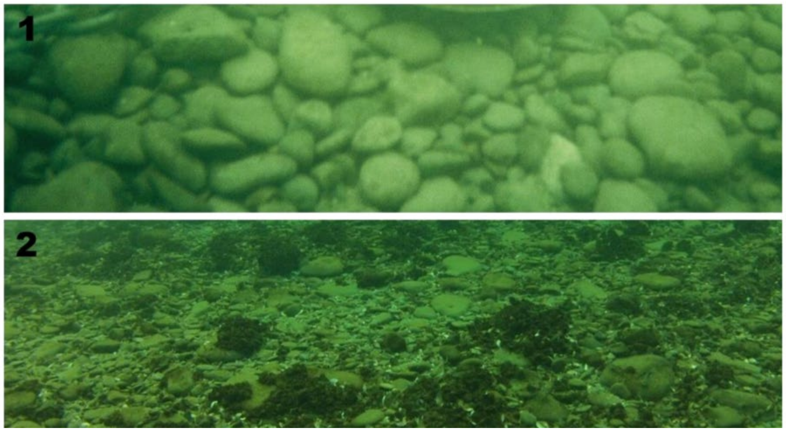

Figure 4. Photo of spawning substrate from the Lake Ontario nearshore Stony Island spawning reef (~5m) in 1987 (panel 1; courtesy. J. Ellen Marsden) and again in 2017 (panel 2; Furgal, 2019).

increasing egg deposition, warranting further research to verify cleaning as a method for habitat remediation (Baetz et al., 2020; Gatch et al., 2021).

Insufficient thiamine for eggs and juvenile lake trout –

Thiamine deficiency complex (TDC) is a nutritional disorder that occurs when insufficient levels of vitamin B1 (thiamine) leads to a disruption of key thiamine-dependent metabolic pathways (Bettendorff 2013). Severe thiamine deficiency has been shown to induce acute mortality in early life stages of salmonines and has been implicated as a source of recruitment failure for lake trout and Atlantic salmon in Great Lakes, including Lake Ontario (Fitzsimons 1995b; Honeyfield et al. 2005a; Riley et al. 2011; Futia and Rinchard 2019; Harder et al. 2018). Thiamine levels in Lake Ontario lake trout have increased since reaching their lowest recorded levels in 1998 (Fitzsimons et al. 2009b; Futia and Rinchard 2019). However, a recent evaluation of thiamine deficiency in Lake Ontario salmonines revealed that TDC induced acute mortality still occurred in a portion of lake trout free embryos, and that most females produced eggs with thiamine concentrations below those seen in populations considered to be thiamine replete (Figure 5; Fitzsimons et al. 2010; Futia and Rinchard 2019). Furthermore, while much effort has been made to estimate the effects of TDC on direct acute mortality and secondary (sub-lethal) effects of TDC have been investigated in laboratory settings (Fitzsimons 1995b; Jaroszewska et al. 2009; Carvalho et al. 2009; Fitzsimons et al. 2009a; Lee et al. 2009; Ottinger et al. 2014), considerably less effort has been made to measure the effect of TDC on survival in the wild, where mortality may be much higher (Balk et al. 2016; Ivan et al. 2018). Conversely, the abundance of thiamine in natural waters and early exogenous feeding by lake trout free embryos on thiamine-rich zooplankton may mitigate thiamine levels prior to the potential onset of TDC (Ladago et al. 2016). Although the exact cause for TDC in lake trout remains uncertain (Harder et al. 2018), strong correlations have been made between TDC and diets consisting mainly of non-native alewife (*Alosa pseudoharengus*; Honeyfield et al. 2005; Fitzsimons et al. 2009a, 2010). While the recovery of deepwater sculpin (*Myoxocephalus thompsonii*) populations (Weidel et al. 2017) and the invasion and proliferation of round goby (*Neogobius melanostomus*) have led to an increase in diversity of prey items consumed by lake trout in Lake Ontario (Dietrich et al. 2006; Mumby et al. 2018), alewife still comprise 83.9 – 96.7% lake trout diets (Nawrocki et al. 2020), a range previously shown to cause TDC in this species (Honeyfield et al. 2005). As such, TDC may still be serving as an impediment to lake trout restoration efforts in Lake Ontario and

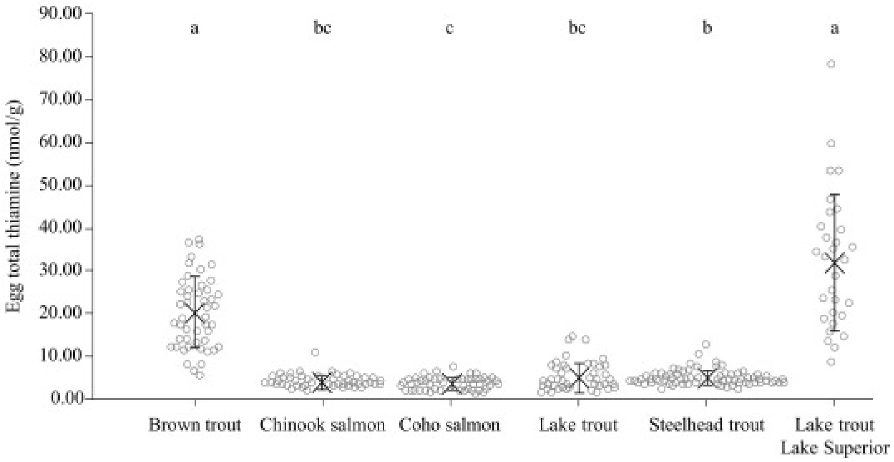

Figure 5. Egg total thiamine concentrations of salmonines from Lake Ontario and a thiamine replete population of lake trout from Lake Superior (Futia and Rinchard, 2019)

continued monitoring of thiamine concentrations and investigations into the rates of TDC induced mortality in the wild are needed.

Predation of egg and juvenile lake trout –

Species such as slimy sculpin (*Cottus cognatus*), round goby, rainbow smelt (*Osmerus mordax*), crayfish, and alewife prey on lake trout eggs and post-embryo, and if distributions of these species coincide with lake trout egg deposition or hatch, predation may be severe (Chotkowski and Marsden, 1999; Fitzsimons et al., 2002; Krueger et al., 1995b; Savino et al., 1999). Unfortunately, quantifying predation of lake trout eggs and post-embryo is challenging because they rapidly degrade (e.g., < 3 hours) in the guts of predators, making them unidentifiable unless predators are captured quickly after consumption (Krueger et al., 1995b). Due to the challenges associated with quantifying predation on lake trout eggs and post-embryos (e.g., fast digestion rates), most estimates of egg loss due to predation are derived from laboratory experiments and statistical models and not *in situ* observations (Savino et al., 1999; Fitzsimons et al. 2006), highlighting the uncertainty of the effect of predation on wild lake trout recruitment. Predation of juvenile lake trout age-1 and greater should be easier to detect due to slower digestion rates; however, routine diet analysis of Lake Ontario salmonids shows very little evidence of predation or cannibalism (Mumby et al., 2018), pointing to earlier life stages (i.e., egg and post-embryo) as potential bottlenecks if predation is an impediment to lake trout restoration.

Resources for juvenile lake trout –

Lake trout free embryos and early post-embryos (age-0) feed mainly on Bosmina and calanoid and cyclopoid copepods while absorbing their yolk sac (Ladago et al., 2016). Since the early 1990s, epilimnetic zooplankton abundance has decreased 10-fold, potentially limiting the resources available to newly hatched free embryos (Holeck et al., 2010, 2020). Alternatively, variability in the timing of spring warming and lake trout hatch may create a match/mismatch of zooplankton emergence with hatch leading to starvation of wild lake trout (Cushing, 1990; Simard et al., 2020). However, lake trout are buffered from starvation for several weeks post-hatch by their large yolk sac, unlike coregonine larvae. By summer (> 30 mm TL) post-embryos switch to mostly consuming *Mysis diluviana* (Marsden et al. in revision). If Mysis are not available, young-of-year are unlikely to acquire sufficient resources to survive through their first winter. Once lake trout reach age-1, however, lake trout begin to switch from *Mysis* to juvenile alewife and rainbow smelt, which are readily available. Therefore, if prey availability is impeding survival of juvenile lake trout, the critical period is likely occurring before age-1 (Elrod, 1983; Elrod and O'Gorman, 1991; Weidel et al., 2020).

Thermal influence on egg development –

Lake trout eggs incubate from October to May; because egg development rates are driven by temperature, even small changes in the timing of water cooling in fall and warming in spring may substantially alter the timing of hatch (Goetz et al., 2021). As a result, under warming conditions lake trout free embryos may hatch at suboptimal times relative to peak abundance of zooplankton and experience a prey match-mismatch (Pothoven 2020). Although changes in incubation temperatures affect the development and survival of other salmonines such as cisco (*Coregonus artedi*) and lake whitefish (*Coregonus clupeaformis*; Karjalainen et al., 2015; Stewart et al. 2021), it is unknown to what extent changing water temperatures will in fact affect lake trout development and survival, particularly if eggs are spawned at deeper depths that are not affected by early spring warming.

Epigenetic effects on stocked lake trout –

The tendency for hatchery-reared salmonids to exhibit different phenotypic and physiological characteristics and experience reduced fitness relative to wild conspecifics has been well documented (Araki et al. 2007, 2008; Fraser 2008; Araki and Schmid 2010; Lorenzen et al. 2012). As a result, much effort has been made to implement management practices that mitigate sources of unintended genetic changes (e.g., domestication selection or genetic drift) in fish while in captivity (Fraser 2008; Attard et al. 2016; Milla et al. 2020). However, there is a growing body of evidence demonstrating that captive spawning and rearing can cause gene expression profiles and epigenetic characteristics of captive fish to differ substantially from their wild progenitors and conspecifics without any detectable changes to the underlying DNA sequence (Sauvage et al. 2010; Chittenden et al. 2010; Christie et al. 2016; Leitwein et al. 2021). These epigenetic responses to hatchery-rearing have been shown to alter the expression or methylation of genes involved in immune function, developmental pathways, metabolism, visual acuity, and other important biological processes, which may contribute to reduced post stocking performance (Le Luyer et al. 2017; Best et al. 2018; Gavery et al. 2018; Rodriguez Barreto et al. 2019). Importantly, the epigenetic changes induced by hatchery rearing in salmonines appear to be heritable (Gavery et al. 2018; Rodriguez Barreto et al. 2019; Nilsson et al. 2021), which may reduce the recruitment success of the wild-origin progeny of hatchery-reared fish (Araki et al. 2008; Leitwein et al. 2021). While the hatchery methods currently implemented in the federal hatcheries to rear lake trout have proven effective in maintaining genetic diversity (Page et al. 2004, 2005), the presence and extent of epigenetic alterations induced by hatchery rearing in this species remains unexplored. Although the extent to which transgenerational epigenetic effects of hatchery-rearing impact reproductive fitness in the wild is still poorly understood, the potential detriments that might arise from such effects merit further investigation. Furthermore, the prevalence of this phenomenon reported in other salmonines suggest that it is likely that similar epigenetic perturbations are occurring in the lake trout being used in restoration stocking efforts in Lake Ontario, which may be contributing to poor recruitment of wild-born lake trout.

Competition between hatchery-reared and wild-produced juveniles –

One stocking practice is to release hatchery-reared lake trout in close proximity to known spawning reefs used by adult lake trout. This practice is thought to help recruit lake trout to spawning areas from where they were stocked, similar to homing in other salmonids. Recent acoustic telemetry work determined that post-stocked juvenile lake trout could stay near stocking sites for months before moving to deepwater habitat (Gatch et al., 2022). If wild lake trout are hatching on spawning habitat near stocking sites, the wild young-of-year may be prey for hatchery lake trout, which are stocked at age-1. Similarly, competition for resources (e.g., *Mysis*) may occur between wild young-of-year and hatchery-reared age-1 juveniles if their habitat[2] ranges overlap.

III. RESEARCH PRIORITIES AND RECOMMENDATIONS

Given current impediments to lake trout restoration in Lake Ontario and the research needs they present, the Working Group identified four research priorities. Identifying lake trout spawning distribution across the lake, and in what habitats they currently deposit eggs are paramount to the subsequent research priorities. The research priorities are presented in the order that they should be accomplished to address the impediments to wild recruitment of lake trout in Lake Ontario. It is likely that all impediments previously stated in this document have some effect on early life survival of lake trout, however, it is imperative that we determine the relative ranking or importance of each impediment on early life survival thereby allowing managers to best allocate limited resources to remediation actions or management levers. The priorities listed below use a stepwise approach to quantifying the relative impact of impediments to lake trout restoration.

Research Priority 1: Identify and evaluate lake trout spawning locations

Objectives:

a) Determine the spatial distribution of Lake Ontario lake trout spawning habitat at the lake scale.
b) Determine site-specific habitat (e.g., depth, substrate, flow, aspect) where lake trout are depositing eggs.

Recommendations:

- Use a lake-wide acoustic array (already in place) to characterize the lake-scale distribution of lake trout spawning (high spatial coverage with low site-specific inference-positioning)
- Use fine-scale acoustic arrays (i.e., InnovaSea VPS; low spatial coverage with very high geo-positioning precision) to identify specific habitats where Lake Trout are depositing eggs
- Create bathymetric maps and evaluate physical substrate types in areas identified as primary spawning sites.

Research Priority 2: Adopt standardized methods to collect early life stages of lake trout and record environmental variables at spawning locations

Objectives:

a) Develop standardized quantitative methods for collecting egg and post-hatch juveniles that can be adapted for different types of spawning habitats.
b) Implement methods to track environmental conditions during egg incubation and post-hatch time periods (e.g., temperature, sedimentation rate, physical disturbance, prey availability, predation rate).

Recommendations:

- Evaluate existing or develop methods to quantify habitat specific lake trout density at various stages potentially including egg deposition, incubating eggs, hatch, free embryo, post embryo and age 0. Methods should be standardized among all research groups.
- Methods used to collect early life stages should rely on vessel deployment/recovery due to limited SCUBA resources.
- Creation of annual surveys at site-specific locations to measure early life survival should be considered.

Research Priority 3: Identify relative impact of different impediments on early life survival with use of time series and cross gradient experiments

Objectives:

a) Establish long-term monitoring sites (recognized in research priority one) to track life stage survival across years
b) Determine the role of spawning habitat degradation and thiamine deficiency on egg and free embryo survival at monitoring sites using control and manipulation treatments.
c) Determine the role of environmental and biological factors such as predation of lake trout, prey availability, and conspecific competition at early life stages at monitoring sites.
d) Quantify seasonal prey abundance (e.g., invertebrate biomass) and timing of prey emergence at monitoring sites.

e) Identify the role of epigenetic effects of hatchery rearing on lake trout survival and successful reproduction after release in Lake Ontario.

f) Rank the impediments to early life survival

Recommendations:

- Develop spawning substrate manipulation studies using cleaning devices or augmenting existing habitat to determine the effect of degraded spawning substrates on egg survival.
- Support the continuation of lake-wide thiamine sampling from eggs, free embryo, post-embryo, juvenile, and adult lake trout.
- Develop thiamine-based manipulation studies using thiamine enrichment on spawning areas or in pre-spawn females to determine the effect of thiamine on post-hatch survival.
- Support studies measuring biological interactions of early life stages with predator and prey near spawning locations (e.g., impact of predator abundance and predation on early life stages).
- Evaluate hatchery practices that induce epigenetic shifts in gene expression that may affect survival and reproductive success of hatchery-reared lake trout (e.g., pseudo predators within hatchery raceways).

Research Priority 4: Continue assessment of lake trout population dynamics

Objectives:

a) Develop model-based estimates of lake trout density and biomass for wild reproduced fish and individual strains of stocked lake trout.
b) Quantify and annually report on lamprey wounding of the adult lake trout population.
c) Develop year class strength indices for naturally reproduced lake trout from historical data.

Recommendations:

- Evaluate current annual survey methods with regards to reducing redundancy, standardizing methods across agencies and countries, and providing information needs noted above.
- Develop model-based estimates of lake trout density and biomass for wild reproduced fish and stocked strains.
- Develop and implement methods to determine natal origin (stocked vs. wild) of unmarked lake trout (e.g., otolith microchemistry, genetic methods) and identify a lab that can handle high throughput otolith isotope analysis for natal origin (i.e., stocked vs wild).
- Agree upon standardized reporting metrics and combine the OMNDMNRF and NYSDEC annual lake trout reports.

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