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Spatio-temporal variation in total lipid content of stocked and wild juvenile lake trout (Salvelinus namaycush) in Lake Champlain

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Abstract:

After more than 40 years of stocking, lake trout (*Salvelinus namaycush*) in Lake Champlain have started to exhibit strong, natural recruitment which suggests a change in limiting factors such as the prey base or overwinter survival. The distribution of juvenile wild lake trout shows variation in abundance and condition factor among regions of Lake Champlain. These differences suggest the prey base, or foraging success, may vary geographically within the lake. Stocked and wild lake trout may differ in their ability to utilize resources and in overwinter survival. One metric that may indicate differences in resources across regions is lipid content, which reflects the quality of available food and acts as an important energy reserve for overwinter survival. We quantified total lipid content of stocked and wild juvenile lake trout across spatial (lake regions) and temporal (seasonal) scales. No spatial differences in lipid content were apparent. Wild fish were significantly greater in lipid content than stocked fish. Seasonally, stocked fish showed a drop in lipid content from pre-winter levels to the following spring, and lipids continued to drop through autumn. Wild fish showed a cyclical summer increase in lipids following replenishment from winter depletion, which plateaued by autumn. Results suggest that hatchery conditions cause stocked juvenile lake trout to be less competitive in the Lake Champlain environment than wild juveniles, evidenced by their lower lipid content and seasonal depletion. Hatchery practices could be modified to produce more competitive juvenile lake trout and support the goal of restoring a self-sustaining population.

Keywords: Lake trout, recruitment, lipids, Lake Champlain

Introduction

Lake trout *(Salvelinus namaycush)*, a popular recreational species, were extirpated from Lake Champlain, Vermont by 1900 (Plosila and Anderson, 1985). Restoration efforts began in 1972 with the implementation of an intensive stocking program to reestablish a self-sustaining population and a sustainable fishery (Marsden et al., 2010; Marsden and Langdon, 2012). Successful spawning and fry emergence were documented at several sites starting in 2000 but sustained natural recruitment did not begin until 2012 (Marsden et al., 2018). Recruitment in this case is defined as fish who have survived initial critical periods and progressed past the fry stage, attaining a large enough size to be captured.

Wild yearling and older lake trout have been absent from the lake trout population for decades (Marsden et al., 2018). Annual assessments by the Vermont Department of Fish and Wildlife evaluate the abundance and year classes of stocked lake trout by assessing fin clips; all stocked fish are clipped before release into Lake Champlain on a 5-year rotation between paired and adipose fins (Marsden et al., 2018). Annual autumn assessments of lake trout at two known spawning sites found that unclipped (wild) fish composed 2% or less of the adult lake trout since 2002. Two percent unclipped lake trout is below the level expected from missed fin clips in the hatchery or regrown fins, thus natural recruitment was not occurring (Marsden et al., 2018). All known sampling efforts for juvenile and adult lake trout between 2001 and 2012 yielded no wild juveniles (Marsden et al., 2018).

In 2015, sampling efforts focused on juvenile lake trout found high numbers of wild juveniles age 0 – 2; the first documented occurrence of juvenile wild lake trout in Lake Champlain in decades (Marsden et al., 2018). Subsequently, a sampling program for juvenile lake trout was implemented and included intensive sampling concentrated in the Main Lake basin and seasonal sampling across Lake Champlain to document juvenile lake trout distribution and quantify recruitment of wild fish (Marsden et al., 2018). Sampling between 2015 and 2018 provided evidence of sustained natural recruitment: the low proportion of unclipped fish from autumn spawning assessments indicate that natural lake trout recruitment is likely a recent phenomenon in Lake Champlain because no wild lake trout had yet been captured during spawning (Marsden et al., 2018). Evidence of natural recruitment is important for the recovery of lake trout in Lake Champlain, as it represents the first step towards establishment of a self-sustaining population.

Recent surveys have revealed that relative abundance of stocked and wild fish varies across regions of Lake Champlain in addition to providing evidence of recruitment. Between 2015 and 2016, the highest proportion of wild fish was consistently found in the central Main Lake, while the highest catch-per-unit-effort was found in the southern Main Lake (Marsden et al., 2018). Such differences in distribution contradict what might be expected from spawning site locations (Marsden et al., 2018). The spawning sites known to produce the most wild-hatched lake trout are located near Whallon Bay and Gordon Landing, which are south and north, respectively of the central Main Lake (Ellrott and Marsden, 2004). In the absence of other information, we might expect highest densities of fish and highest abundance of wild fish to be in the southern and northern regions of the Main Lake, reflecting these stocking and known spawning sites. The difference in expected versus observed distributions suggest that spatial differences in lake resources may exist that contribute to successful juvenile recruitment, or that unknown but successful spawning sites exist in the central Main Lake.

The cause(s) of the surge in natural recruitment is unknown, but its suddenness indicates a recent change in limiting factors such as a change in food quality or quantity that leads to improved overwinter survival (Marsden et al., 2018). For example, the Lake Champlain prey base was diversified in 2003 by the invasion of alewife (*Alosa pseudoharangus*), a known component of juvenile lake trout diets (Marsden unpubl. data; Madenjian et al., 2006). Winter has been well-documented as a period of mortality for juvenile freshwater fish when the risk of starvation, thermal stressors, predation and pathogens is high (Hurst, 2007; Needham et al., 1945). A change in overwinter survival as a result of milder winter conditions, increased prey availability, or other factors could help juvenile lake trout survive the winter critical period.

Why lake trout suddenly started to naturally recruit in Lake Champlain, and what drives spatial differences in their abundance, are two leading questions that, if answered, can help achieve a self-sustaining lake trout fishery. Lipids may provide some insight into these questions because of their role in fish health. Lipid content of lake trout likely reflects differences in foraging success and overwinter survival, and may help to uncover the reasons behind recent increases in recruitment. Lipids serve as energy resources, promote overwinter survival, are important during reproduction and early life history, and help fish to cope with environmental stressors (Adams, 1999; Tocher, 2003). Fish without energy reserves are dependent upon consistent energy acquisition; interruption of energy flow results in decreased health or condition (Adams, 1999). The lipid content of fish relates to lipid content of prey species. For example, the whole-body lipid content of juvenile Atlantic halibut (*Hippoglossus hippoglossus*) increased in response to manipulation of dietary lipid intake (Martins et al., 2007). Energy stores provided by lipids allow organisms to survive periods of low prey availability, such as the overwintering period (Adams, 1999; MacKinnon, 1972; Rikardsen and Elliott, 2000). During winter, many fish species use lipid stores for basic maintenance and other metabolic needs such that lipids are typically reduced by the end of winter (Adams, 1999). For example, juvenile rainbow trout (*Oncorhynchus mykiss*) and juvenile Atlantic salmon (*Salmo salar*) exhibited depleted lipid reserves (60-90% and 34-57% depletion, respectively) over winter (Biro et al., 2004; Naesie et al., 2006).

Available energy in the form of lipids can be used for growth, storage, reproduction and immediate metabolic needs (Adams, 1999; Sheridan, 1988). For juvenile fish in the pre-reproductive stages, the most important functions of lipids are likely growth and metabolic needs, and energy reserves for overwinter survival and migration or feeding efforts (Martin et al., 2017). The health and resilience of fish can often be predicted by lipid content; fish with low growth and condition factor (Fulton's K) have been shown to have correspondingly low lipid content (Amara et al., 2007). Total lipid content can provide an accurate measure of the energy status of a fish, and changes in lipid composition results in changes in energy density (Naesie et al., 2006; Trudel et al., 2005). Ultimately, lipids provide an energy resource for energy-costly processes such as reproduction (Adams, 1999). High lipid levels during reproduction may therefore indicate a self-sustaining population of wild lake trout.

Differences in lipid content may help to explain why lake trout are exhibiting natural recruitment and how different areas of the lake might support the growth of juvenile wild fish. Additionally, lipid content can indicate how well-prepared fish are to survive the winter months, and how they respond to winter depletion of energy reserves. Stocked and wild juvenile lake trout might also display differences in lipid content. Stocked fish are typically fed a high-fat diet prior to their release into Lake Champlain, while wild lake trout rely on the lake prey base and must capture food. Variation in lipid content between stocked and wild juvenile fish could reveal differences in the ability of wild fish compared to the ability of stocked fish to survive stressors such as the winter season.

Lipid content can help us to better understand lake trout recruitment in Lake Champlain, inform stocking and conservation efforts, and support the goal of naturally reproducing fish populations. Spatial differences can provide insight in the potential suitability of different areas of the lake to support juvenile lake trout growth, and seasonal differences can provide insight on how fish respond to winter conditions, which may impact juvenile survival rates. We hypothesized that total lipid content of lake trout would be greatest in the central Main Lake where wild recruits are most abundant, and in the summer when the prey base is most abundant. We also hypothesized that the high-ration diet fed to stocked lake trout would cause stocked juveniles to have a higher lipid content than wild juveniles. To test our hypotheses, we measured total lipid content of stocked and wild juvenile lake trout (ages 0-3) in Lake Champlain from three areas of the Main Lake basin duringthree seasons, as well as fish from the hatchery.

Methods

Study System

Lake Champlain is situated between New York and Vermont, USA, and Quebec, Canada (Figure 1). The lake is 193 km in length, has a maximum width of 20 km, and an average depth of 19.5 m. Lake Champlain is divided into five trophically distinct basins: Missisquoi Bay, the Inland Sea, Malletts Bay, the Main Lake, and the South Lake (Marsden and Langdon, 2012). Lake trout are stocked at four locations: mainly in Burlington Bay and Whallon Bay, and to a lesser extent in Gordon Landing and Arnold Bay (Marsden et al., 2018).

Sample Collection

Fish capture took place at three areas in the Main Lake: near Burlington Bay, Whallon Bay, and Grand Isle (hereafter referred to as the central, south, and north sites) (Figure 1). We selected these locations to assess the condition of lake trout spatially across Lake Champlain. Additionally, sampling efforts for lake trout have been concentrated at these locations over the past four years, which provided evidence of variation in relative abundance of stocked and wild lake trout across the lake (Marsden et al., 2018).

Sampling was conducted between 8 June and 28 September 2018 to assess potential seasonal changes in lake trout condition. The central site was sampled every 2-3 weeks, and north and south sites were each sampled twice (June and August). We used a three-in-one bottom trawl with a 8 m headrope, 9.3 m footrope with chains attached, and 1.25 mm stretch cod end liner (Marsden et al., 2018). Tows were 20 minutes at ~5.5 km/h. Trawling was conducted along contours at depths from 28.2 m to 63.5 m, with the majority of tows concentrated around 40 m. Approximately 30 lake trout were systematically selected from the trawls on each sampling date to represent the range of sizes captured up to 300 mm and included both stocked and wild fish from each site (i.e., 15 stocked and 15 wild fish). Stocked fish were identified based on presence of a fin clip. Fish were immediately frozen on dry ice and stored at -80°C until lipid extraction. A sample of hatchery-raised lake trout (15 fish) was collected from the Ed Weed Fish Culture Station, Grand Isle, VT, on 15 November 2018 to assess lipid content of the lake trout a week prior to release into Lake Champlain.

Sample Preparation

All lake trout were thawed and measured (total length), weighed, re-assessed for fin clips, aged based on fin clips and non-overlapping size classes, and dissected to remove the stomach contents. Stomach contents were removed to avoid any influence of recently consumed prey on the estimate of total lipid content. Each lake trout >150 mm in total length was homogenized in a Ninja BL500 Professional Blender, and a ~30 g subsample was removed. Lake trout <150 mm in total length were dried whole. Subsamples and whole small fish were dried to a constant mass at 65°C. Once dry, samples were ground in a mortar and pestle to produce a fine powder.

Lipid Extractions

Three 1g (for lake trout >150mm) or 0.5 g (for lake trout <150mm) aliquots were measured from the dried mass of each fish, and placed into pre-weighed 50 ml conical centrifuge tubes. Samples were analyzed for total lipid content according to a modified version of the Folch et al., (1957) method. Briefly, 10 or 20 ml (depending on sample size) of a 2:1 chloroform:methanol solution was added to each centrifuge tube. Samples were agitated for 30 seconds using a vortex, and centrifuged for 10 minutes at 3,000 rpm. The lipid-containing supernatant was carefully pipetted off to avoid disturbing the pellet, and the process from addition of chemicals to removal of the supernatant was repeated once more. Samples were then dried for 24 hours at 65°C to ensure evaporation of any remaining chloroform:methanol solution. Samples were weighed again in the centrifuge tubes to find the final lipid-free dry mass measurement.

Data Analysis

Mean percent total lipid content (MPTLC) of the dry fish weight (hereafter referred to as mean percent lipid content) was determined by dividing the pre-extraction weight of each sample by the post-extraction weight and converting to a percent, after subtracting the weight of each centrifuge tube. The percent total lipid content of the three subsamples per fish was averaged together to find the MPTLC for each fish. MPTLC was compared across sites (north, south, and central) and seasons (spring, summer, autumn) using two-way ANOVAs. We ran interactive tests, incorporating the source (stocked vs wild) variable in all analyses as a covariate, along with total length as a scaling factor. We also ran a Tukey HSD test for pairwise comparisons using glht and mcp from the multcomp package v1.4-10 in the R™ statistical environment v3.5.2. (Hothorn et al., 2019; R Core Team, 2018).

Results

A total of 197 juvenile lake trout (85 wild and 112 stocked, including 15 hatchery-sampled fish) were analyzed for mean percent total lipid content. Average (± SD) MPTLC content was 15.2 ± 7.1% of dry mass for stocked fish in the lake and 17.0 ± 6.8% for wild fish. Average percent lipid content of lake trout from the hatchery was 35.1 ± 2.9% of dry mass.

We found no differences in mean percent lipid content spatially across the three Main Lake sites ($F_{2,175} = 1.744$, $p = 0.178$) (Figure 2). However, we did find significant differences in mean percent lipid content between stocked and wild fish ($F_{1,175} = 24.8$, $p < 0.001$) (Figure 2). In the central and southern Main Lake, wild fish showed significantly greater mean percent lipid content than their stocked counterparts ($F_{1,175} = 3.6$, $p = 0.004$) and ($F_{1,175} = 3.0$, $p = 0.03$), respectively.

Juvenile lake trout from the central Main Lake varied significantly in mean percent total lipid content seasonally ($F_{2,94} = 14.3$, $p < 0.0001$) (Figure 3). Mean percent lipid content was slightly lower in summer (July – August; ($F_{5,94} = -2.9$, $p = 0.01$)) and much lower in Autumn (September; ($F_{5,94} = -4.8$, $p < 0.0001$)) than spring (June) for all fish. A pairwise comparison further revealed that stocked fish specifically are lower in mean percent lipid content during the summer than wild fish ($F_{5.94} = 3.4$, $p = 0.01$).

Discussion

We tested three hypotheses focused on spatial, temporal, and source-based variation in mean percent total lipid content of juvenile lake trout. We found significant differences between stocked and wild fish, where wild fish are higher in lipid content. Seasonally, stocked fish show very different changes in lipid content than wild fish. Finally, we did not find any significant spatial variation in percent total lipid content of juvenile lake trout.

We expected to find greater mean percent lipid content of juvenile lake trout in the central Main Lake basin near Burlington Bay than in the northern or southern Main Lake. The greatest proportion of wild juvenile lake trout have consistently been captured in the central Main Lake region (Marsden et al., 2018). However, during this study, the greatest proportions of wild lake trout were not found near locations of known spawning sites, Whallon Bay and Gordon Landing, suggesting movement by juvenile lake trout across the Main Lake. Alternatively, recruitment could be low in the north and south Main Lake and an unknown but successful spawning site in the central Main Lake could exist to explain spatial differences.

We expected that differences in prey quantity or quality might draw juvenile lake trout to the central Main Lake or lead to greater survival in the region. The lack of variation in lipid content suggests that lake trout do not experience differences in prey availability among the areas of the Main Lake where we sampled. For example, an assessment of rainbow smelt (*Osmerus mordax*), a common prey source for juvenile lake trout in Lake Champlain from 2001 to 2002 found that age-0 and age-1 smelt varied in density across the lake (Thomson et al., 2011, Madenjian et al., 1998). Because rainbow smelt density appears spatially and annually variable, the likelihood that the central Main Lake consistently provides food resources in markedly different quantities than the rest of the Main Lake seems slim. The lack of spatial differences in lipid content could therefore reflect this lack of difference in prey resources. An analysis of total abundance, relative species abundance, and total lipid content of forage base available to juvenile lake trout (e.g. alewife (*A. pseudoharangus*), *M. diluviana,* rainbow smelt (*O. mordax*), slimy sculpin (*Cottus cognatus*)) could provide more definitive evidence on the potential effects of the prey base on total lipid content of juvenile lake trout.

We also considered the effects of Lake Champlain's internal seiche on juvenile lake trout distribution. Lake Champlain experiences an internal seiche that can produce currents up to 50 cm/s; these currents might cause juvenile lake trout to use excess energy to maintain their position (Manley et al., 1999; Marsden et al., 2018). The axis of the seiche is in the central Main Lake, so we expected that juvenile lake trout may take refuge in the central Main Lake to avoid the effects of seiche-driven currents, or may be driven to the central Main Lake by the seiche currents. High water velocity has been shown to deplete lipid content. Juvenile Atlantic salmon inhabiting streams of different water velocities showed lower lipid content in high velocity waters compared to low velocity waters, as maintenance of body position against water currents requires increased use of energy reserves (Cleary et al., 2012). However, any potential effects on lipid content from moving against the seiche in areas further from the axis of rotation do not appear strong enough to cause noticeable spatial differences in mean percent lipid content for the juvenile lake trout in this study.

We expected to find that stocked juvenile lake trout would possess a higher percent lipid content than their wild counterparts. Hatchery-raised fish are typically fed a high-ration diet rich in lipids that is reflected in their body composition (Reinitz, 1983). Populations of Stocked fish have been documented to have higher total body lipid content than wild fish, such as hatchery-reared Atlantic salmon parr and smolts relative to wild Atlantic salmon (Bergstrom, 1989). However, the wild fish that we analyzed had significantly greater mean percent lipid content than the stocked fish. Analysis of the stocked lake trout sample collected from the Ed Weed Fish Culture Station showed that stocked lake trout are released with a mean percent lipid content roughly three times greater than what we found for a typical wild fish of the same size in Lake Champlain. Lipid content of newly stocked lake trout drops markedly over their first winter to the level of wild fish and continues to drop throughout summer until by autumn the stocked juvenile lake trout are lower in mean percent lipid content than wild juvenile lake trout of the same age class, although larger in size.

The high lipid content of wild compared to stocked juvenile lake trout suggests that wild fish may compete for prey in Lake Champlain better than stocked fish. Stocked fish are raised in artificial environments where non-living food is typically added to the surface of the water – spatial and temporal variation in prey availability is not a component of the hatchery experience for young salmonids (Brown and Laland, 2002; Brown et al., 2003; Saikkonen et al. 2011). Such conditions select for bold fish that stay at the surface of the water, and for aggressive fish that can outcompete conspecifics for food (Saikkonen et al., 2011). Relatively unlimited feeding in the absence of predators may also encourage the bold behavior seen in hatchery lake trout. In the hatchery environment, such traits enable fish to feed more efficiently but are less applicable to natural conditions (Saikkonen et al., 2011). For example, hatchery-raised fish are less competitive in the wild, where they consume less food, fewer prey types, and exhibit a reduced ability to switch to new prey types (Saikkonen et al., 2011). Density-dependent growth and condition factor, decreased fin quality, and inferior anaerobic capacity and swim performance have also been documented for fish raised in hatcheries (McDonald et al., 1998). Hatchery-raised brook trout (*Salvelinus fontinalis*) also exhibited lower survival rates once released compared to wild fish because of poor foraging ability (Ersbak and Haase, 1983). The body of evidence suggests that hatchery-raised salmonids, such as the lake trout that we examined, are less competitive in the natural lake environment, and could lead to lower lipid levels compared wild lake trout, as we found in this study.

We also found seasonal differences in mean percent lipid content of juvenile lake trout in the central Main Lake. For all fish collected from the central Main Lake, we found that summer mean percent lipid content was slightly lower than spring lipid levels, and that autumn lipid levels were much lower than spring. These findings contradict patterns reported for other piscivorous fish, where lipids are usually low in the springtime after overwinter depletion, greatest in the midsummer months when feeding opportunities are best, and plateau by autumn when productivity drops before winter (e.g. Madenjian et al., 2000; Metcalfe et al., 2002).

When we analyzed temporal patterns in mean percent lipid content separated by source, stocked and wild fish showed very different trends in lipid levels; the pattern in lipid content exhibited by the stocked fish appears to influence the overall trend when all fish were analyzed together. Lipid content of wild fish was consistent with other salmonid fishes where lipids are greatest in the summer and lower in spring and autumn (e.g. Madenjian et al., 2000; Metcalfe et al., 2002). Lipid content would logically be greeatest in the summer months when food is most abundant (e.g. changes in abundance of prey items such as rainbow smelt and alewife in Lake Champlain found by Simonin et al., (2012)). Stocked fish, however, exhibited significant declines in lipid content from spring to summer to autumn. The rate of decline in lipid content for stocked fish seems to slow throughout the seasons, as both summer and autumn lipid content are significantly lower than spring, but autumn lipid content is not significantly lower than summer lipid content. Lipid levels of the November hatchery fish were also much greater than the spring lipid levels of stocked fish caught in the lake. The drop in lipid content from pre-winter hatchery lipid levels to spring post-winter levels and further decrease through the summer season into August suggests that stocked lake trout experience a decline in lipid content even through the increase in foraging opportunities that summer provides.

Winter has been well-established as a critical period for young fish that can impact recruitment (e.g. Hurst, 2007; Needham et al.,1945). The consistent seasonal decline that we found in lipid content of stocked juvenile lake trout suggests that these fish will have less energy reserves than wild juveniles to survive through winter. The high-nutrient diet that stocked lake trout were fed in the hatchery does not appear to give them an advantage over wild lake trout, as wild fish surpass stocked fish in lipid content by the summer following their first winter in the lake. The competitive strategies that stocked lake trout learn in hatchery conditions highlighted earlier in this discussion may contribute to the seasonal changes in lipid content that differ between stocked and wild fish.

Future work should focus on several areas to better understand the recent increase in wild recruitment, spatial differences in wild juvenile abundance, seasonal effects, and the effects of the stocking program on juvenile lake trout. Most importantly, more lake trout from a wider range of age classes are needed to form a more complete picture of lipid levels of juvenile lake trout. The number and size range of lake trout in this study were limited given the time constraints under which sampling took place. Additionally, data from consecutive years will add power to the analyses completed in this study. The study period (June-September 2019) limits conclusions that can be drawn about long-term trends, and changes in lipid levels of the lake trout population from year to year.

To re-examine the spatial component of this study, more intensive sampling of the prey base across the Main Lake could help to definitively understand if prey is a factor in spatial differences in juvenile lake trout distribution. Additionally, sampling efforts across more of Lake Champlain would broaden the spatial implications of this study. While noticeable differences in the prey base may not exist in the Main Lake basin, they may very well exist when all of Lake Champlain is under consideration. The seasonal element of this study could greatly benefit from winter sampling of juvenile lake trout. We suspect a winter dip in lipid content based on spring and autumn trends, and on our analysis of dropping lipid levels of stocked fish on a sample from fish pre-release. However, winter sampling efforts would provide more definite evidence of the trends that we suspect from this study. Additional years of sampling including winter sampling would also provide a more complete picture of the drop in lipid levels from the release of stocked fish to the following spring, as fin clip data would allow us to assess the same cohort of fish across seasons and years.

The ultimate goal of the lake trout stocking program in Lake Champlain is to restore a self-sustaining population (Marsden and Langdon, 2012; Marsden et al., 2010). The recent phenomenon of natural recruitment in the lake trout population suggests that factors that promote survival of wild juvenile fish have changed in Lake Champlain. Our results suggest that current hatchery practices may not be best suited to produce the most competitive juvenile lake trout for the Lake Champlain environment. Stocked juvenile fish appear less competitive than wild fish, evidenced by their low lipid levels in comparison to wild juvenile fish and seasonal decline in lipid content while wild fish show a normal cyclic increase in summer months. Hatchery practices should emphasize growth of juvenile lake trout that are suited for life in the lake environment. Practices could include the reduction of rearing densities, which has been shown to increase growth, condition, lipid stores, and swimming performance (McDonald et al.,1998; Saikkonen et al., 2011). The exposure to live prey items prior to release into the natural environment has also been shown to increase foraging success of hatchery-raised fish (Brown and Laland, 2002). Additionally, a more feasible change to hatchery practices could involve investing less resources into raising large fish and releasing hatchery-raised lake trout at a smaller size, as the fish lose their lipid-based advantages over the first winter. The modification of hatchery practices for lake trout restoration in Lake Champlain and potentially other areas struggling to recover self-sustaining populations will likely lead to more lipid-rich, competitive individuals that are better suited for life in their natural environment and the continuation of wild recruitment.

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Figure Captions

Figure 1: Sampling sites in Lake Champlain: north (A), central (B), and south (C) Main Lake. The three locations were sampled between 8 June and 29 September 2019.

Figure 2: Spatial comparison of mean percent total lipid content of the dry weight of juvenile lake trout ages 1-3 in Lake Champlain captured between 8 June and 29 September 2019. Grey bars denote stocked (fin-clipped) lake trout, and white bars denote wild (unclipped) lake trout. Error bars show standard deviation. Sample size is indicated at the base of each data bar. North, central, and south refer to the sampling regions in the Main Lake basin.

Figure 3: Seasonal comparison of mean percent total lipid content of the dry weight of juvenile lake trout ages 0-3 in Lake Champlain captured between 8 June and 29 September 2019. Grey bars denote stocked (fin-clipped) lake trout, and white bars denote wild (unclipped) lake trout. Error bars show standard deviation. Sample size is indicated at the base of each data bar. The seasons refer to the month in which lake trout were captured: June (spring), July – August (summer), September (autumn), and a November sample from the Ed Weed Fish Culture Station (pre-winter). We refer to the hatchery sample as pre-winter for comparison between pre-winter and post-winter (i.e., spring) fish.

Figures

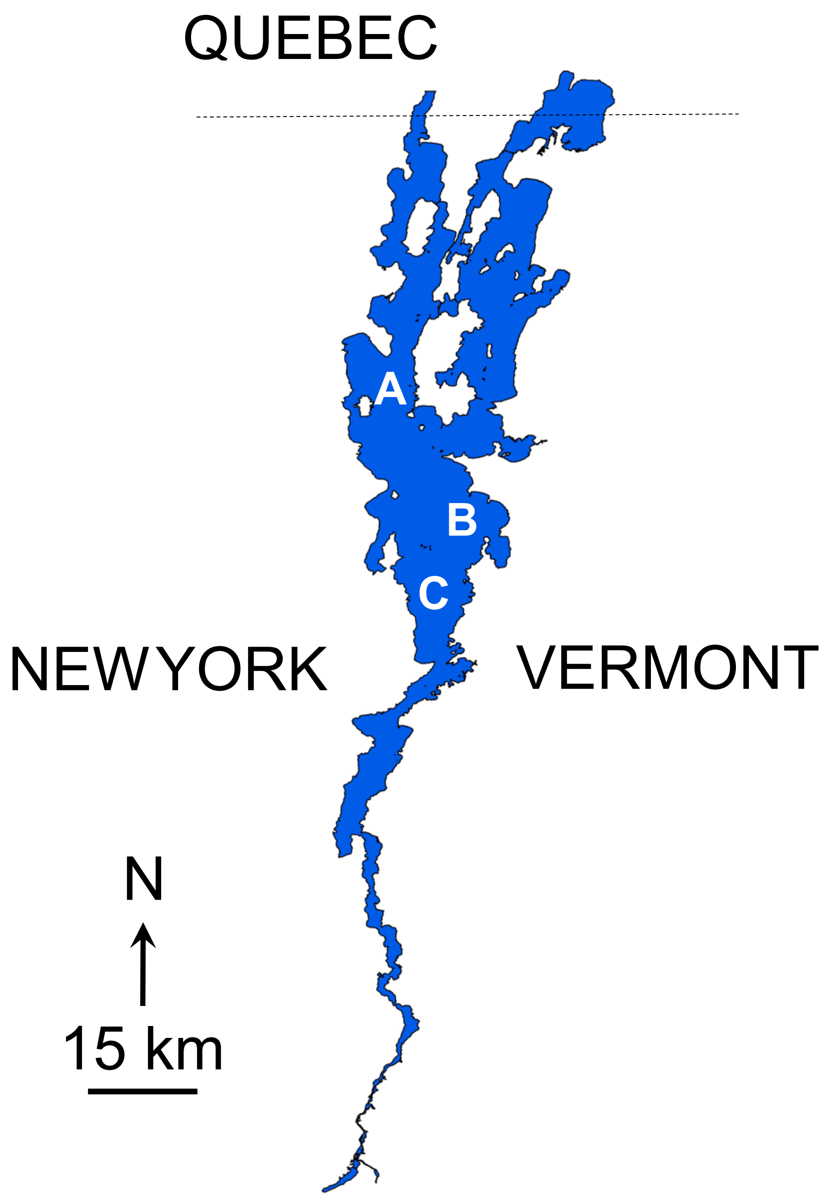

Figure 1

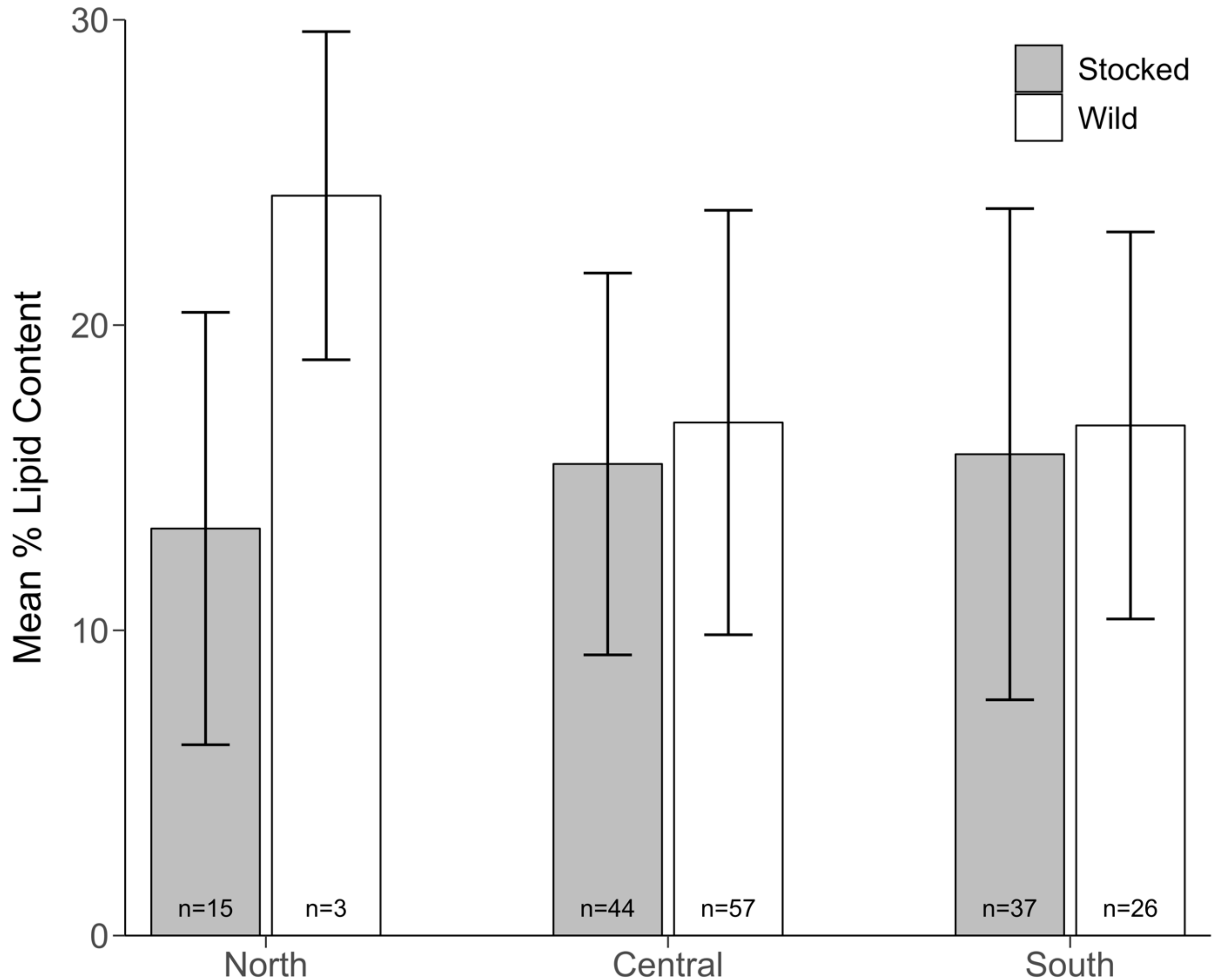
30
20
10
0
Mean % Lipid Content
Stocked
Wild
n=15
n=3
n=44
n=57
n=37
n=26
North
Central
South

Figure 2

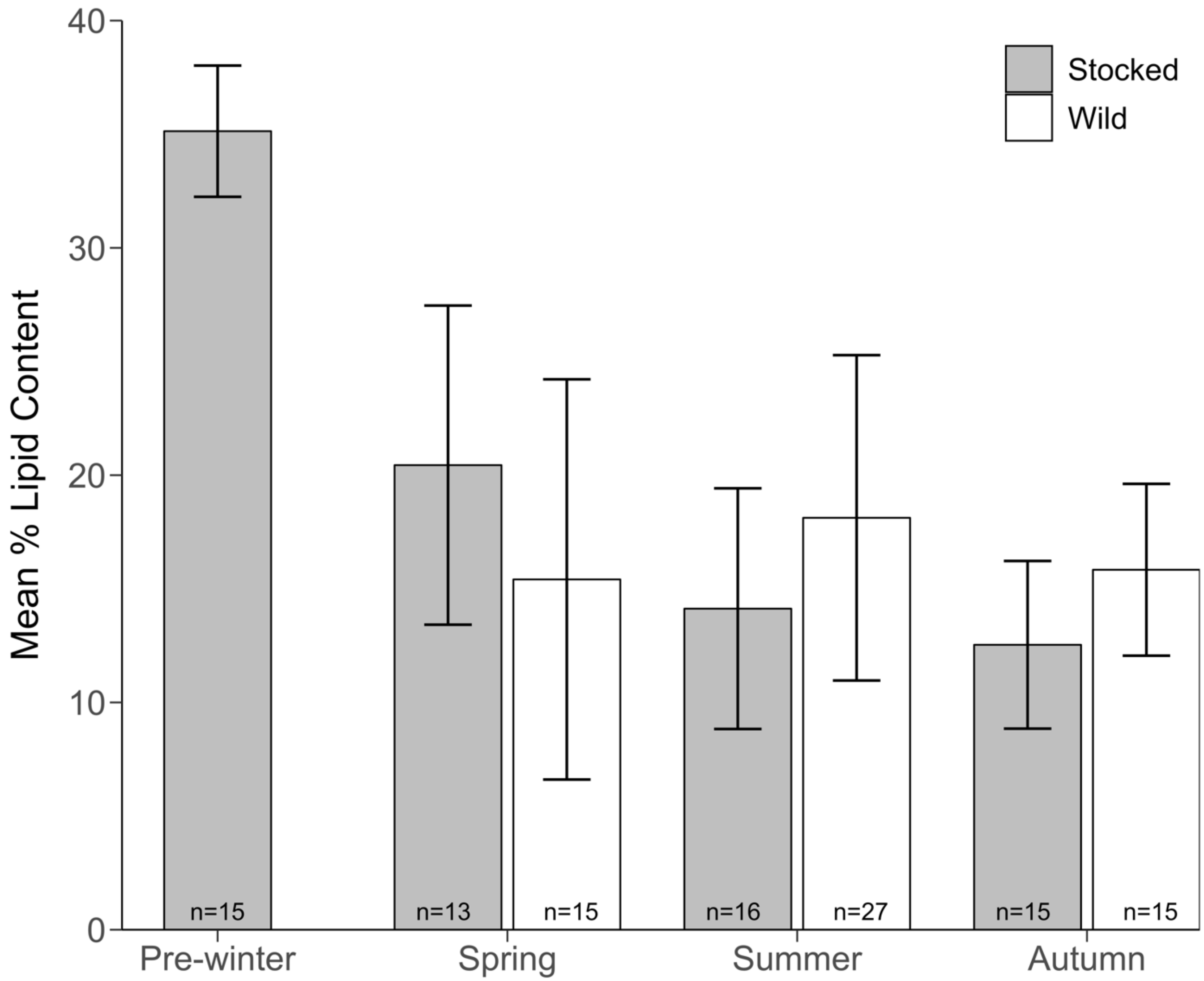
40
30
20
10
0
Mean % Lipid Content
Stocked
Wild
n=15
n=13
n=15
n=16
n=27
n=15
n=15
Pre-winter
Spring
Summer
Autumn

Figure 3