Growth Evaluation And Standardized Assessment Of Juvenile Lake Trout In Lake Champlain

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GROWTH EVALUATION AND STANDARDIZED ASSESSMENT OF JUVENILE LAKE TROUT IN LAKE CHAMPLAIN

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Abstract

Restoration and recovery of lake trout (*Salvelinus namaycush*) has been the focus of research and management in the Great Lakes and Lake Champlain since populations collapsed in the late 19th and 20th centuries. Wild juvenile lake trout recruitment was discovered in Lake Champlain in 2015 after 42 years of stocking efforts. Intensive biweekly bottom trawl sampling during the ice-free season was conducted from 2015 to 2018 to assess the extent of wild recruitment at three different sampling areas (north, central, south) of the Main Lake. The collection of wild and stocked lake trout in bottom trawls enabled analysis and comparison of growth and distribution between wild and stocked juveniles. Lake trout stocked at age-0 in Lake Champlain have established an adult population, therefore if growth of wild lake trout is similar to that of stocked fish of similar size, we assume they will have similar survival. To assess the potential for wild lake trout to survive past their first winter, a critical period in fish life history, I compared growth of juvenile lake trout in Lake Champlain spatially, seasonally, and by origin (wild or stocked). No consistent differences were found in growth rates between wild and stocked juveniles of similar size. In addition, and contrary to general assumptions, the data indicate that juvenile lake trout continue to grow in length while maintaining condition over the winter and therefore must be actively feeding. The percentage of wild juveniles was markedly higher in the central sampling area than the north and south, but no trend in growth was evident among sampling areas. The data from intensive bottom trawling also provided insight into the seasonal depth distribution of juvenile lake trout that can be used to design future juvenile assessments in Lake Champlain. I compared the distribution of wild and stocked lake trout by depth and temperature in the central sampling area of Lake Champlain based on seasonal changes in thermal stratification. Differences in distribution were most pronounced during thermal stratification, when wild lake trout were significantly more abundant in warm, shallow depths and stocked lake trout were more abundant in cold, deep areas. Overall, my results suggest that wild juvenile lake trout survival should be comparable to stocked juveniles in Lake Champlain, and differences in depth and temperature preferences can be used to develop a standardized survey to assess recruitment of wild lake trout.

Citations

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CHAPTER 1: LITERATURE REVIEW

Introduction

Lake trout (*Salvelinus namaycush*) are a top predator and were an important part of the commercial fishing industry in the Laurentian Great Lakes and Lake Champlain. In the 1950s, overharvesting, eutrophication, and predation by invasive sea lamprey (*Petromyzon marinus*) led to the decimation of their populations, and extirpation in the lower four Great Lakes (Smith and Tibbles 1980, Coble et al., 1990, Eshenroder 1992). In Lake Champlain, the lake trout population decline began in the late 1800s, with lake trout extirpation in the early 1900s in the absence of a major commercial fishery (Plosila and Anderson 1985, Marsden and Langdon 2012). Lake trout restoration efforts began in the Great Lakes and Lake Champlain with sporadic stocking of lake trout in the 1950s (Hansen 1999, Marsden and Langdon 2012). Annual stocking of lake trout began in 1951 in Lake Superior, 1965 in Lake Michigan, 1972 in Lake Ontario, 1973 in Lake Champlain, 1974 in Lake Huron, and 1978 in Lake Erie (Plosila and Anderson 1985, Cornelius et al., 1995, Elrod et al., 1995, Eshenroder et al., 1995a, Holey et al., 1995, Hansen 1999). Long-term sea lamprey control programs were initiated in the Great Lakes in 1958 and in Lake Champlain in 2001 to reduce the sea lamprey wounding on salmonids and to improve lake trout growth and survival (Ferreri et al., 1995, Marsden et al., 2003).

The combination of lake trout stocking and sea lamprey programs was successful in establishing adult lake trout populations in the Great Lakes and Lake Champlain, with documentation of wild reproduction of stocked lake trout everywhere except Lake Erie

(Marsden et al., 1988, Cornelius et al., 1995, Johnson and VanAmberg 1995, Schram et al., 1995, Ellrott and Marsden 2004). Sustained natural recruitment and survival of wild lake trout to the adult population has only been successful in Lake Superior and sections of Lake Huron where wild populations were still present (Hansen et al., 1995, Reid et al., 2001, Riley et al., 2007). Recruitment of wild juvenile lake trout past the first winter in lakes where lake trout were extirpated has not been documented until recently, with even fewer lakes reporting survival of wild lake trout to the adult population (Rybicki 1991, Roseman et al., 2009, Hanson et al., 2013, Landsman et al., 2017, Marsden et al., 2018).

Although natural recruitment has been documented in lakes Michigan, Ontario, and Champlain, stocking is the primary source of lake trout in each lake (Marsden et al., 1988, Hanson et al., 2013, Marsden et al., 2018). The inability of stocked lake trout populations to develop sustainable wild populations in extirpated lakes has been a focus of extensive research and evaluation of spawning and recruitment in the Great Lakes and Lake Champlain (Fitzsimons 1995a, Ellrott and Marsden 2004, Sitar and He 2006).

Geographic range and diversity of lake trout

Expansion of lake trout occurred during and after the last major glacial period, as the current native range was almost entirely covered by ice during the Pleistocene glaciation (Lindsey 1964). Lake trout likely used refugia along the Appalachian Mountains and upper Mississippi River for survival during the glacial period and used large glacial lakes and waterways as the glacial boundary receded to migrate to their current range (Lindsey 1964, Khan and Qadri 1971). Introducing lake trout outside their native range became popular in the early 20th century, and resulted in expansion of lake trout populations to the western region of the United States, and several South American and European lakes (Figures 1.1 and 1.2; Welcomme 1988, Crossman 1995, Martinez et al., 2009). In most of these lakes, lake trout introductions have produced undesirable effects. For example, lake trout introduced to several lakes in the western United States have outcompeted and, in some cases, have eliminated salmonids native to the region and the waterbody (Martinez et al., 2009, Hansen et al., 2016a).

Lake trout are successful as an introduced species in part due to their behavioral, morphometric, and life history plasticity that allows them to fill available niches in various environments (Martin and Olver 1980, Eshenroder et al., 1995b, Muir et al., 2016). Lake trout are successful invaders because they are generalist predators, but colonization success is also improved when the system into which lake trout are introduced has a simple community structure with low species richness, providing more available niches and fewer potential predators of their eggs and embryos (Evans and Olver 1995, Pazzia et al., 2002). When introduced to a new area, lake trout colonize effectively by outcompeting native residents (Martinez et al., 2009). The combination of abundant prey, limited predation, and being a successful competitor makes lake trout an excellent colonizer of new environments.

The diverse habitat historically found in the Great Lakes allowed lake trout to adapt behaviorally and morphometrically to fill multiple niches, resulting in several sympatric morphotypes in each lake (Muir et al., 2014, Hansen et al., 2016b). Several of these unique morphotypes were lost when lake trout were extirpated (Krueger et al., 1995a). Therefore, stocking and restoration is limited to the remaining morphotypes (Evans and Olver 1995). Without the unique lake trout morphotypes available to match the habitats and niches previously utilized in the Great Lakes, the complete restoration of lake trout to their previously occupied roles is extremely unlikely. Furthermore, the loss of historic habitat and prey resources combined with the invasion and introduction of additional species to the community makes restoration of all morphotypes functionally impossible (Fitzsimons 1995b, Bronte et al., 2003a, Zimmerman and Krueger 2009).

Lake trout diversity and life history

Lake trout morphotypes

Lake trout spawning habitat and timing are highly variable among lakes and morphotypes. Morphotypes of lake trout are separated and maintained by differences in resource use in a waterbody (Skulason and Smith 1995). Differences in resource use can be habitat-specific, such as benthic versus pelagic foragers, prey-specific, such as piscivores or planktivores, or a combination of the two. Multiple lake trout morphotypes are found in large, oligotrophic lakes with simple community structures and diverse habitat such as Lake Superior, Great Slave Lake, and Great Bear Lake (Blackie et al., 2003, Zimmerman et al., 2009, Hansen et al., 2016b). Lake Superior, once home to as many as ten distinct lake trout morphs, now has only four morphs (lean, humper, siscowet, and redfin) to occupy the available spawning habitat and access forage resources (Goodier 1981, Hansen et al., 2016b, Muir et al., 2016). Great Slave Lake, the deepest lake in North America, is home to three (lean, humper, and siscowet) distinct lake trout morphs (Zimmerman et al., 2009). Great Bear Lake, the largest Canadian lake, has four shallow-water morphs distinguished by foraging habitat (benthic vs pelagic) and by prey source (insectivore vs piscivore; Chavarie et al., 2016).

Lake trout morphotypes can vary by size, coloration, osteology, morphometry, habitat depth, spawning time, and by differing fat content (Lawrie and Rahrer 1973, Goodier 1981, Burnham-Curtis and Bronte 1996, Moore and Bronte 2001, Zimmerman et al., 2006, Sitar et al., 2008, Goetz et al., 2010, Muir et al., 2016). Siscowet lake trout are large piscivores, inhabiting some of the deepest regions of Lake Superior and Great Slave Lake. Siscowets have a higher fat content and deeper body than the lean lake trout, a shallow-water piscivore (Zimmerman et al., 2006, Bronte and Moore 2007, Goetz et al., 2010, Muir et al., 2016). Humpers are a deepwater lake trout, named for primarily inhabiting deep offshore "humps" or "reefs", with lower fat content than siscowets, foraging on zooplankton and insects, and are smaller in size than lean lake trout (Burnham-Curtis and Bronte 1996, Zimmerman et al 2006). Most research has focused primarily on the lean morphotype because they are more common than the other lake trout morphotypes, although recent research in Lake Superior and Great Slave Lake has included the deepwater morphs (Muir et al., 2014, Hansen et al., 2016b, Chavarie et al., 2019).

Early life history terminology and developmental stages in lake trout

The terminology used for early life history and developmental stages of lake trout is difficult to decipher in scientific literature due to the use of general terms that are neither directly relevant to lake trout nor specific enough to classify aspects of developmental growth. For the remainder of this thesis, the following terms and subsequent definitions, proposed by Marsden et al., (in press - a), are used to define developmental stages of lake trout. *Eggs* are unfertilized (haploid) gametes released from female lake trout over spawning substrate. *Pre-hatch embryo* refers to a fertilized egg incubating within substrate overwinter. Lake trout become *post-hatch/free embryos* when they hatch, and carry an external yolk-sac. Free embryos typically stay within the spawning substrate, but can avoid predators. Once the yolk-sac is fully absorbed, lake trout are labeled as *post-embryos*. Lake trout are distinguished as young-of-year or age-0 from the time they leave the spawning reef until the end of the year, December 31. Lake trout are defined as *juveniles* after December 31 and remain juveniles until they reach reproductive maturity, i.e., adulthood. *Adult* lake trout travel to spawning sites in the fall to reproduce. When lake trout no longer reproduce, they are termed *senescent*.

Lake trout spawning preferences

Lake trout spawn primarily in lakes, although there are several populations that spawn in rivers (Goodier 1981, Jones et al., 2018). Most lake trout spawn in the fall from September to December, during or after the thermal stratification breakdown and when temperatures approach 10ºC (Gunn 1995). However, siscowet lake trout, a deep-water morphotype found in Lake Superior, have been documented in spawning condition in April (Bronte 1993). Lake trout are iteroparous broadcast spawners, releasing their eggs over rocky crevices in the substrate to incubate over the winter. Spawning typically occurs along rocky shorelines or mid-lake shoals. Preferences for substrate features such as substrate particle size, area, and depth, vary considerably within and among lakes (Martin and Olver 1980, Marsden et al., 1995a, Jones et al., 2018). Ideal lake trout spawning areas are primarily on cobble with deep interstitial spaces and good water quality near a steep slope with access to deeper water and prey items for post-embryos (Marsden and Krueger 1991, Marsden et al., in press - b, Fitzsimons 1995a). Deep interstitial crevices in cobble and large boulders provide protection from epifaunal predators and wave turbulence (Claramunt et al., 2005, Jonas et al., 2005). Man-made structures, such as breakwalls and artificial reefs, have also been found to be successful lake trout spawning habitat (Marsden et al., 1995b). However, nearshore spawning sites such as breakwalls and rocky shorelines are more likely than offshore locations to be affected by physical changes to the watershed, such as urbanization and logging (Krueger et al., 1995a). Deterioration and human alteration of the watershed can lead to increased sedimentation and siltation, filling in interstitial spaces with silt and causing lake trout pre-hatch embryos to suffocate (Gunn 1995, Bronte et al., 2003b).

Not all spawning lake trout select sites with cobble, interstitial crevices, and a steep slope. Some lake trout also use atypical substrates such as bedrock, boulders, and macrophytes for spawning (Beauchamp et al., 1992, Marsden 1994, Binder et al., 2018). Introduced lake trout in lakes with low species diversity may be more likely to use atypical spawning substrate because there are few or no predators of pre-hatch embryos and free embryos in the system (Simard 2017). The flexibility to use a variety of spawning habitats enhances the ability of lake trout to colonize new systems effectively.

Lake trout spawning in the Great Lakes

Historically, lake trout morphotypes each spawned in different areas of the Great Lakes due to their preference for shallow, intermediate, or deep-water spawning sites (Eshenroder et al., 1995a, Krueger and Ihssen 1995, Muir et al., 2014). After the decimation of lake trout in the Great Lakes, most of these morphotypes were lost. After the initial stocking effort in the Great Lakes, stocked spawning lake trout exhibited weak homing behavior and many spawned on nearshore cobble reefs close to stocking sites (Krueger et al., 1986, Bronte et al., 2003b, Zimmerman and Krueger 2009). Great Lakes stocking strategies were subsequently modified to also release lake trout at historic spawning areas and along offshore reefs to expand colonization of additional spawning sites (Bronte et al., 2007). Multiple lake trout strains from additional lakes were also used to increase genetic diversity (Holey et al., 1995, Elrod et al., 1996).

Sampling methods to assess presence of spawning lake trout and pre-hatch embryos in the Great Lakes have focused primarily at or near shallow, nearshore spawning reefs due to the difficulty of sampling at deep, offshore sites. Sampling occurs in the fall for adults and pre-hatch embryos, or in the spring for free embryos. Advances in technology, such as underwater cameras, satellite imagery, acoustic telemetry, and remotely operated vehicles, have been used to improve assessment and visualization of habitat and spawning activity at nearshore, intermediate, and deepwater spawning sites (Ellrott and Marsden 2004, Janssen et al., 2006, Grimm et al., 2016, Johnson et al., 2018).

Development of acoustic telemetry technology has been instrumental for assessing and discovering new lake trout spawning habitat (Binder et al., 2018). Acoustic telemetry involves tracking aquatic organisms by surgically attaching or implanting acoustic transmitters and using individual receivers or receiver arrays to detect the signals from the tagged individuals (DeCelles and Zemeckis 2014). During the spawning season, telemetry can be used to locate congregations of fish on potential spawning sites within a receiver's detection radius (Pinheiro et al., 2017) or track fish movements among sites with an array of receivers that triangulates position (Binder et al., 2018). The use of acoustic telemetry tags has made assessment of deep, offshore spawning sites in the Great Lakes and Lake Champlain considerably easier.

Lake trout spawning in Lake Champlain

In Lake Champlain, eight strains of lake trout were stocked during the 1970s and 1980s. By the 1990s, the strains were reduced to the Seneca Lake strain and egg collection from stocked spawning lake trout in Lake Champlain (Marsden et al., 2003). Annual fall adult spawning assessments are conducted by state agencies at two spawning sites: Whallon Bay, New York and Gordon Landing breakwall off from Grand Isle, Vermont, to evaluate sea lamprey wounding rates and proportion of unclipped (naturally produced in the wild) fish, and collect broodstock for the hatcheries. Surveys of other potential spawning habitat in Lake Champlain by Ellrott and Marsden (2004) found 12 additional potential nearshore spawning sites, 6 natural and 6 artificial. The spawning sites consisted mostly of shallow cobble and boulders with an adjacent slope (Ellrott and Marsden 2004). Lake Champlain spawning sites had the highest density of pre-hatch embryos and free embryo lake trout compared with known spawning sites in lakes Ontario, Michigan, and Huron (Jonas et al., 2005, Marsden et al., 2005). The highest density of pre-hatch and free embryos were produced at Gordon Landing, a man-made breakwall adjacent to a hatchery effluent, and one of the smallest spawning sites sampled (Ellrott and Marsden 2004). Acoustic telemetry was used in Lake Champlain in 2015 and 2016 to assess movement of spawning lake trout to the known spawning sites in Lake Champlain. Results from the telemetry data found the majority of tagged lake trout return to same spawning area each year, but a small proportion stray to other spawning sites (Pinheiro et al., 2017).

Lake trout recruitment

In most fish species, survival from hatching to age-1 has been thought to involve several critical periods, including the progression from yolk-sac adsorption to exogenous feeding, advection from optimal nursery areas, and starvation during the first winter due to a deficiency of stored resources (Hjort 1914, 1926, Cushing 1974, 1990, Lasker 1978, Cury and Roy 1989, Houde 2008). The first critical period limiting recruitment to age-1 is the transition from feeding on the yolk-sac to feeding exogenously (Hjort 1914). Advection of eggs or larvae away from essential prey resources and juvenile habitat by current or wind was also identified by Hjort as a potential factor in recruitment in the aberrant drift hypothesis (Hjort 1926). The temporal alignment of yolk-sac adsorption with prey availability is also important because the non-overlap with abundant prey can reduce survival (Cushing 1974, 1990). The 'critical period' and 'aberrant drift' hypotheses were combined with temporal alignment with prey described above to form the match-mismatch hypothesis (Cushing 1974). Cushing proposed that the progression from spawning to egg hatch to yolk-sac adsorption must occur at the correct time in the correct location so that there are available prey nearby. Additional hypotheses, such as Lasker's (1978) "stable ocean" hypothesis, Cury and Roy's (1989) "optimal environmental window" hypothesis, and Iles and Sinclair's (1982) "stable retention" hypothesis expand and elaborate on Hjort's two major hypotheses to include the role of upwelling systems or changes in water current, winds, and turbulence to alter recruitment patterns (Houde 2008).

Although the hypotheses referenced above are applicable to many fish species, not all of them are relevant to lake trout recruitment. Once hatched, free embryo lake trout remain primarily demersal, limiting exposure to most wind-driven currents. Exogenous foraging has been documented in lake trout while the yolk-sac is still present, providing a buffer in both resources and time for the individual to acquire foraging skills and adjust to resource availability (Ladago et al., 2016). As young-of-year lake trout grow throughout the summer and fall, they move deeper and shift from foraging primarily on smaller zooplankton such as copepods to the benthic invertebrate, *Mysis diluviana*, and small benthic fish species (*Cottus* spp.; Bronte et al., 1995, Hudson et al., 1995, Roseman et al., 2009, Holbrook et al., 2013). For many freshwater fish species in the northern hemisphere, winter is assumed to be a period of limited foraging because primary production slows down, ice cover reduces visibility, and the cold water slows metabolism (Shuter et al., 2012). If a winter lasts too long, fish can starve due to the lack of available resources and exhaustion of stored resources. Lake trout recruitment does not appear to be affected by starvation due to insufficient stored resources during the first winter. Lake trout are coldwater fish, thus, their winter foraging should not be as limited as cool- and warmwater fishes (Snucins and Gunn 1995, Plumb and Blanchfield 2009). *Mysis diluviana* are an ideal prey resource for young-of-year lake trout during winter due to shared temperature and habitat preferences. If young-of-year lake trout can forage effectively over winter, growth should be sustained through to the following spring without expending stored resources. Sustained growth should continue for lake trout after the first winter, as an increase in primary production in the spring and summer leads to an abundance of prey resources (*Mysis,* planktonic predators) to forage readily during the warmer months.

Another major factor affecting lake trout recruitment to age-1 is predation. Pre-hatch embryos can be consumed by epifaunal predators such as burbot (*Lota lota*), yellow perch (*Perca flavescens*), and invasive alewife (*Alosa pseudoharengus*) prior to settling into crevices (Martin and Olver 1980, Riley and Marsden 2009). Predation of pre-hatch embryos in interstitial crevices occurs during the winter by infaunal predators such as invasive round goby (*Neogobius melanostomus*), sculpins (*Cottus* spp.), crayfish

(*Orconectes* spp.; Jonas et al., 2005, Fitzsimons et al., 2006). Lake trout free embryos are consumed by epifaunal predators such as rainbow smelt (*Osmerus mordax*), yellow perch, and alewife in the spring (Krueger et al., 1995b, Riley and Marsden 2009).

Although the introduction of alewife into Lake Champlain caused concern due to their potential predation on lake trout free embryos, their role as a prey resource for adult lake trout is equally problematic. Alewife invasion in the Great Lakes began in Lake Ontario in the 1870s and spread through canals and waterways to the remainder of the Great Lakes by 1955 (Smith 1970). Introduced alewife rapidly became a prey resource for adult lake trout in the Great Lakes and Lake Champlain (Fitzsimons et al., 2010, Marsden et al., 2018). Alewives contain high concentrations of thiaminase, so consumption of alewives by adult lake trout leads to vitamin-B deficiency in pre-hatch embryos and potentially to a variety of symptoms, including lethargy, convulsive swimming, and mortality collectively termed thiamine deficiency complex (TDC; Fisher et al., 1996, Brown et al., 2005). However, foraging while the yolk-sac is present likely allows lake trout to obtain thiamine from zooplankton, reducing the risk of thiamine deficiency and improving the probability of survival (Ladago et al., 2016).

Lake trout stock assessment

Pre-hatch embryo, free and post-embryo assessment

Pre-hatch embryo sampling on spawning reefs have been conducted in the Great Lakes since the late 1970s to investigate lake trout reproduction and spawning habitat (Eshenroder et al., 1995c, Marsden and Kruger 1991). Techniques to collect pre-hatch embryo lake trout on spawning shoals and reefs have improved from both an efficiency and economic standpoint since sampling began, shifting from containers buried in the substrate (Peck 1986) and diver assessments (Kelso et al., 1995) to use of egg nets (Horns et al., 1989), egg traps (Marsden et al., 1991), and egg bags (Perkins and Krueger 1994). Lake trout pre-hatch embryo collections from the 1970s through 2000s confirmed natural reproduction in lakes Ontario, Michigan, Huron, Superior and Champlain. These collections provided information on quantity of fertilized eggs, timing and depth of egg deposition, and habitat preference and use by spawning adults (Marsden and Krueger 1991, Eshenroder et al., 1995c, Schreiner et al., 1995, Jonas et al., 2005, Marsden et al., 2005). The focus of sampling shifted to free- and post-embryos after evidence of lake trout natural spawning was discovered in most of the Great Lakes and Lake Champlain.

Free- and post-embryo collections from spawning reefs have been conducted in the Great Lakes since the late 1970s to investigate spawning habitat use and preferences. Sampling began with small fry trawls and minnow traps (Peck 1981) then transitioned to placing emergent fry traps on spawning reefs in the spring (Marsden et al., 1988). Fry traps and fry collectors have also been used to identify potential spawning sites and evaluate survival of embryos to hatching (Chotkowski et al., 2002).

Standardized lake trout assessment

Standardized sampling methods involve the consistent use of designated sampling gear at consistent locations using repeatable methods at the same season each year (Bonar and Hubert 2002). The repeatability of standardized methods makes comparison among waterbodies and development of long-term monitoring possible. Lake trout standardized sampling methods used throughout the Great Lakes include index gill nets and bottom trawling assessments that focus on different ages and sizes of fish (Hansen et al., 1994, Bronte et al., 2008). Annual index sampling provides managers with a data series to assess changes in relative abundance of different year classes, growth rates, mortality rates, and catch rates over time.

Juvenile assessment

Juvenile assessment involves sampling sub-adult lake trout to evaluate growth and survival to the adult population (Elrod et al., 1996, Madenjian et al., 1998). Juvenile assessment can also be used to examine growth, mortality rates, and year class strength of stocked and wild lake trout. Sampling methods used for juvenile lake trout assessment vary among lakes and even among agencies in the same lake (Brenden et al., 2011, Lantry et al., 2011). Bottom trawling using three-in-one, otter, Yankee, or beam trawls during the summer are the methods most commonly used to target age-0 to age-4 lake trout (Hudson et al., 1995, Madenjian and DeSorcie 1999, Riley et al., 2007, Marsden et al., 2018). Beam and otter trawls can be used to target age-0 lake trout near to or on top of spawning reefs and nursery areas 4 m to 80 m deep after the transition to exogenous feeding has occurred (Bronte et al., 1995, Hudson et al., 1995, Madenjian and DeSorcie 1999, Riley and Marsden 2009). Sampling with three-in-one and Yankee bottom trawls along the substrate at depths from 10 m to 150 m in the Great Lakes and 35 m to 55 m in Lake Champlain is typically conducted in conjunction with annual prey fish abundance assessment and provides insight on year class abundance, annual growth and mortality rates, and health of the forage base (Selgeby and Hoff 1996, Yule et al., 2008, Lantry et al., 2011). Depending on time of sampling, size of net, speed of sample, and depths sampled, bottom trawls can target lake trout from age-0 to age-4 (Hansen et al., 1994, Marsden et al., 2018). Standardized annual bottom trawling assessments are conducted in all of the Great Lakes to assess broader fish communities, but Lake Ontario is the only

Great Lake that currently uses standardized bottom trawling to target lake trout (Bunnell et al., 2006, Riley et al., 2007, Yule et al., 2007, Lantry et al., 2011). Gill net surveys have also been used to target age-3 juvenile lake trout in Lake Ontario (Brenden et al., 2011) and for community index gill net surveys targeting age-2 and older lake trout in Lake Huron (He et al., 2012). Evidence of natural recruitment of wild lake trout to the juvenile population has been documented from bottom trawl samples in regions of lakes Champlain, Huron, Michigan, Ontario, and Superior (Selgeby and Hoff 1996, Roseman et al., 2009, Brenden et al., 2011, Hanson et al., 2013, Marsden et al., 2018). Continued annual juvenile assessment is important for monitoring potential shifts in year class strength.

Adult assessment

Assessment of adult lake trout has been conducted in all of the Great Lakes and Lake Champlain since stocking efforts began in the early 1970s, but the methodology for sampling the adult lake trout has not been consistent in all locations. Trap nets are currently used to collect spawning lake trout at spawning sites in lakes Huron and Champlain (Reid et al., 2001, Marsden and Langdon 2012). Electroshocking was used until 2009 in Lake Champlain to sample adult lake trout at two spawning sites (Marsden and Langdon 2012). Gill nets set overnight are used for annual adult lake trout index assessments in all of the Great Lakes to monitor fluctuations in the adult populations (Hansen et al., 1994, Bronte et al., 2008, Brenden et al., 2011, He et al., 2012, Coldwater Task Group 2019). Gill net sampling has documented lake trout recruitment to the adult population in lakes Superior, Huron, and most recently Lake Michigan (Sitar and He 2006, He et al., 2012, Landsman et al., 2017).

Current status of lake trout in Lake Champlain and the Great Lakes

To date, lake trout spawning has been documented in Lake Champlain and in all of the Great Lakes with the exception of Lake Erie (Jude et al., 1981, Peck 1981, Marsden et al., 1988, Eshenroder et al., 1995a, Ellrott and Marsden 2004). Recruitment of naturally produced lake trout past the first winter has been documented in lakes Champlain, Huron, Michigan, Ontario, and Superior (Sitar and He 2006, Schaner et al., 2007, Roseman et al., 2009, Hanson et al., 2013, Marsden et al., 2018), but has only resulted in sustained natural recruitment in Lake Champlain, Lake Superior, and sections of Lake Huron, where wild populations were still present (Hansen et al., 1995, Reid et al., 2001, Riley et al., 2007). Degradation of quality spawning habitat by siltation and sedimentation, introduction of invasive species such as alewife and round goby, and loss of unique morphotypes have all contributed to slow progress towards restoration in the Great Lakes (Smith and Tibbles 1980, Holey et al., 1995, Rogers et al., 2019). However, after more than 40 years of stocking, progress towards naturally recruiting lake trout populations has been made, with spawning, free embryos documented since the late 1990s and juvenile recruitment being first documented in Lake Champlain in 2015 (Ellrott and Marsden 2004, Ladago et al., 2016, Marsden et al., 2018). Continued research on obstacles to spawning and recruitment should provide further insight into lake trout population dynamics that affect the restoration and recovery of lake trout in the Great Lakes and Lake Champlain.

Moving forward

Lake trout spawning and free embryos have been documented in the Lake Champlain since the late 1990s (Ellrott and Marsden 2004, Ladago et al., 2016). Wild age-0 through age-3 lake trout first appeared in bottom trawls during the 2015 sampling season in Lake Champlain, and have been collected each subsequent year (Marsden et al., 2018). Documentation of annual changes in stocked and wild juvenile year class strength and continued wild recruitment to age-1 is necessary to assess progress towards restoration of self-sustaining lake trout populations in Lake Champlain.

The abundance of wild and stocked juvenile lake trout in bottom trawls has raised question to how wild and stocked lake trout compare spatially within the lake. Wild spawning adults have not yet been documented in Lake Champlain and stocking of age-0 lake trout continues annually. Determining how wild and stocked lake trout distribute spatially and by depth in Lake Champlain will improve understanding of habitat use and access to forage, and inform development of standardized assessment methods to track annual recruitment. Researchers in other lakes have studied bathythermal and habitat distribution differences between different strains, morphotypes, and development stages of lake trout, but have not looked at depth and spatial distributions between wild and stocked juveniles (Eck and Wells 1986, Elrod et al., 1996, Chavarie et al 2016, 2019).

Data on seasonal growth of juvenile lake trout are rare because juvenile lake trout sampling typically occurs during one period of the year in the form of a standardized assessment. Consistent bottom trawl sampling through the ice-free season in Lake Champlain provides information on distribution of juveniles by depth, temperature, and season. These data can be used to determine the optimal sampling period, locations, depths, and duration for a standardized assessment protocol that will provide valuable information for managers and researchers to assess recruitment of juvenile lake trout in Lake Champlain.

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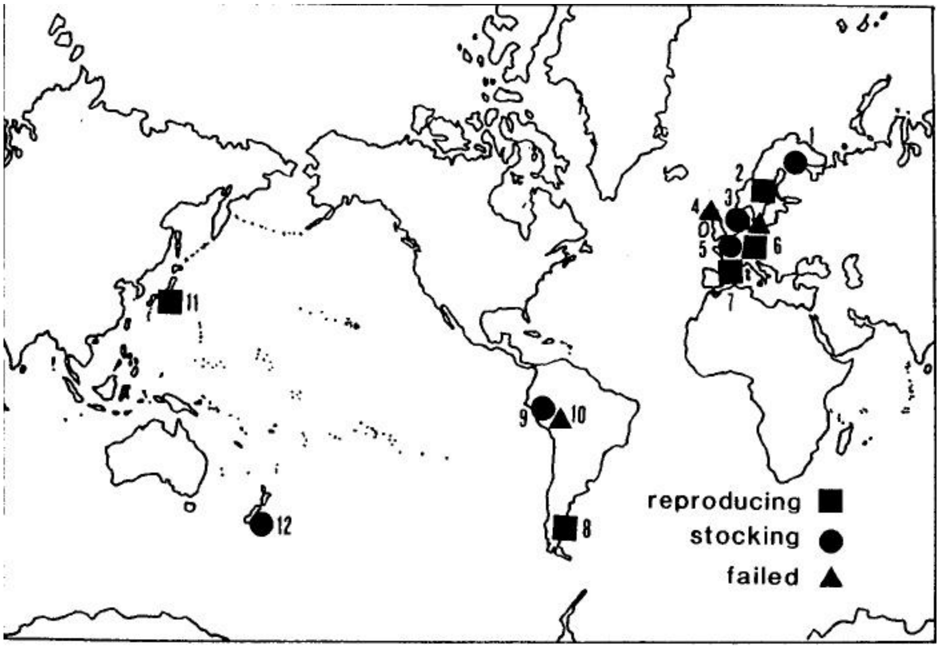

Figure 1.1: Introductions of lake trout outside North America. These are classified as Reproducing, Stocking (requiring annual or irregular fish-culture support), and Failed (did not establish a self-sustaining population and not supported by regular stocking). 1. Finland, 2. Sweden, 3. Denmark, 4. Scotland, S. France, 6. Germany, 7. Switzerland, 8. Argentina, 9. Peru, 10. Bolivia, 11. Japan, 12. New Zealand. From Crossman (1995).

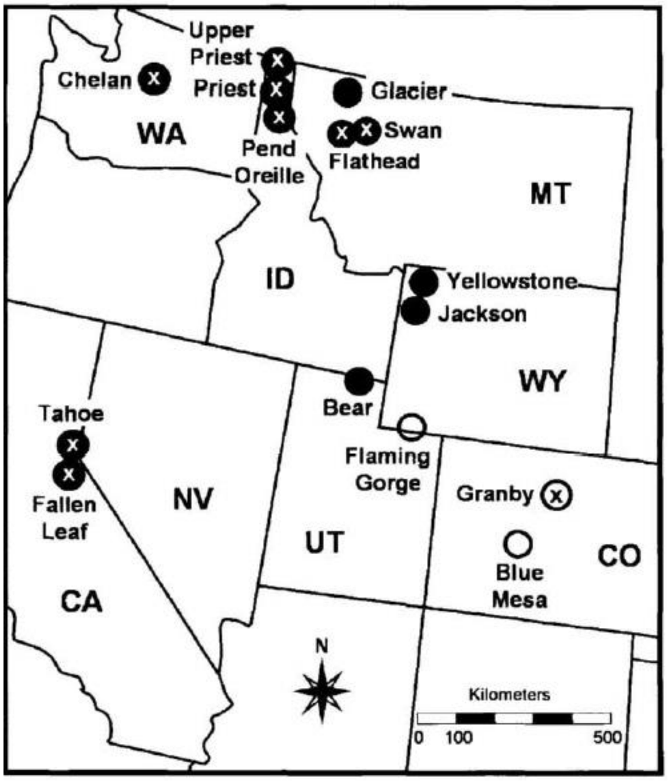

Figure 1.2: Lakes (solid dots) and reservoirs (open circles) in the western U.S. with management issues concerning introduced lake trout. Waters marked with an "x" indicate the presence of non-native *Mysis diluviana* (formerly *Mysis relicta*). From Martinez et al., 2009.

CHAPTER 2: SPATIAL AND SEASONAL COMPARISONS OF GROWTH OF WILD AND STOCKED JUVENILE LAKE TROUT IN LAKE CHAMPLAIN

Abstract

After 42 years of stocking in Lake Champlain, recruitment of wild juvenile lake trout (Salvelinus namaycush) was observed in 2015 and has continued. The percentage of wild juvenile lake trout increased from 27.8% of the total juvenile catch collected in 2015 to 65.7% in 2018. Bottom trawling was conducted in the central, north, and south Main Lake every two to four weeks during the ice-free season. The presence of both wild and stocked juvenile lake trout raised several questions focusing on differences in growth based on origin (wild or stocked), location (north, central, south), and season (winter, sampling season). Based on these questions, our objectives were to determine whether rates of growth in length and change in condition of juvenile lake trout differed among sampling areas, origin, and season, to evaluate progress towards population restoration. Lake trout stocked at age-0 in Lake Champlain have established an adult population, therefore if growth of wild lake trout is similar to that of stocked fish of similar size, we assume they will have similar survival. No consistent differences were found in growth rates in length between wild and stocked juveniles of similar size. The percentage of the total catch composed of wild juveniles was markedly higher in the central sampling area than the north and south, but no trend in growth was evident among sampling areas. Growth rates in length and change in condition during winter was equal to or less than during the sampling season for both stocked and wild juveniles.

Introduction

Lake trout (*Salvelinus namaycush*) is an apex predator and was an important component of fisheries throughout their native range during the 1800s. Overharvesting, habitat degradation, and predation by invasive sea lamprey (*Petromyzon marinus*) led to the decimation or extirpation of lake trout in the Great Lakes by 1960 (Coble et al., 1990, Eshenroder 1992). Extirpation of lake trout in Lake Champlain occurred by 1900 in the absence of a major commercial fishery and prior to reports of high sea lamprey wounding rates, making the cause of their disappearance not well understood (Marsden and Langdon 2012). The ecological and economic importance of lake trout has motivated efforts to restore self-sustaining populations of lake trout in all of the lakes where they were eliminated or greatly reduced; however, progress has been slow.

In Lake Champlain, lake trout stocking began in 1973 (Marsden and Langdon 2012), and use of lampricides to reduce sea lamprey populations began in 1990 (Marsden et al., 2003). Since 1997, an average (± SD) of 84,000 ± 5,100 age-0 lake trout have been stocked into the lake annually (unpublished data, Vermont Fish and Wildlife Department). Survival of stocked lake trout to maturity has been sufficiently high to maintain an adult population. The goal of lake trout stocking in Lake Champlain, since development of the 2010 Strategic Plan for Lake Champlain Fisheries, has been to develop a self-sustaining population of lake trout (Marsden et al., 2010). If reproduction occurs and wild juvenile lake trout, i.e., naturally-spawned individuals, exhibit similar or better growth than stocked juveniles, then they are likely to recruit to the adult population. Thus, assessment of reproduction, recruitment, and growth is critical to inform progress towards restoration.

Natural reproduction by stocked lake trout occurs at nearshore areas throughout the main basin of Lake Champlain (Ellrott and Marsden 2004), but recruitment, i.e., survival of naturally produced lake trout past the first winter, was not observed until 2015 (Marsden et al 2018). A bottleneck appears to be present in wild lake trout between hatching and survival to age-1. The first year of life is thought to be a decisive period in most fish species (Cushing 1974, 1990; Hjort 1914, 1926, Houde 2008). High mortality during this period is due to a failed transition from yolk-sac to exogenous feeding, advection from optimal nursery areas, and overwinter starvation due to insufficient stored resources (Cushing 1974, 1990; Hjort 1914, 1926). However, lake trout lack a larval stage and have a long free embryo stage in which the stress of transition to exogenous feeding is buffered by feeding prior to yolk sac adsorption (Ladago et al., 2016). Advection is also less likely for lake trout than for species with pelagic larvae because age-0 lake trout are demersal. Overwinter survival should not be as stressful for lake trout, a coldwater species, as for species with higher temperature optima; in fact, lake trout are likely to actively feed throughout the winter months (Shuter et al., 2012). However, little is known about growth of age-0 lake trout after they leave spawning reefs or their likelihood of overwinter starvation. The appearance of wild recruits in Lake Champlain in 2015 created an opportunity to compare growth rates of natural and stocked juvenile lake trout to better understand the drivers of recruitment.

Juvenile lake trout assessment was initiated in Lake Champlain in 2015, with annually increasing proportions and catch-per-unit-effort (CPUE) of wild juveniles (Marsden et al., 2018). We refer to age-0 through age-3 as ‘juveniles’, although age-4 to age-7 are also usually pre-reproductive (Elrod et al., 1996, Madenjian et al., 1998). Four year classes of wild lake trout, identifiable by the absence of a fin clip that is used to mark all stocked individuals, were caught in 2015. The absence of unclipped adults in angler's catches and annual state assessments of spawning lake trout indicated that either recruitment had not occurred prior to 2012, or was sufficiently low that no wild fish survived to maturity. Fortnightly sampling each year from April to November provided data to evaluate growth in length and change in condition over the sampling and non-sampling seasons. In addition, spatially extensive sampling in southern and northern areas of Lake Champlain occurred two to three times each year. Here we document the results of two additional years of juvenile lake trout assessment, and use the temporally and spatially intensive data to compare rates of growth in length and change in condition between stocked and wild lake trout among locations, seasons, and cohorts. We supplemented trawling data with collection of free embryo lake trout in 2018 to evaluate growth of age-0 lake trout.

The presence of wild recruitment raised several questions regarding juvenile lake trout growth in Lake Champlain: We hypothesized that wild and stocked juveniles would have similar growth rates. Lake trout stocked in fall as fingerlings (age-0), but at the size of age-1 wild lake trout, have established an adult population, therefore if growth of wild lake trout is similar to that of stocked fish we assume they would have similar survival and are likely to enter the adult population. We hypothesized that growth rates would be similar among locations in the lake. The observed variability in the spatial distribution of juveniles may be a result either of movement to areas with the best growth potential, high mortality in areas with low growth potential, or reproduction in unknown areas in the Main Lake. The first two possibilities are difficult to distinguish, but absence of differences in growth among areas of the lake would suggest that the abundant juveniles in the central lake are the result of higher spawning in that area of the lake. We hypothesized that growth would occur over winter, but growth rates would not be as pronounced in winter as during the sampling season when lake trout are closer to their optimal temperature. To assess these hypotheses we developed three objectives: (1) compare rates of growth in length and change in condition of wild and stocked lake trout by size. (2) Compare rates of growth in length and change in condition of juvenile lake trout by sampling area in Lake Champlain. (3) Determine whether winter growth occurs, and compare winter and sampling season growth rates in length and rates of change in condition.

Methods

Study area

Lake Champlain is situated among New York and Vermont, USA, and Quebec, Canada. The lake is 193 km long and up to 19 km wide, with an average depth of 19.5 m and maximum depth of 122 m. The lake is divided by islands and causeways into four basins; Malletts Bay, Inland Sea, Missisquoi Bay, and the Main Lake (Fig. 1). Lake trout are restricted to the Main Lake in summer, likely due to a fairly small hypolimnetic volume and hypolimnetic hypoxia in the three eastern basins. Sampling was conducted throughout the Main Lake basin in areas where substrate below the thermocline was suitable for bottom trawling. Sampling areas were classified as south (south of the Boquet River), north (north of Colchester Point), and central (between the Boquet River and Colchester Point; Fig. 1).

Sampling methods

Lake trout were sampled using a three-in-one bottom trawl (DeAlteris et al., 1989) with an 8 m headrope, 9.3 m footrope with chains attached, 1.25 mm stretch cod end liner, towed at 5.5 km/h parallel to bottom contours. Tows in 2015-2017 were 20-min unless an impediment forced early retrieval. In fall, 2018, we changed to 10-min trawls so that the variability in depth of each trawl could be reduced by sampling within a narrower depth contour than the 20-min trawls. Trawling depths ranged from 18.6 to 61.6 m, with the majority of tows between 35 and 50 m; trawl depth was calculated as the mean of the start and end trawl depths. Sample tows began in June in 2015, May in 2016, and April in 2017 and 2018, and ended in November each year. Sampling occurred every two to three weeks in the central sampling area, except for August and September 2016 when mechanical issues limited sampling to one day for each month (Marsden et al., 2018). Juvenile lake trout sampling was conducted at the northern and southern sampling areas of the lake two to three times each year. Fifteen fry traps (Marsden et al., 1988) were used from April-June 2018 to collect free-embryo lake trout from a spawning site at Gordon Landing on Grand Isle (Fig. 1). Traps were checked weekly and total length was measured to the nearest millimeter prior to preservation; the site and methods were described by Ellrott and Marsden (2004).

Lake trout captured in trawls were measured for total length to the nearest mm and frozen on board the boat. After thawing, each fish was evaluated for hatchery fin clips, remeasured to evaluate shrinkage due to freezing, and weighed. Total length of juvenile lake trout (age-0 through age-3) shrank by 3.8% due to freezing (frozen length (mm) = 0.9622 * fresh length (mm) – 0.7363, R_2 = 0.9963). For consistency we used fresh lengths of juveniles throughout the analyses except for calculations of condition, for which we used the length and weight of thawed individuals to get a condition value. Length data were collected for all sampling seasons, while condition data were collected from 2016 through the 2018 sampling season. CPUE was calculated as the number of juvenile lake trout (either total, wild, or stocked) per 10 min of trawling. Stocked lake trout were identified by presence of a fin clip; all stocked lake trout have a single fin clipped, using a 5-year rotation of paired fins and adipose fin. Age of stocked fish was determined using the five-year fin clip rotation schedule, and age of wild fish was determined from non-overlapping length-frequency cohorts for each month (Marsden et al., 2018). Only age-0 to age-3 lake trout were fully recruited to the trawl. Lake trout condition was determined using Fulton's condition factor, K:

$$K = (W \times L^{-3}) \times 100000$$

where W is the weight of the fish (g) and L is the total length (mm; Nash et al., 2006, Ricker 1975). Fulton's K has been criticized because it assumes isometric growth (e.g., Cone 1989); however, we used this metric to compare lake trout within the same limited size ranges, in which the slope of condition is effectively linear.

Data analysis

All data analyses were conducted using lake trout less than age-4, as sample sizes of lake trout older than age 4 (>400 mm) were too small for analysis. Analyses included data from 2015 and 2016 reported by Marsden et al., (2018) plus 2017 and 2018 samples as described above. All lake trout were classified by age, origin (stocked or wild), lake sampling area (north, central, or south), and date collected (Julian date). Adjusted Julian date, a continuous count of days throughout the study starting January 1, 2015 (the first year of sampling) was used to document changes in length or condition over the course of several sampling seasons. All analyses except spatial comparisons used lake trout data only from the central sampling area, where sample sizes were greater, and sampling was more frequent than the north or south sampling areas. Because the same depth strata were sampled on each date of trawling, and fish data were aggregated by date, we did not include depth as a factor in the analyses. If there were fewer than three individuals available for any group (e.g., a particular year class in a given year and sampling area), the group was removed from the analysis. Analyses were performed with the abd (Middleton and Pruim, 2015) and stats (R Core Team, 2019) packages using the statistical software R (v. 3.5.2; http://www.r-project.org).

We structured analyses to compare rates of increase in length and change in condition between subsets of juvenile lake trout by comparing slopes of length and condition over Julian date using generalized linear models (GLM, structure for each model detailed below). We used only age-1 through age-3 wild and stocked juvenile lake trout for the models as age-0 fish were only caught in fall each year. Assumptions of normality, linearity, and homogeneity of residuals were tested using quantile-quantile plots, histograms, observed vs. fitted plots, and fitted vs. residuals plots for each model (alpha = 0.05). An analysis of variance (ANOVA) was then used for each GLM, and if the GLM was found to have a significant difference from the null (alpha = 0.05) and the interaction effect(s) pertinent for a given objective were significant (alpha=0.05), we used pairwise comparisons to assess differences in the rates of change in length or condition between subsets of lake trout using additional ANOVA’s.

Pairwise comparisons were only conducted on lake trout that were subset by sampling area, age, season, or origin, as these were the only comparisons relevant to the research objectives. Rates of growth in length and change in condition were assessed using Julian date as the time metric, so pairwise comparisons focused on the interaction of Julian date and the target variable (origin, sampling area, season). Estimated linear regression coefficient values were derived from the ANOVA summary tables for each significant pairwise comparison and used to assess differences in the slope of length or condition over time (i.e. growth rate). All pairwise comparisons assessed similar size classes of lake trout rather than age classes because growth is relative to size. Stocked lake trout were one year advanced in size compared to wild lake trout (see below), so when stocked fish were compared to wild fish, we would match wild and stocked lake trout by size by creating a "pseudoage" for each wild fish to match their stocked counterpart by size (e.g., age-2 wild fish became a pseudoage-1 to match stocked age-1).

Objective 1: We compared rates of change in length and condition between stocked and wild juvenile lake trout using a GLM with length (mm) or condition (Cond) as the dependent variable, and Julian date (JD), age (age), origin (Or), and their interactions as the explanatory variables:

$$Length\ or\ Cond \sim Or + age + JD + Or * age + Or * JD + age * JD + Or * age * JD$$

If the full model was found to have a significant difference from the null and the interaction effects pertinent to the objective were significant, we used pairwise comparisons for wild and stocked lake trout of similar size.

Objective 2: To determine whether rates of change in length and condition of juvenile lake trout varied among sampling areas in Lake Champlain, the effects of sampling area, age, Julian date of capture, and their interactions were assessed using separate GLMs for wild and stocked juveniles for length and condition (Cond):

$$Length\ or\ Cond \sim SA + age + JD + SA * age + SA * JD + age * JD + SA * age * JD$$

Analyses were conducted separately for length and condition, with length or condition as the dependent variable, and Julian date, age, sampling area (SA), and their interactions as the explanatory variables. If the model was found to have a significant difference from the null (alpha = 0.05) and the interactions pertinent to the objective were significant, we used pairwise comparisons for wild or stocked subsets from each location (e.g., wild central vs. wild south). Age-3 juveniles were not used for this objective as there were not enough collected in the northern or southern sampling areas to conduct comparisons.

Objective 3: To determine whether growth occurred in winter, and compare winter and sampling season rates of change in length and condition, we first examined relative growth rates, i.e., rate of growth proportional to initial mean size for a given year class on the starting date of calculation (Guy and Brown 2007), for wild and stocked cohorts overwinter. We defined April to November as the ‘sampling season’; winter was defined by the last trawling date of each year to the first trawling date of the following year. If fewer than three individuals from a given cohort and origin were collected from the first and last day, we included individuals from the next adjacent sampling date as long as the dates were no more than 10 days apart. Only age-1 and age-2 lake trout were assessed, as the age-3 sample sizes from the first and last days of each sampling season were too small.

Relative growth rates in length and change in condition in the winter season were calculated for stocked and wild fish from each available cohort of age-1 and age-2 lake trout for each sampling year for which sufficient sample sizes were available. The relative winter growth equation was constructed as,

$$Relative\ Winter\ Growth\ Rate = \frac{(\mu_{f(x+1)} - \mu_{lx})}{\mu_{lx}(t_{f(x+1)} - t_{lx})} x100$$

where ‘f’ = first sampling day, ‘l’ = last sampling day, ‘x’ = year, such that μ_{lx} = mean total length (mm) or condition from last day of sampling for year x and $\mu_{f(x+1)}$ = mean total length (mm) or condition from first day of the following sampling year (x+1), t_{lx} and $t_{f(x+1)}$ = adjusted Julian date of last sampling trawl day of year x and adjusted Julian date of first sampling trawl day of year (x+1). Mean length and condition values from the first and last day of each season (winter) were used for stocked or wild lake trout to calculate the relative growth rates.

To compare winter to sampling season growth rates, we used separate GLMs for wild and stocked lake trout to assess the effects of season, age, adjusted Julian date of capture (AJD), and their interactions on length or condition (Cond):

$$Length\ or\ Cond \sim S + age + AJD + S * age + S * AJD + age * AJD + S * age * AJD$$

Analyses were conducted separately for wild and stocked juveniles, with length or condition as the dependent variable, and Julian date, age, season (S), and their interactions as the explanatory variables. If the full model was found to have a significant difference from the null (alpha = 0.05) and the interactions pertinent to the objective were significant, we used pairwise comparisons for wild or stocked subsets from each season (e.g., wild sampling season vs. wild winter). Pairwise comparisons were used to assess differences in rates of change for length and condition between the sampling and winter seasons separately for wild and stocked juveniles.

Results

We conducted 33 to 124 trawls each year and collected between 263 to 1,474 age-0 to 3 juvenile lake trout per year (Table 2.1). An additional 2 to 63 lake trout from older year classes were also collected each year. Of collected lake trout age-4 and older fish, an increasing proportion each year were wild, from 0 in 2015 to 20% in 2018; sizes of older wild fish ranged from 420 mm to 552 mm, and the oldest wild fish was caught in 2017 was estimated at age-5. We collected 371 free embryos in fry traps between April 26th and June 5th with a seasonal CPUE of 0.51 free embryos per trap per day. During each sampling season, CPUE of wild trout was highest in the central sampling area of Lake Champlain (1.3-6.2 fish/10-min trawl), lowest in the north sampling area (0.3-0.6), and intermediate in the south sampling area (0.7-2.8). Maximum CPUE for wild lake trout in a single trawl was 29 fish/10-min trawl in October 2018 in the central sampling area. Maximum CPUE for stocked lake trout in a single trawl was 25.5 fish/10-min trawl in August 2016 in the southern sampling area. CPUE of wild lake trout increased each year in the central and southern sampling areas of the Main Lake in Lake Champlain, from 1.3 to 6.2 in the central sampling area and 0.7 to 2.8 in the south sampling area (Table 2.1). The percentage of the total catch comprised of wild lake trout increased each year in all sampling areas of the Main Lake, from 27.8% (2015) to 65.7% (2018).

Age-0 hatchery fish stocked annually at 149-211 mm (unpublished data) in late October and early November were collected in November of the same year (150-208 mm), approximately equivalent to the size of age-1 wild lake trout in November (145-232 mm). This one-year advantage in length was maintained until they no longer fully recruited to the trawl at age-4 (Fig. 2.2). Age-0 wild lake trout were first collected in trawls each year in late September in 2015 and 2016 (minimum size 61 mm), early August in 2017 (minimum size 49 mm), and mid-July in 2018 (minimum size 38 mm). Free embryos ranged from 18 mm on April 26th to 30 mm on May 30th (Fig. 2.2).

Objective 1: The full model analyzing the effects of Julian date, age, and origin on length explained a significant amount of variation in length (Table 2.2). The growth rate in length of wild juveniles was equal to or greater than stocked juveniles at the same size. One of the two pairwise comparisons had a significant difference in growth rate of length between wild and stocked fish, indicating wild age-2 (pseudoage-1) fish grew faster in length than age-1 stocked fish (Table 2.3).

The full model analyzing the effects of Julian date, age, and origin on condition explained a significant amount of variation in condition (Table 2.2). All two-way interactions between predictors (origin*age, origin*Julian date, and age*Julian date) were significant, but the three-way interaction was not. Rate of change in condition of stocked juveniles was greater than wild juveniles (Table 2.3).

Objective 2: The full model analyzing the effects of Julian date, age, and sampling area on length explained a significant amount of variation in length for wild juveniles (Table 2.2). Only two (age*Julian date and sampling area*Julian date) of the two-way interactions between predictors were significant. One of the two pairwise comparisons for rate of growth in length had a significant interaction for wild juveniles, indicating the north wild fish increased length faster than central wild fish (Table 2.3).

The full model analyzing the effects of Julian date, age, and sampling area on length explained a significant amount of variation in length for stocked juveniles (Table 2.2). One of the two pairwise comparisons for growth rates in length had a significant interaction for stocked juveniles, indicating the central stocked fish increased length faster than south stocked fish (Table 2.3).

The full model analyzing the effects of Julian date and sampling area on wild juvenile lake trout condition explained a significant amount of variation in condition, but the interaction effect necessary to assess differences in the rate of change in condition between sampling areas (sampling area * Julian date) was not significant (Table 2.2). The full model analyzing the effects of Julian date, and sampling area on condition explained a significant amount of variation in condition for stocked juveniles (2.2). One of the two pairwise comparisons for the rate of change in condition had a significant interaction for stocked juveniles, indicating the north stocked fish increased condition faster than central stocked fish (Table 2.3).

Objective 3: Relative growth rates in length and change in condition during the winter season were calculated for all stocked and wild cohorts with a sufficient sample size; all relative growth rates are reported here at the same order of magnitude (exp$_{-4}$) to facilitate comparisons. Relative winter growth in length was positive in all 10 cohorts (3.7exp$_{-4}$ to 19.8exp$_{-4}$ mm•day$_{-1}$, Table 2.4). Relative winter change in condition per day decreased in six of seven cohorts (-0.6exp$_{-4}$ to -5.3exp$_{-4}$ K•day$_{-1}$,Table 2.5). The remaining cohort, which had a positive relative winter change in condition, was stocked age-2 (6.2exp$_{-4}$ K•day$_{-1}$).

The full model analyzing the effects of Julian date, age, and season on length explained a significant amount of variation in length for wild juveniles (Table 2.2). One of the two pairwise comparisons for growth rate in length had a significant interaction for wild juveniles, indicating the sampling season age-1 wild fish increased length faster than winter age-1 wild fish (Table 2.3).

The full model analyzing the effects of Julian date, age, and season on length explained a significant amount of variation in length for stocked juveniles (Table 2.2). Only two (age*Julian date and season*Julian date) of the two-way interactions between predictors were significant. Rates of change in length of stocked juveniles during the sampling season was not significantly different than during the winter season (Table 2.3).

The full model analyzing the effects of Julian date, age, and season on condition explained a significant amount of variation in condition for wild juveniles (Table 2.2). One of the two pairwise comparisons for growth rate in condition had a significant interaction for wild juveniles, indicating the sampling season age-1 wild fish increased condition faster than winter age-1 wild fish (Table 2.3).

The full model analyzing the effects of Julian date, age, and season on condition explained a significant amount of variation in condition for stocked juveniles (Table 2.2). One of the two pairwise comparisons for growth rates in condition had a significant interaction for stocked juveniles, indicating the sampling season age-1 stocked fish increased condition faster than winter age-1 stocked fish (Table 2.3).

Discussion

The abrupt successful wild lake trout recruitment and post-age-0 survival noted by Marsden et al., (2018) has continued. The percentage and CPUE of wild juvenile lake trout in Lake Champlain increased annually from 2015 (27.8%, 1.3 wild juvenile lake trout/10 min trawl) to 2018 (65.7%, 5.1 wild juvenile lake trout/10 min trawl). CPUE of stocked lake trout remained fairly constant, so the change in proportion of wild fish was due to an increase in wild recruitment, not a reduction in survival or change in distribution of stocked fish. The highest overall abundance of juveniles was in the southern sampling area of the Main Lake, consisting mostly of stocked fish, but the relative abundance and proportion of wild lake trout was consistently higher in the central sampling area than the northern or southern sampling areas. However, there were no consistent differences in growth rate for length or change of condition between wild and stocked or among sampled areas of the lake, indicating that growth potential is not the likely driver for the increased wild lake trout density in the central sampling area or a detriment to increased population densities.

The absence of consistent differences in growth rates between wild and stocked juveniles may be partially explained by differential mortality. Each year class of stocked juveniles from a given hatchery are raised under identical conditions (i.e., fertilized, hatched and raised as one group). Based on this symmetry, we would expect stocked lake trout to have a tighter variance in both length and condition than wild juveniles. However, the stocked juveniles we sampled had high variation in length, leading to overlapping length ranges between year classes. In contrast, fall spawning and the subsequent spring hatch occurs over a period of 6-8 weeks (Ellrott and Marsden 2004, Ladago et al., 2016), and should result in wide variation in length for post-hatch embryo lake trout. However, the length distributions we observed for each year class of wild fish had limited variation with no overlap between year classes. This may be due to severe size-selective mortality during the first year of life (age-0). Stocked lake trout are released with lipid content up to five times higher than wild lake trout at the same age, making mortality due to a lack of stored resources less likely (Sorrentino et al., in revision).

The differences between wild and stocked fish in the first year of life may also explain their differences in growth rates. Age-1 stocked lake trout tend to grow more allometrically than wild lake trout juveniles, i.e., their mass typically increases faster than length, leading to an increase in condition. In contrast, wild lake trout are leaner then stocked lake trout and tend to grow faster in length rather than girth.

The higher abundance of wild juveniles in the central sampling area could indicate higher growth and therefore survival in the central sampling area, migration of fish from the north and south into the central sampling area, or the presence of major spawning sites in the central Main Lake. Our analysis indicates that geographic variation in abundance and proportion of juveniles in the Main Lake is not explained by differences in growth rates for length or condition. Alternatively, if migration is occurring from the north and south to the central sampling area, a difference favoring the central sampling area in growth rate in length and/or condition could help explain the shift to the central sampling area. As we saw no difference in growth between the three sampling areas, migration to the central sampling area to improve growth potential does not seem likely. Additional spawning sites, with production of free embryos, have been documented in the lake (Ellrott and Marsden 2004), but investigations did not extend to offshore areas of the Main Lake. Several sites in the central sampling area of the Main Lake have the potential to be highly productive spawning reefs, based on bathymetric maps and geological formations; reproduction at these sites may be the source of the abundant wild juveniles in our samples.

Juvenile lake trout grew in length overwinter and maintained condition, suggesting that both stocked and wild juvenile lake trout actively forage during the winter. Winter is an underestimated period of potential growth in coldwater fish species with low temperature preferences, as the autumn-winter transition to isothermal temperatures provides increased access to habitat and food resources for fish species that can tolerate the colder water (Blanchfield et al., 2009, Shuter et al., 2012). Juvenile stocked lake trout age-2 to age-4 in Lake Michigan actively forage and undergo significant growth in length over winter (Eck and Wells 1986). The ability to grow and maintain condition during the winter at these young ages should reduce the likelihood of mortality from starvation and lack of stored resources. Alternatively, the increase in length we observed over winter could be due to size-selective mortality of the smaller individuals, leading to a bias in the data.

If wild lake trout can survive to age-1 in Lake Champlain, they should exhibit similar survival to stocked fish because lake trout stocked in fall at the size of age-1 wild fish have successfully established an adult population (Marsden et al., 2018). The first year class of wild recruits detected in our samples hatched in 2012, and thus should have been age-6 in 2018. Lake trout typically mature at age-4 to age-6 in males and age-5 to age-7 in females, with higher variance among some strains (Elrod et al., 1996, Madenjian et al., 1998). Therefore, we expected to see wild fish in spawning site assessments by 2018. Despite the increase in the proportion of age-4 and older wild trout from 0% in 2015 to 22.6% in 2018 from the central sampling area, no wild spawners have yet been documented at Gordon Landing or Whallon Bay, so either the wild cohorts have not yet reached maturity, have been killed prior to maturity due to sea lamprey predation, or are spawning elsewhere (as discussed above). The early cohorts of wild fish may not have been sufficiently large to see high numbers of them at spawning areas by 2018. High mortality of wild juveniles due to sea lamprey predation seems unlikely because sea lamprey prefer larger hosts, which are abundant in Lake Champlain. Lake trout survival to maturity has been sufficiently high in stocked lake trout to build and maintain a spawning population, despite lamprey wounding rates that are 5-20X higher in Lake Champlain than in any of the Great Lakes (Marsden et al., 2018, Marsden and Siefkes 2019). Most age 4+ wild lake trout caught in trawls were found in the central area, supporting the likelihood that they remain in this area and may spawn there.

My study indicates that wild juvenile lake trout are actively foraging over winter and are increasing in both abundance and proportion in the central and southern sampling areas of the Main Lake in Lake Champlain. Increased proportions of wild lake trout age-4 and older suggests that the older cohorts of wild trout are approaching maturity. The abundance of wild juveniles in the central lake and absence of wild spawners at either of the two spawning assessment sites suggests that unidentified, productive spawning sites may be present elsewhere in the lake. The steadily increasing population of wild lake trout, with potential for an increase in the spawning stock, is likely to affect the forage base and has raised concerns about whether and how much stocking levels should be reduced.

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Table 2.1: Total number of trawls, juvenile lake trout, percent wild (unclipped) lake trout, total catch per unit effort (CPUE, # fish per 10 min), and CPUE of wild lake trout sampled with bottom trawls in Lake Champlain, 2015-2018.

Year	Location	# of Trawls	Age-0 to 3	% Wild 0-3	Total CPUE	Wild CPUE	Age 4+	% Wild 4+
2015	Central	30	250	28.8	4.6	1.3	2	0.0
	North	3	13	7.7	4.3	0.3	0	-
	Total	33	263	27.8	4.6	1.3	2	0.0
2016	Central	60	778	44.7	6.5	2.9	17	11.8
	North	28	198	18.2	3.4	0.6	5	0.0
	South	22	356	9	8.1	0.7	9	0.0
	Total	110	1,332	31.2	6	1.9	31	6.5
2017	Central	75	670	72.8	4.9	3.6	54	5.6
	North	27	109	20.2	2.2	0.4	3	0.0
	South	8	167	11.4	10.4	1.2	5	20.0
	Total	110	946	55.9	4.7	2.6	63	4.8
2018	Central	99	1,232	73.3	8.4	6.2	31	22.6
	North	14	44	22.7	1.8	0.4	1	0.0
	South	12	198	28.3	9.9	2.8	3	0.0
	Total	124	1,474	65.7	7.7	5.1	35	20.0

Table 2.2: F-Test (ANOVA) summary statistics for each component GLM (generalized linear model). The three-way interaction effects were assessed for each model, if found to not be significant (α = 0.05), it was subsequently removed from the formula and the two-way interaction effects were then assessed for significance in the same manner. Model formulas detailed below are the full or reduced versions based on the significant interaction effects. NS indicates a p-value that is not significant (α = 0.05).

Comparisons	Components	Model	F-stat	df	R_2 value	F-test p value	Interaction p value
Origin	Length	L~Or+age+JD+Or*age+Or*JD+age*JD+Or*age*JD	569.3	7, 1638	0.71	<0.001	0.002
	Condition	C~Or+age+JD+Or*age+Or*JD+age*JD	30.7	6, 1230	0.13	<0.001	<0.003
Location	Length						
	Wild	L~SA+age+JD+SA*JD+age*JD	2087.0	7, 1599	0.90	<0.001	<0.006
	Stocked	L~SA+age+JD+SA*age+SA*JD+age*JD+SA*age*JD	394.1	11, 1876	0.70	<0.001	0.004
	Condition						
	Wild	C~SA+JD+SA*JD	18.1	5, 1463	0.05	<0.001	NS
	Stocked	C~SA+JD+SA*JD	29.0	5, 1253	0.10	<0.001	0.010
Season	Length						
	Wild	L~S+age+AJD+S*age+S*AJD+age*AJD+S*age*AJD	1930.0	7, 1410	0.91	<0.001	<0.001
	Stocked	L~S+age+AJD+S*age+S*AJD	499.5	5, 1015	0.71	<0.001	<0.02
	Condition						
	Wild	C~S+age+AJD+S*age+S*AJD+age*AJD+S*age*AJD	143.0	7, 1330	0.43	<0.001	<0.001
	Stocked	C~S+age+AJD+S*age+S*AJD+age*AJD+S*age*AJD	21.9	7, 667	0.18	<0.001	<0.001

Table 2.3: F-Test (ANOVA) summary statistics for all pairwise comparison GLMs (generalized linear models). The model and interaction effects were assessed for each comparison, if found to not be significant (α = 0.05), differences in slope were not assessed. NA indicates summary statistics that were not available for analysis of pairwise comparisons due to insignificant interaction effects in the full model. NS indicates a p-value that is not significant (α = 0.05).

			Length						Condition					
Comp.	Pairwise Comparisons	Contrast	F-stat	df	R_2 value	F-test p value	int. p value	diff. in slope	F-stat	df	R_2 value	F-test p value	int. p value	diff. in slope
Origin	Wild vs Stock	Age-1	305.0	3, 1303	0.41	<0.001	0.002	(W>S)	NA	NA	NA	NA	NA	NA
	Wild vs Stock	Age-2	21.9	3, 335	0.16	<0.001	NS	NS	NA	NA	NA	NA	NA	NA
	Wild vs Stock	All	NA	NA	NA	NA	NA	NA	17.0	3, 1233	0.04	<0.001	0.05	(S>W)
Location	South vs Cent	Wild	6.1	3, 1540	0.01	<0.001	NS	NS	NA	NA	NA	NA	NA	NA
	North vs Cent	Wild	8.7	3, 1512	0.01	<0.001	0.030	(N>C)	NA	NA	NA	NA	NA	NA
	South vs Cent	Stocked	32.0	3, 1596	0.05	<0.001	0.004	(C>S)	33.8	3, 1060	0.08	<0.001	NS	NS
	North vs Cent	Stocked	44.2	3, 1296	0.09	<0.001	NS	NS	24.8	3, 862	0.08	<0.001	0.014	(N>C)
Season	SS vs Winter	Age-1 W	1347.0	3, 897	0.82	<0.001	<0.001	(S>W)	203.1	3, 869	0.41	<0.001	<0.001	(S>W)
	SS vs Winter	Age-2 W	245.3	3, 513	0.59	<0.001	NS	NS	5.9	3, 461	0.03	<0.001	NS	NS
	SS vs Winter	Age-1 S	NA	NA	NA	NA	NA	NA	28.7	3, 532	0.13	<0.001	0.001	(S>W)
	SS vs Winter	Age-2 S	NA	NA	NA	NA	NA	NA	1.7	3, 143	0.01	NS	NA	NA
	SS vs Winter	All S	53.4	3, 1017	0.13	<0.001	NS	NS	NA	NA	NA	NA	NA	NA

Table 2.4: Mean lengths (mm) and relative growth rates in length of wild and stocked juvenile lake trout from the first and last sampling day during each sampling season during the winter in the central sampling area of Lake Champlain from four seasons, 2015-2018, by cohort, origin, and age. Relative winter growth rates in each row are calculated using the mean lengths from the last sampling date in that row and the first sampling day in the row containing data from the first sampling day for the same cohort one year older. The number of individuals (N) collected and sampling months for each age, origin, and cohort class are also reported. All relative growth rates are reported here at the same order of magnitude (exp-4) to facilitate comparisons.

			Mean length (mm) and sample size					
Cohort	Age	Origin	first sampling day		last sampling day		Relative winter growth	Sampling season
2014	1	Stocked	294.7	6	276.1	41	4.3	Jun-Nov
2015	1	Stocked	226.6	21	272.7	6	9.6	May-Nov
2016	1	Stocked	225.6	11	278.1	7	3.7	Apr-Nov
2013	2	Stocked	343	5	337.4	5	9.3	Jun-Oct
2015	2	Stocked	315.9	8	334.8	11	4.2	Apr-Nov
2014	1	Wild	168.3	11	167	6	19.8	Sept-Oct
2015	1	Wild	107	5	192.4	8	13.9	May-Nov
2016	1	Wild	103.5	13	198.9	54	9.4	Apr-Nov
2014	2	Wild	230.6	11	279.7	6	14.3	May-Nov
2015	2	Wild	236.5	10	288	4	11.8	Apr-Oct

Table 2.5: Mean condition (K) and relative rate of change in condition of wild and stocked juvenile lake trout from the first and last sampling day of each sampling season during the winter in the central sampling area of Lake Champlain from four sampling seasons, 2016-2018, by cohort, origin, and age. Relative winter rates of change in each row are calculated using the mean condition from the last sampling date in that row and the first sampling day in the row containing data from the first sampling day for the same cohort one year older. All relative growth rates are reported here at the same order of magnitude (exp$_{-4}$) to facilitate comparisons. The number of individuals (N) collected and sampling months for each age, origin, and cohort class are also reported.

			Mean condition (K) and sample size					
Cohort	Age	Origin	first sampling day		last sampling day		Relative winter change	Sampling season
2015		Stocked	0.9	21	1.0	5	-2.3	May-Nov
2016		Stocked	0.9	11	1.1	10	-0.8	Apr-Nov
2015		Stocked	1.0	7	1.0	9	6.2	Apr-Nov
2015		Wild	0.8	5	0.9	8	-5.3	May-Nov
2016		Wild	0.7	13	0.9	54	-0.6	Apr-Nov
2014		Wild	0.9	10	0.9	5	-1	May-Nov
2015		Wild	0.8	10	1.1	3	-1.7	Apr-Oct

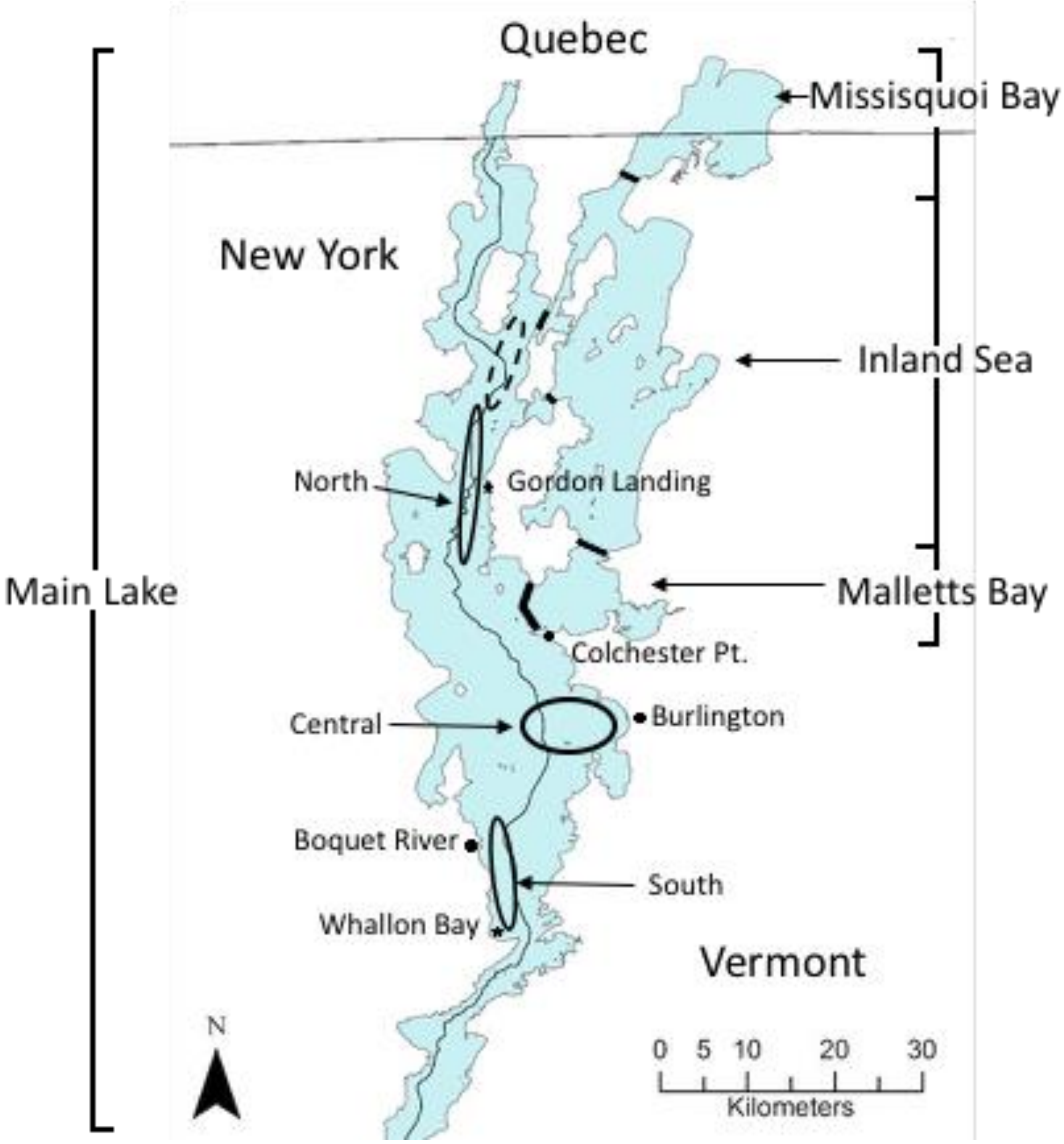

Figure 2.1: Map of the northern two thirds of Lake Champlain where juvenile lake trout were sampled to assess growth. Spawning sites mentioned in paper denoted with stars (★). Solid ellipses indicate the three sampling areas, with the dashed ellipse indicating area of additional trawls during the 2016 and 2017 seasons. Basins and sampling areas identified with arrows.

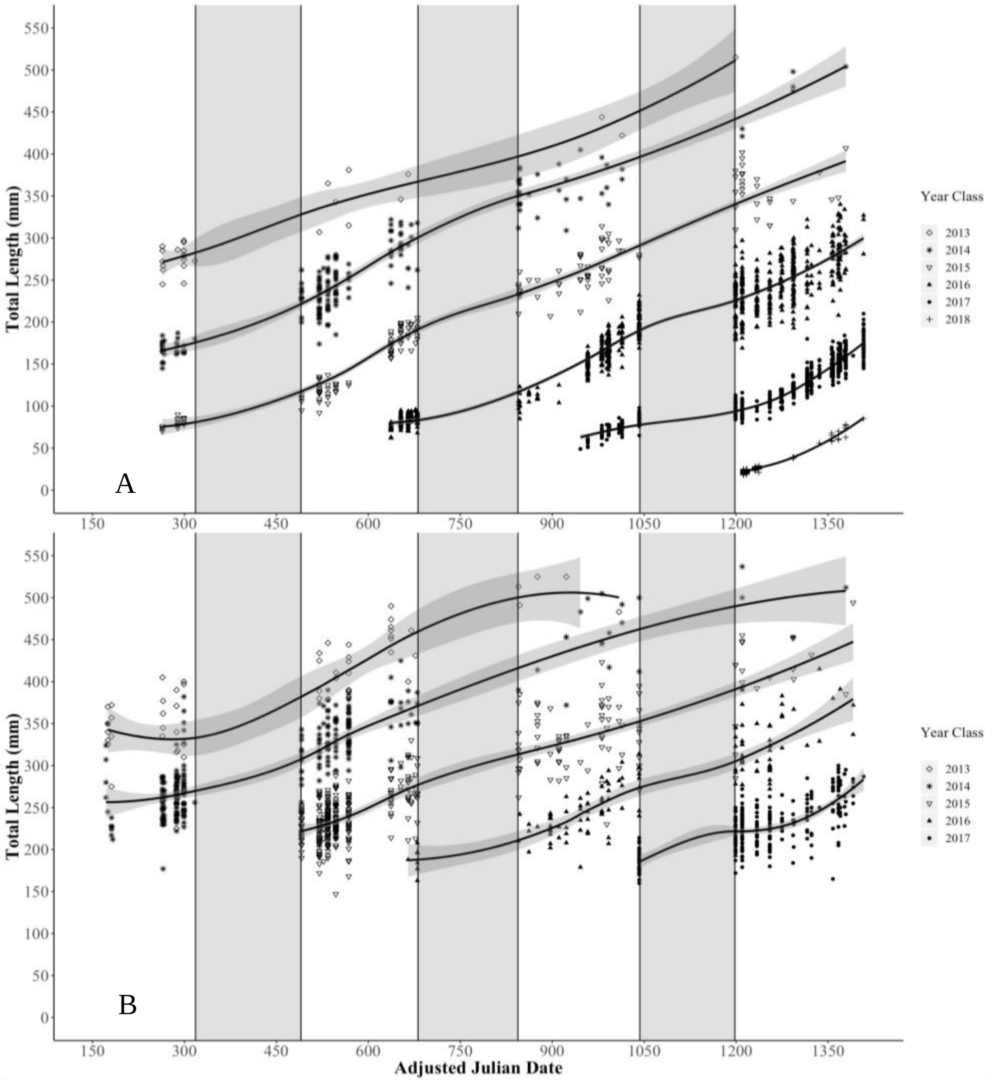

Figure 2.2: Lake trout total length (mm) of each juvenile year class collected in bottom trawls in Lake Champlain in 2015-2018. Panel (A, upper) is wild lake trout, (B, lower) is stocked lake trout. Grey vertical bars indicate the non-sampling season (i.e., winter). 2018 Wild cohort includes age-0 lake trout measurements from free embryo trapping at Gordon Landing, April-June.

CHAPTER 3: DIFFERENCES IN SEASONAL DISTRIBUTION OF WILD AND STOCKED JUVENILE LAKE TROUT BY DEPTH AND TEMPERATURE IN LAKE CHAMPLAIN

Abstract

Distribution of wild and stocked juvenile lake trout (*Salvelinus namaycush*) relative to depth and temperature was determined from bottom trawl samples in Lake Champlain, 2015-2019. Our objective was to describe habitat use and seasonal distribution of wild and stocked juvenile to inform sampling strategies focused on evaluating recruitment and progress towards restoration. Bottom trawling was conducted in the central Main Lake every two to four weeks during the ice-free season. Differences in distribution of wild and stocked lake trout were most pronounced during thermal stratification, when wild juveniles were more abundant than stocked juveniles at shallower depths and warmer temperatures and stocked juveniles were more abundant at deeper depths and colder temperatures. Temperature preferences may be a consequence of different early rearing environments; wild lake trout are acclimated to lake temperatures and forage, whereas stocked fish have high lipid content and little foraging experience. Unbiased assessment of the proportion of wild lake trout and growth and survival of the entire juvenile lake trout population using bottom trawl sampling should either take place in the pre- and post-stratification seasons when wild and stocked fish are at the same depths, or include a range of depths and temperatures in the stratified period.

Introduction

Restoration of lake trout (*Salvelinus namaycush*) populations has been the focus of research and management in the Great Lakes and Lake Champlain since populations collapsed during the late 19th and 20th centuries (Hansen 1999, Marsden and Langdon 2012). Reproduction by stocked lake trout has been documented in all of these lakes except Erie (Hanson et al., 2013, Marsden et al., 2018, Roseman et al., 2009, Schaner et al., 2007, Sitar and He 2006). However, sustained natural recruitment has only been documented in Lake Superior and sections of Lake Huron (lakes with remnant wild populations present), and most recently in Lake Champlain (Hansen et al., 1995, Marsden et al., 2018, Reid et al., 2001, Riley et al., 2007).

The recent surge in natural recruitment of wild lake trout in Lake Champlain has occurred in conjunction with continued annual fall stocking of age-0 lake trout, creating populations of both wild and stocked juveniles (Marsden et al., 2018, Wilkins and Marsden in review). Wild and stocked lake trout experience very different conditions during their first year of life that may affect their behavior, habitat use, and distribution. Hatchery lake trout are raised at elevated temperatures and provided pelletized artificial food to accelerate growth, and are released either as fall fingerlings (age-0) or spring yearlings (age-1), usually the size of age-1 or age-2 wild lake trout. In contrast, age-0 wild lake trout forage on plankton and Mysis while avoiding predation (Hudson et al., 1995, Holbrook et al., 2013). Lake trout in hatcheries are raised in shallow, lotic raceways in higher densities than commonly found in the wild, while wild age-0 lake trout can inhabit a wide array of depth and temperature ranges in a lentic system (Bronte et al., 1995). Differences in the first year of life may result in long-term differences in diet, behavior, distribution and habitat use from age-1 onwards.

Description of habitat differences between wild and stocked lake trout after the first year in Lake Champlain is important from both an ecological and lake management perspective. Habitat use (e.g., distribution of fish by depth or temperature) can affect, and is influenced by, diet and growth. Differences in environmental preference between wild and stocked lake trout also dictates assessment sampling for both populations. The purpose of this study was to describe habitat use and seasonal distribution of wild and stocked juveniles and inform sampling strategies focused on evaluating recruitment.

Methods

Study area and data collection

Lake Champlain is bordered by New York and Vermont, USA, and Quebec, Canada. The lake is 193 km long and up to 19 km wide, with a mean depth of 19.5 m and maximum depth of 120 m. We conducted depth-stratified bottom trawling for wild and stocked lake trout in the central portion of the Main Lake every two to four weeks from April to November in 2015-2019 (Fig. 1).

Lake trout were collected using a three-in-one bottom trawl (DeAlteris et al., 1989) with an 8 m headrope, 9.3 m footrope with chains attached and 1.25 mm stretch cod end liner, towed at 5.5 km/h parallel to bottom contours. Trawl durations were 20-min from 2015-2017 before a shift to 10-min tows in fall 2018 so that a narrower depth range could be maintained with each tow. Trawl depth was calculated as the mean of the start and end trawl depths. Temperature profiles and temperature at the mean depth of each trawl were obtained from vertical temperature profiles measured within 11 days of each bottom trawling event. Trawling was conducted every two to four weeks, except in August and September 2016 when mechanical issues restricted sampling to one day each month (Marsden et al., 2018).

Lake trout captured in trawls were measured for total length to the nearest millimeter and evaluated for presence of a hatchery fin clip. Hatcheries use a 5-year single fin-clip rotation of paired fins and the adipose fin to identify stocked lake trout by age. Hatchery-raised (stocked) lake trout are released in October and November of each year at a size similar to age-1 wild lake trout. Ages of wild lake trout were assessed from non-overlapping length-frequency cohorts each month (Marsden et al., 2018). Total catch per unit effort (CPUE) and CPUE of wild and stocked lake trout were calculated as the number of juvenile lake trout per 10 min of trawling.

Data analysis

Only age-0 to age-3 lake trout were fully recruited to the trawl, so analysis focused on these age classes. We use the term “juveniles” to denote age-0 through age-3 fish, although age-4 through age-7 lake trout can also be pre-reproductive (Elrod et al., 1996, Madenjian et al., 1998). We examined distribution of lake trout during three seasonal periods based on thermal structure of the water column. Thermal stratification was defined as a temperature gradient of at least 5ºC between 10 m and 60 m. Trawls conducted prior to and after thermal stratification were designated as “pre-stratification” and “post-stratification”. Each trawl tow was categorized by trawl depth, temperature at trawl depth, presence/absence of thermal stratification, and catch of wild and stocked juveniles. Each juvenile lake trout was categorized by mean trawl depth and temperature at capture, stratification period, and origin (wild or stocked).

Seasonal differences in CPUE by depth and temperature for wild and stocked juvenile lake trout were summarized with 95% confidence intervals (CIs) using ggplot2 (Wickham 2016) and ggpubr (Kassambara 2019) packages in the statistical software R

(v. 3.5.2; http://www.r-project.org). For each stratification period, we then generated two bootstrap samples by randomly selecting either depth or temperature for *n* fish from the original data with replacement, where *n* was the number of fish (wild or stocked) collected in the stratification subset. The bootstrap samples were generated using the boot package (Canty and Ripley 2019) in statistical software R. The mean depth or temperature was calculated for each bootstrap sample. This process was replicated 1,000 times, creating a randomized bootstrap distribution of means for the habitat variables (depth and temperature) for wild and stocked lake trout in each stratification period. We calculated 95% confidence intervals (CI) for mean depth and temperature for each stratification period using the bootstrapped replicates. Observed juvenile catches were summarized using kernel density estimation for each stratification period.

Results

We conducted 30 to 99 trawls and collected between 250 and 1,232 juvenile lake trout each year from 2015 to 2019 (Table 1). Mean trawl depths ranged from 20 m to 64.9 m. Temperature at mean trawl depth in the central sampling area ranged from 1.8 to 6.2ºC pre-stratification, 4.2 to 12.3ºC during thermal stratification, and 7.4 to 13.0ºC post-stratification.

Differences between wild and stocked juvenile abundance were related to stratification period. Different depth distributions of wild and stocked fish were most pronounced during the thermal stratification period, when wild juveniles were more abundant than stocked juveniles in shallower water and stocked juveniles were more abundant than wild juveniles in deeper water (Fig. 2). The bootstrapped 95% CI around mean depth ranges did not overlap for wild and stocked juveniles during any of the three stratification periods, with the greatest difference in mean depths between wild and stocked juveniles occurring during thermal stratification (Fig. 3).

There were no clear distribution differences during pre- or post-stratification periods based on temperature (Fig. 4), and the bootstrapped 95% CI around the observed mean temperature overlapped for wild and stocked juveniles (Fig. 5). However, during thermal stratification wild juvenile lake trout were more abundant in warmer water and stocked juveniles were more abundant in colder water.

Discussion

The distribution of wild and stocked juvenile lake trout ages 0 to 3 in Lake Champlain indicated changing depth and temperature preferences throughout the sampling season. Wild juveniles were slightly shallower than stocked juveniles pre-stratification, but wild and stocked juveniles were found at similar temperatures because the water was close to isothermal at the depths inhabited by lake trout. During thermal stratification, wild and stocked distributions differed in both depth and temperature, with the wild juveniles in shallower and warmer areas than stocked lake trout. Wild juvenile lake trout were also slightly shallower than stocked juvenile lake trout post-stratification, but wild and stocked temperature distributions overlapped. The temperature overlaps pre- and post-stratification indicate that the depth differences during those periods are not temperature-related.

Observed disparity in the distribution of wild and stocked juvenile lake trout is either due to inherent, i.e., genetic differences or a result of early experience in different environments. Early studies in the Great Lakes, in the absence of wild juveniles, focused on comparison of depth and temperature distributions among stocked lake trout strains. In

Lake Ontario, Seneca Lake strain juveniles were found at intermediate depths (24-31 m) relative to shallower Clearwater strain and deeper Lake Superior strain (Elrod et al., 1996). After dreissenid mussels invaded Lake Ontario in the early 1990s, distributions of all strains of stocked lake trout shifted deeper (O’Gorman et al., 2000). Dreissenids filter-feed and increase water clarity, so altered light levels may have been a more important factor than temperature motivating the change in lake trout depth preferences. Stocked juveniles in Lake Champlain descend primarily from the Seneca Lake strain, and zebra mussels have been established since 1993 (Ellrott and Marsden 2004, Marsden and Hauser 2009). The depth distribution of these stocked juveniles during thermal stratification is similar to Seneca Lake strain in Lake Ontario after dreissenid mussel invasion (O’Gorman et al., 2000). Wild Lake Champlain lake trout are offspring of stocked fish and therefore are largely derived from the Seneca Lake strain; therefore, the different distributions of wild and stocked juveniles are likely a result of differences in their early rearing environment rather than genetic strain.

Hatchery lake trout are reared at 10ºC and mostly stocked in Lake Champlain at age-0 in November, they must learn to forage in late fall and over winter, when lake productivity declines and optimal temperatures are unavailable. In contrast, wild age-0 lake trout hatch and begin foraging in spring and early summer at a time of high lake productivity near their preferred temperature range of 8 to 12ºC (Magnuson et al., 1990). Differences in prey availability and previous foraging experience for age-0 wild and stocked lake trout at the time of initial foraging in the lake could lead to differences in foraging behavior and therefore habitat preferences. Wild lake trout benefit from warmer temperatures to maximize foraging efficiency. In contrast, lake trout are stocked in Lake

Champlain with lipid content up to five times higher than wild lake trout at the same age (Sorrentino et al., in revision). The motivation for stocked lake trout to seek lower temperatures to slow metabolism and conserve their high lipid content could partially explain their preferences to colder water.

In Lake Champlain, wild age-0 and age-1 lake trout forage heavily on *Mysis diluviana* before incorporating small pelagic and benthic fishes into their diets (age-0 and age-1 alewife, rainbow smelt (*Osmerus mordax*), and slimy sculpin *Cottus cognatus;* Marsden et al., in prep). Alewives and age-0 rainbow smelt reside in the epilimnion and metalimnion during periods of thermal stratification (Simonin et al., 2012), so wild lake trout would have the best access to these prey by remaining close to the metalimnion. However, differences in depth and temperature distributions do not appear to have an effect on growth, as wild and stocked juveniles at the same size had similar growth (Wilkins and Marsden, in review).

Discovery of significant differences in depth and temperature distributions of wild and stocked juvenile lake trout during thermal stratification is important for juvenile lake trout assessment. Unbiased sampling of both wild and stocked juveniles is necessary to document recruitment and year class strength of wild lake trout throughout the Great Lakes and Lake Champlain. Based on our results, assessment of wild lake trout would be least biased in the pre- and post-stratification periods. Bottom trawl sampling during thermal stratification should include a broad range of sampling depths and temperatures. However, changes to the lake could continue to shift lake trout habitat preferences. Juvenile lake trout assessment in Lake Champlain began after zebra mussels (*Dreissena polymorpha*) and alewife (*Alosa pseudoharengus*) invaded and altered the community structure of the lake, and likely altered the depth distribution of lake trout (Marsden and Langdon 2012). Potential invasion of quagga mussels (*Dreissena bugensis*) or alternative prey such as round goby (*Neogobius melanostomus*) to Lake Champlain could further alter depth and temperature distributions of lake trout similar to stocked lake trout in Lake Ontario, and require adjustments in juvenile lake trout sampling methods (O'Gorman et al., 2000).

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Table 3.1: Total number of trawls, juvenile lake trout, percent wild (unclipped) lake trout, mean total catch per unit effort (CPUE, # fish per 10 min (SD)), and mean CPUE of wild lake trout (SD) sampled with bottom trawls in the central sampling area in Lake Champlain, 2015-2019.

Year	# of Trawls	Age-0 to 3	% Wild 0-3	Total CPUE (SD)	Wild CPUE (SD)
2015	30	250	28.8	4.8 (4.5)	1.3 (1.7)
2016	60	778	44.7	6.5 (4.2)	2.9 (3.0)
2017	75	670	72.8	4.8 (4.8)	3.5 (4.3)
2018	99	1,232	73.3	8.6 (6.3)	6.5 (5.3)
2019	66	556	57.4	7.2 (6.6)	4.3 (4.8)

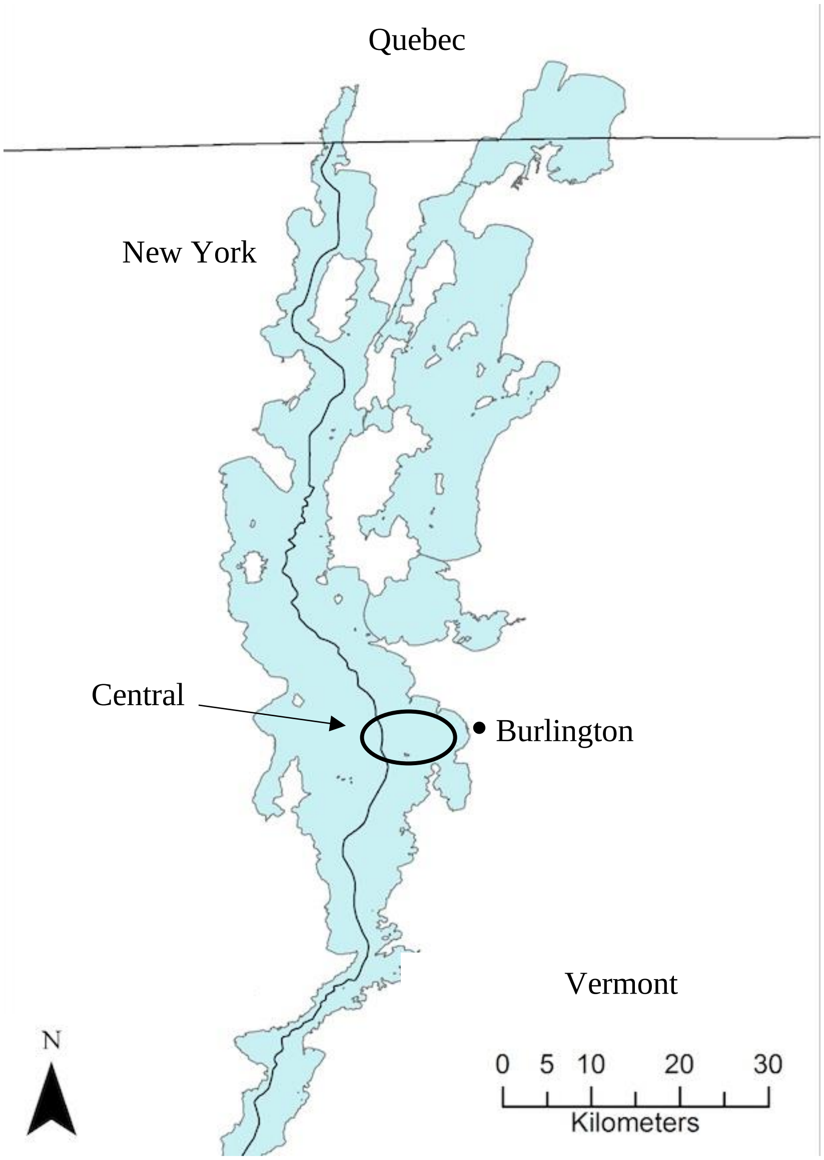

Figure 3.1: Map of the northern two thirds of Lake Champlain indicating the central Main Lake where juvenile lake trout were sampled in 2015-2019.

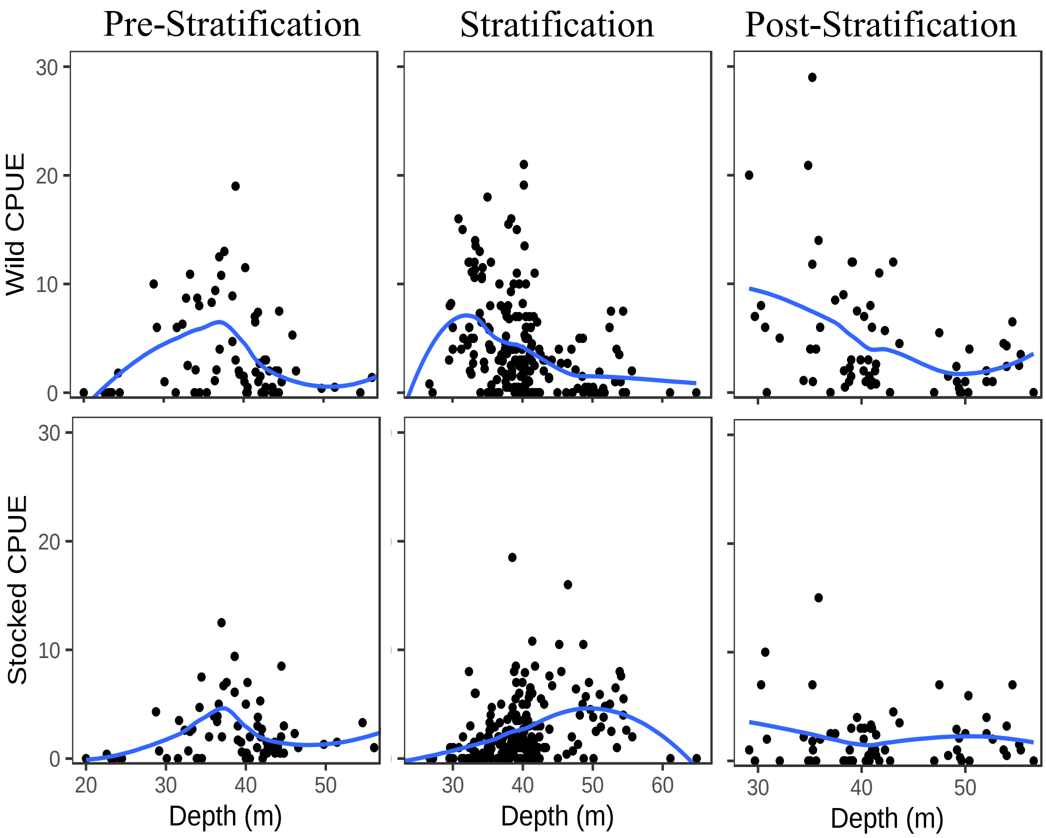

Figure 3.2: Mean and 95% confidence intervals for wild and stocked juvenile lake trout CPUE by mean depth (m) based on stratification period. Black dots represent individual trawl catches.

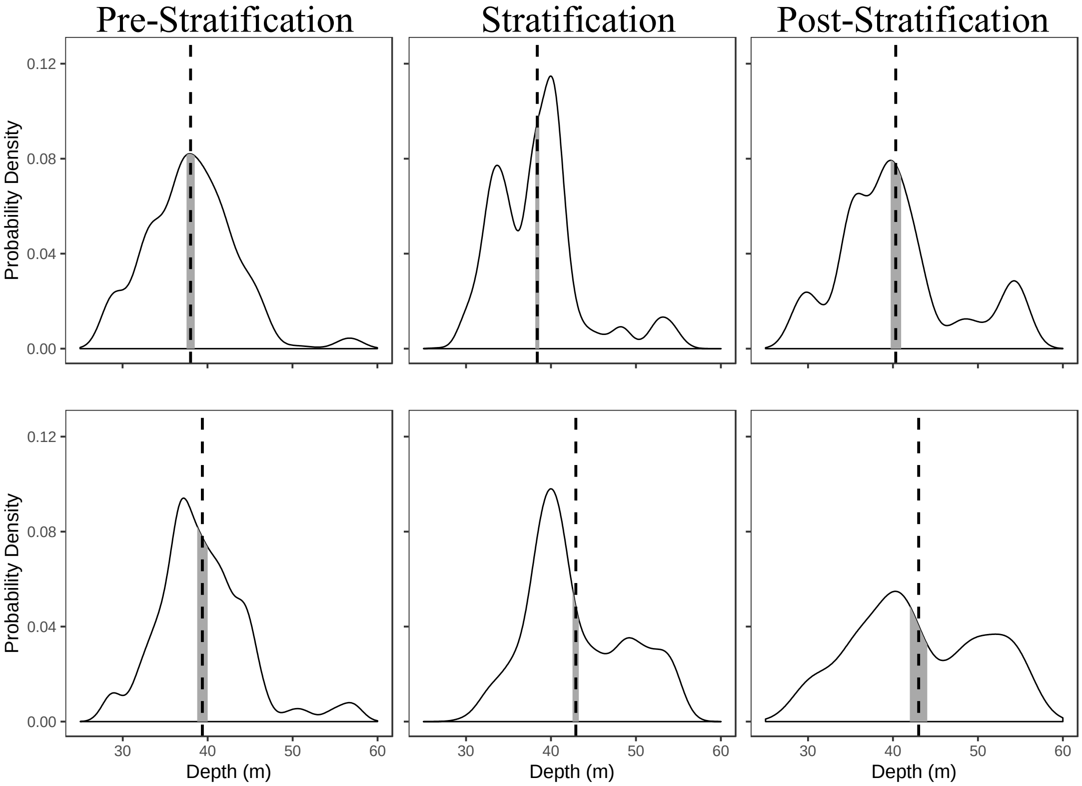

Figure 3.3: Kernel density plot with mean and 95% confidence interval of wild (top) and stocked (bottom) juvenile lake trout by depth (m) based on stratification period. Shaded area represents the 95% confidence interval for the mean depth from 1,000 bootstrap replicates. The dashed line represents the mean depth from the observed data.

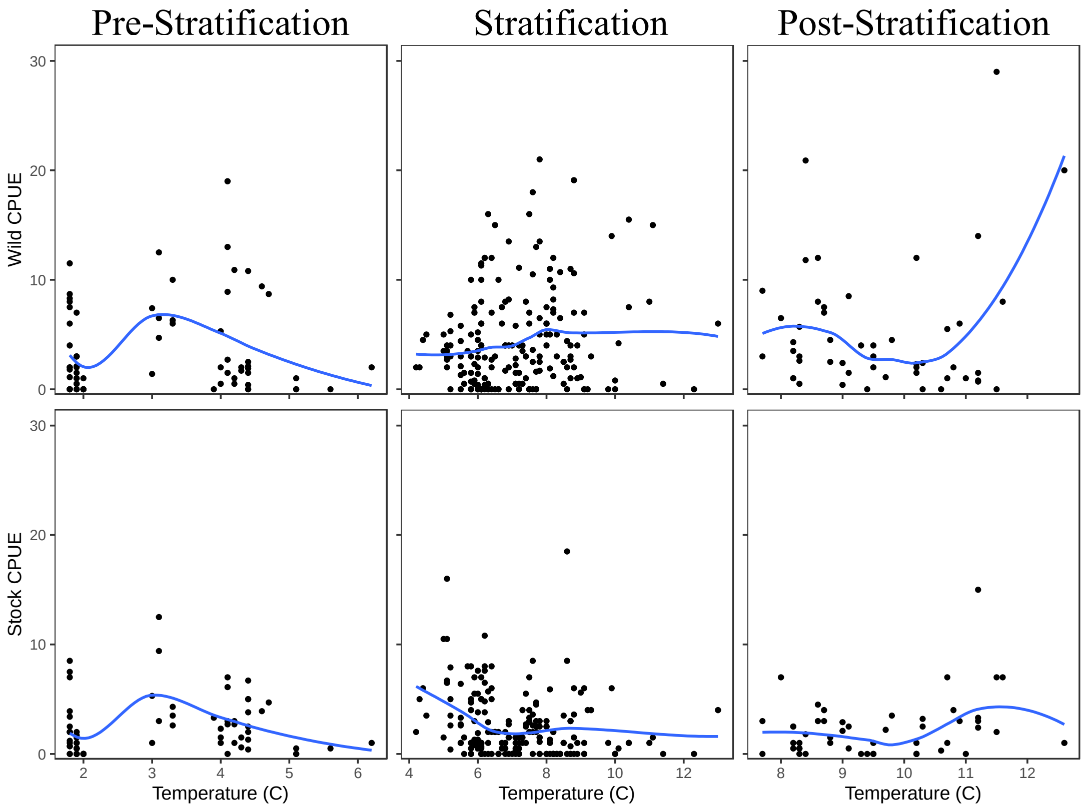

Figure 3.4: Mean and 95% confidence intervals for wild and stocked juvenile lake trout CPUE by mean temperature (ºC) based on stratification period. Black dots represent individual trawl catches.

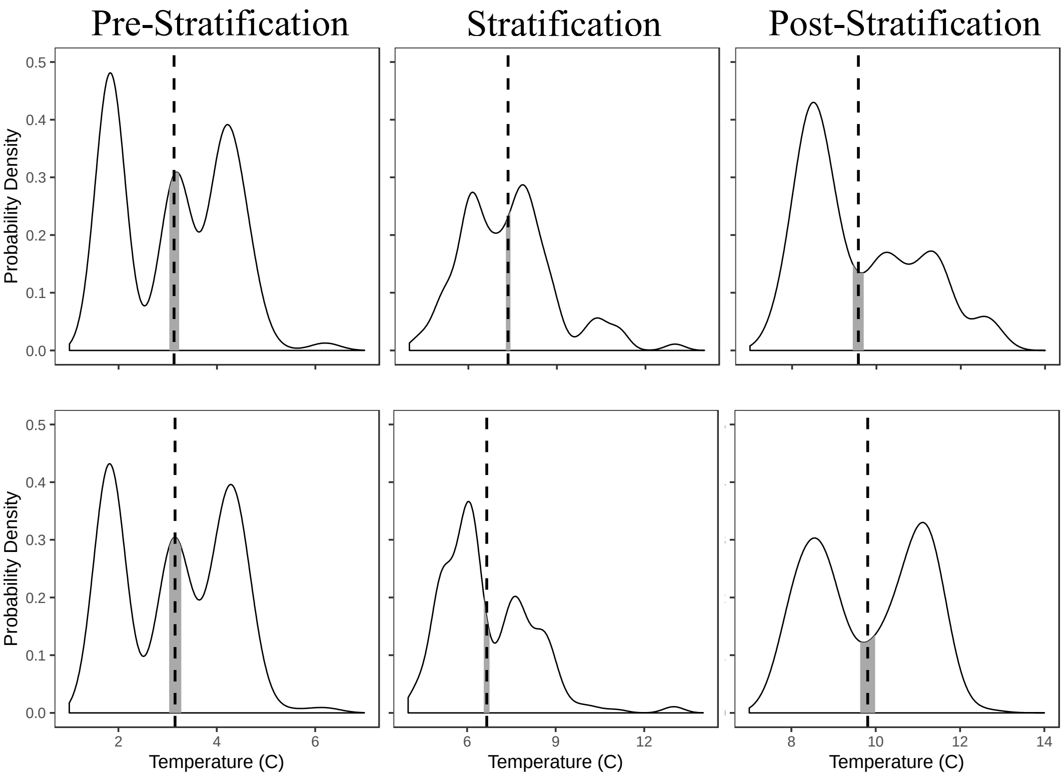

Figure 3.5: Kernel density plot with mean and 95% confidence interval of wild (top) and stocked (bottom) juvenile lake trout by temperature (ºC) based on stratification period. Shaded areas represent the 95% confidence interval for the mean depth from 1,000 bootstrap replicates. The dashed lines represent the mean temperature from the observed data.

CHAPTER 4: BIBLIOGRAPHY

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APPENDIX A

A.1 Introduction

The discovery of wild juvenile lake trout recruitment in Lake Champlain led to intense bottom trawl sampling over the course of five years at three different sampling areas (north, central, south), providing an abundance of information on juvenile lake trout growth, distribution, and diet (Marsden et al., 2018, Marsden et al., in prep, Sorrentino et al., in revision, Wilkins and Marsden in review, chapter 3). Although the concerted sampling effort provided insight into the extent of wild lake trout recruitment in the lake, the cost in terms of effort, funding, and sampling pressure is not sustainable. I used the prior five years to data to outline elements of a standardized trawling assessment. The goal of future sampling is to design an annual bottom trawl assessment protocol that will (1) maximize juvenile lake trout catch-per-unit-effort (CPUE, catch per 10 min of trawling), (2) provide an unbiased sample of wild and stocked juveniles to evaluate annual changes in percent of wild juveniles, (3) optimize sampling effort and cost (i.e., trawling focused on locations and depths most likely to collect juvenile lake trout), and (4) provide a repeatable standardized method that remains constant (i.e. same gear, duration, locations, depths, and times of year) to assess the juvenile population and provide researchers and managers with data to detect changes in the juvenile population (i.e., increase/decrease in wild and stocked juvenile lake trout abundance, presence/absence of age-0 wild lake trout recruiting to trawl).

A.2 Methods

Power analyses ($\alpha = 0.05, \beta = 0.20$) were used to determine the sample size required to assess annual changes to the juvenile lake trout population based on the proportion of wild juveniles. Two sets of power analyses were conducted, with one set using the 2019 proportion of wild juveniles in the central sampling area (0.57) as the baseline, and the other using no prior information (Table A.1). Plots of CPUE of wild and stocked juveniles by mean depth (m) and mean temperature at trawl depth (ºC) were used to visualize distributions of juvenile lake trout over the entire sampling period in the Main Lake of Lake Champlain. Mean catch (SD) and mean CPUE (SD) were binned into 5-min trawl duration ranges for the entire sampling period in both the Main Lake and more specifically in the central sampling area of Lake Champlain, where the majority of wild juveniles have been documented, to determine the most effective trawl duration. Mean total and wild CPUE (SD) was compared in each sampling area over the last five years of sampling, at different trawl depths, locations, and times of year to determine which could be removed to reduce unnecessary sampling effort and improve efficiency.

A.3 Results and Conclusions

Overall, the central sampling area had the highest mean wild CPUE and has the most habitat available for bottom trawling at multiple depths. The south sampling area had the highest mean total and stocked CPUE and the north sampling area had the lowest total, stocked, and wild mean CPUE values. CPUE of wild lake trout was highest at shallower depths (30-40 m) and CPUE of stocked lake trout was highest at deeper depths (45-55 m) based on the last five years of sampling in the Main Lake of Lake Champlain (Fig A.1). CPUE of wild juvenile lake trout were higher at warmer temperatures (7-12ºC) than colder temperatures (2-7ºC; Fig. A.2). Mean abundance of juvenile lake trout increased with trawl duration in the Main Lake, although the highest CPUE was in the 13-17 min duration range (Table A.2). Mean abundance and CPUE of juvenile lake trout were highest in the 13-17 min duration range in the central sampling area (Table A.3). In the north sampling area, the mean total and wild CPUE were both higher in trawls south of the Gordon Landing ferry crossing at Grand Isle, VT (Table A.4). In the south sampling area, mean total and wild CPUE was consistently higher than the north sampling area at both sampling locations, making the location closer to Burlington, Vermont (Essex to Boquet river, NY) preferable for future sampling (Table A.4).

To consistently catch high numbers of both wild and stocked juveniles and collect age-0 wild lake trout to assess annual recruitment, sampling in the central area in September and October at depths 30-45 m for 12-17 min is recommended (Table A.5). With additional time and funding, supplemental sampling in April could be used to document survival of wild age-0 lake trout past the first winter. Alternatively, extending the depth range to 25-55 meters in September and October in the central area would provide better coverage of both wild and stocked juvenile lake trout depth distributions.

Table A.1: Power analyses ($\alpha = 0.05, \beta = 0.20$) outputs to determine the sample size of juvenile lake trout required each year to correctly reject the null hypothesis (H_o, the proportion of wild lake trout in a total sample remaining the same) for a given effect size or difference in proportion, using 0.57, the 2019 proportion in the central sampling area, or no prior information as the baseline.

Prior information			No prior information	
Difference in proportion	Effect size	Sample size	Effect size	Sample size
-0.20	0.40	97	0.40	99
0.20	0.43	85	0.35	129
-0.15	0.30	174	0.30	175
0.15	0.32	159	0.25	252
-0.10	0.20	391	0.20	393
0.10	0.21	369	0.15	698

Table A.2: Mean total juvenile lake trout CPUE (catch per 10 min trawling) (SD), mean total juvenile catch (SD), total minutes of trawling, and number of trawls based on duration range (in minutes) of individual trawls conducted throughout the Main Lake of Lake Champlain, 2015-2019.

Trawl duration (min)	Total CPUE (SD)	Total catch (SD)	Total minutes	# of trawls
<8	1.2 (1.5)	0.7 (0.8)	33	6
8-12	7.1 (7.4)	7.2 (7.5)	1,475	146
13-17	7.8 (5.7)	12.1 (9.0)	507	33
18-22	6.0 (5.3)	12.0 (10.6)	4,760	239
23-27	5.0 (4.4)	12.5 (11.3)	398	16
28-32	3.9 (2.6)	13.1 (8.8)	272	9
33+	3.3 (1.6)	13.0 (6.3)	192	5

Table A.3: Mean total juvenile lake trout CPUE (catch per 10 min trawling) (SD), mean total juvenile catch (SD), total minutes, and number of trawls based on trawl duration range (in minutes) in the central sampling area of Lake Champlain, 2015-2019.

Trawl duration (min)	Total CPUE (SD)	Total catch (SD)	Total minutes	# of trawls
<8	1.2 (1.6)	0.6 (0.9)	26	5
8-12	7.6 (7.1)	7.7 (7.3)	1,112	110
13-17	8.3 (5.6)	12.8 (8.9)	476	31
18-22	6.4 (4.8)	12.6 (9.4)	3,120	157
23-27	4.3 (3.7)	10.8 (9.4)	372	15
28-32	3.8 (3.0)	11.5 (9.0)	121	4
33+	3.0 (1.6)	11.3 (5.7)	150	4

Table A.4: Mean total juvenile lake trout CPUE (catch per 10 min trawling) (SD), mean wild juvenile CPUE (SD), and number of trawls in each sampling subsection in the north and south sampling areas of Lake Champlain, 2015-2019.

Sampling area	Sampling subsection	Total CPUE (SD)	Wild CPUE (SD)	# of trawls
North	North of Gordon Landing	1.18 (1.62)	0.10 (0.26)	39
	South of Gordon Landing	3.80 (3.30)	0.95 (1.10)	41
South	Whallon-Essex	12.42 (8.87)	2.21 (2.23)	20
	Essex-Boquet	11.78 (6.63)	1.85 (1.73)	19

Table A.5: Decision table for which months, and how many months should be used for sampling juvenile lake trout in the central sampling area in Lake Champlain for different assessment goals.

# Months	Month(s)	Rationale
1 Month	Sept	High CPUE, assess age-0 abundance
2 Months	Sept, Oct	Most consistent months to collect juveniles
2 Months	April, Sept	Assess overwinter survival of age-0 recruits
3 Months	April, Sept, Oct	Assess summer and winter growth

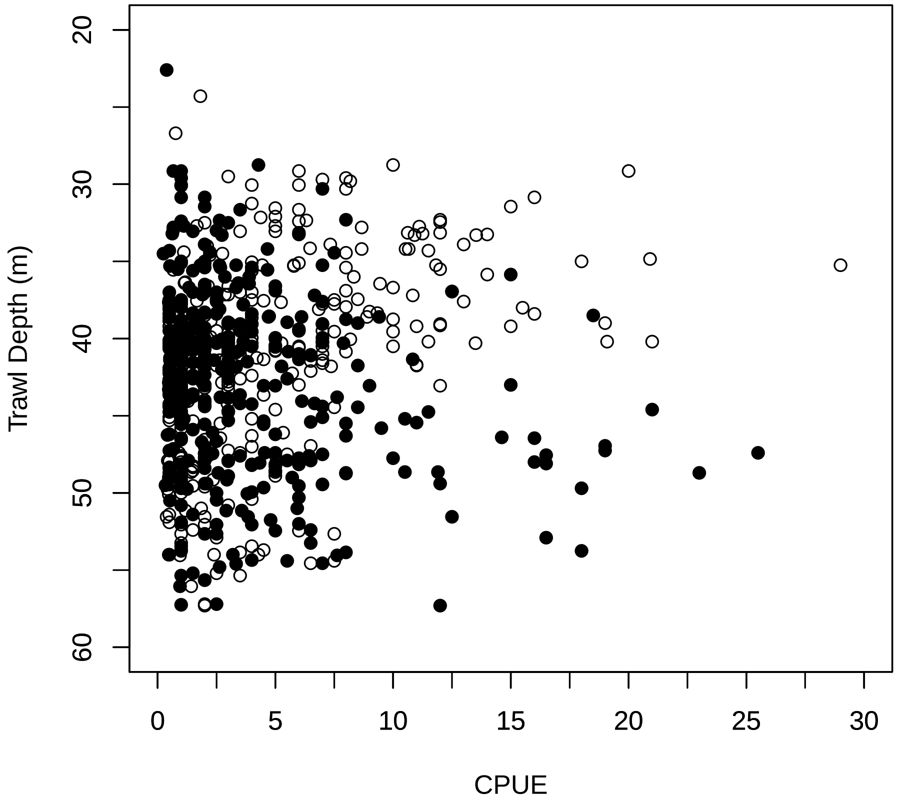

Figure A.1: CPUE (catch per 10 min trawling) of wild (open circle) and stocked (closed) juvenile lake trout by mean trawl depth (m) collected from each trawl in the Main Lake in Lake Champlain in 2015-2019.

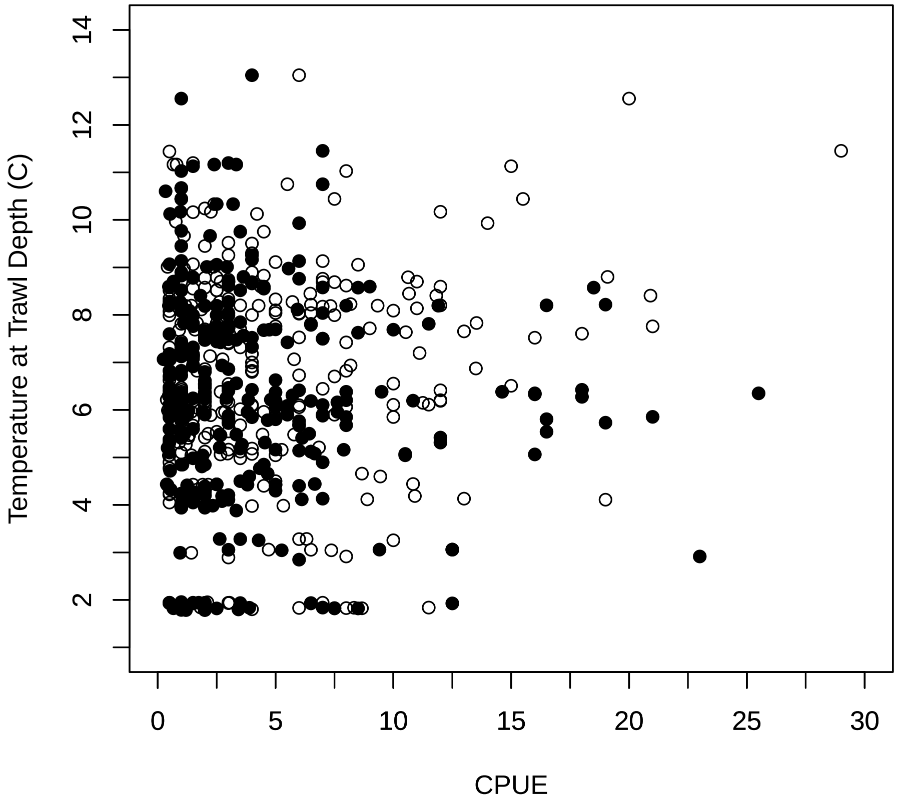

Figure A.2: CPUE (catch per 10 min trawling) of wild (open circle) and stocked (closed) juvenile lake trout by mean temperature at trawl depth (ºC) collected from each trawl in the Main Lake in Lake Champlain in 2015-2019.