**Differential lipid dynamics in stocked and wild juvenile lake trout**

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\*Corresponding author. Email: [ellen.marsden@uvm.edu](mailto:Madelyn.sorrentino@uvm.edu); telephone 802-598-8224; fax 802-656-8683 **Abstract:**

After 45 years of stocking, lake trout in Lake Champlain have started to exhibit strong natural recruitment, suggesting a recent change in limiting factors such as prey availability or overwinter survival. The abundance of juvenile wild lake trout varies among regions of Lake Champlain, which suggest the prey base, or foraging success, may vary geographically within the lake. One metric that can indicate differences in resources across regions is lake trout lipid content, which reflects the availability of food and serves as an important energy reserve for overwinter survival. We quantified total lipid content of stocked and wild age-0 to age-3 lake trout among lake regions and seasons. No spatial differences in lipid content were apparent, but wild fish had higher overall mean ± SE percent total lipid content (17.0 ± 0.7% of dry mass) than stocked fish (15.2 ± 0.7%). Lipids in fish stocked in November were high (35.1 ± 0.7% of dry mass) but dropped by spring (14.9 ± 1.3%) and continued to decline through autumn. Wild fish showed seasonal changes with winter depletion in lipids followed by summer increase, and a plateau in autumn. The lipid depletion in stocked fish poses two competing hypotheses: 1) the high lipid concentration is necessary for stocked age-0 fish to transition to foraging in the wild, or 2) the high lipid concentration is difficult to maintain on a wild diet and reduces survival in the first post-stocking year.

**Keywords:** *Salvelinus namaycush*, recruitment, lipids, Lake Champlain, hatchery

**Introduction**

Lake trout *(Salvelinus namaycush)* were extirpated from Lake Champlain by 1900 (Plosila and Anderson, 1985). Restoration efforts began in 1972 with an intensive stocking program to reestablish a self-sustaining population and a recreational fishery (Marsden et al., 2010; Marsden and Langdon, 2012). Successful spawning and hatching were documented at several sites starting in 2000 but sustained natural recruitment was not observed until 2012, four decades after the stocking program commenced (Marsden et al., 2018). Thus, a survival bottleneck appears to have been present between newly hatched age-0 and age-1 wild lake trout; age-0 lake trout stocked in fall at the size of age-1 wild fish survive to maturity and have established a population in Lake Champlain. Recent natural recruitment may be due to a change in limiting factors such as food quality or quantity. For example, the Lake Champlain prey base was diversified in 2003 by the invasion of alewife (*Alosa pseudoharengus*), a known diet item of juvenile lake trout (Marsden et al. unpublished data; Madenjian et al., 2006). Additionally, winter can be a period of high mortality for juvenile fishes when the risks of starvation, thermal stress, and predation are high (Hjort, 1914; Hurst, 2007). Increased prey availability, milder winter conditions, or other factors could help juvenile lake trout survive through the winter.

Bottom trawl surveys were initiated in 2015 to target age-0 to age-3 juvenile lake trout. Trawl catches indicated that abundance of these year classes of stocked and wild lake trout varied among regions of Lake Champlain (Marsden et al., 2018; Wilkins and Marsden in revision). Annual stocking occurs at two spawning sites, Whallon Bay in the southern Main Lake and Gordon Landing in the northern Main Lake, and both sites produce high densities of newly hatched lake trout (Ellrott and Marsden, 2004). Few spawning sites have been identified in the central lake, so we expected to find higher abundance of wild lake trout near Whallon Bay and Gordon Landing than in the central lake. However, the highest proportion and abundance (catch-per-unit-effort, CPUE) of age-0 to age-3 wild fish has been consistently found in the central lake (Marsden et al., 2018; Wilkins and Marsden in revision). This difference in expected versus observed distributions suggests that (1) unknown spawning sites that successfully produce age-0 lake trout are present in the central Main Lake, (2) wild lake trout move from the northern and southern spawning sites to the central Main Lake, or (3) mortality of age-0 wild lake trout in the north and south is higher than in the central Main Lake. Either of the latter two possibilities may be due to an asymmetrical distribution of prey resources across the lake. Age-0 lake trout primarily consume *Mysis diluviana*. By age-1, juvenile lake trout begin to consume small alewife (*Alosa pseudoharengus*), smelt (*Osmerus mordax*), and slimy sculpin (*Cottus cognatus*) (unpublished data). However, estimates of the abundance of these prey species in different areas of the Main Lake are not available.

Lake trout are stocked in Lake Champlain in fall as ‘fingerlings’, i.e., age-0, but at a range of sizes (149-211 mm) similar to fall age-1 wild lake trout (145-232 mm, Wilkins and Marsden in review, Marsden et al. 2018). Consequently, size may be a more relevant metric than age when evaluating diet, growth, and condition. Lipid concentration in juvenile lake trout could provide insight into the recent surge in natural recruitment as an indirect measure of foraging success – lipids serve as energy resources and help fish to cope with environmental stressors (Adams, 1999; Tocher, 2003). In particular, lipids are used for basic maintenance and other metabolic needs during winter, when prey availability is presumably low and typically reduced by the end of the open-water season (Adams, 1999; MacKinnon, 1972; Rikardsen and Elliott, 2000). For example, juvenile rainbow trout (*Oncorhynchus mykiss*) and juvenile Atlantic salmon (*Salmo salar*) exhibited depleted lipid reserves (by 60-90% and 34-57%, respectively) over winter (Biro et al., 2004; Naesie et al., 2006). Additionally, the health of fish can often be predicted by lipid content; fish with low growth and condition factor have correspondingly low lipid content (Amara et al., 2007). Accordingly, total lipid content provides an assessment of the energy status of a fish (Naesie et al., 2006; Trudel et al., 2005), and may indicate how well fish are prepared to survive the winter. Differences in lipid content may help explain why lake trout in Lake Champlain are exhibiting natural recruitment and how different areas of the lake might support the growth of juvenile wild fish. Variation in lipid content between stocked and wild juvenile fish could also reveal differences in the abilities of wild and stocked fish to survive stressors such as the winter season.

We hypothesized that total lipid content of wild juvenile lake trout would be greatest in the central Main Lake where wild recruits are most abundant (Marsden et al., 2018; Wilkins and Marsden in revision). We also examined seasonal lipid differences that might confound site-related comparisons. We also hypothesized that newly stocked lake trout would have a higher lipid content than wild juveniles because hatchery fish are typically fed a highly nutritious diet under ideal conditions prior to their release. However, post-release stress and adaptation to a wild-caught diet could result in a substantial reduction in lipid content. To test our hypotheses, we measured total lipid content of stocked and wild juvenile lake trout (ages 0-3) captured from three areas of the Main Lake basin of Lake Champlain during three seasons, and lipid content of age-0 hatchery lake trout prior to stocking.

**Methods**

*Study System*

Lake Champlain is situated among New York and Vermont, USA, and Quebec, Canada (Figure 1). The lake is 193 km long, with a maximum width of 20 km. The Main Lake is meso-oligotrophic, with a maximum depth of 122 m. Since 1995, lake trout have been primarily stocked at Whallon Bay, Gordon Landing, and Burlington Bay (Figure 1; Marsden et al., 2018).

*Sample Collection*

Fish were sampled in 2018 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). Sampling efforts for juvenile lake trout have been concentrated at these locations over the previous four years, and provided information on variation in abundance of stocked and wild lake trout throughout the Main 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 an 8-m headrope, 9.3-m footrope with chains, and 1.25-mm stretch cod end liner (Marsden et al., 2018). Trawl tows were taken along-contour at depths from 28 m to 64 m, with the majority of tows concentrated around 40 m, for 10 or 20 min at ~5.5 km/h. Approximately 30 lake trout were 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 were targeted). Stocked fish were identified based on presence of a fin clip (Marsden et al. 2018). Fish were immediately frozen on dry ice and stored at -80°C until lipid extraction. A sample of hatchery-reared 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*

In the laboratory, lake trout were thawed, measured for total length, weighed, and re-assessed for fin clips. Age of stocked fish was known based on fin clips and estimated for wild fish based on non-overlapping size classes (Marsden et al., 2018). Fish were dissected and stomach contents removed to avoid any influence of recently consumed prey on the estimate of total lipid concentration. 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 for 72 hours. Once dry, samples were ground into a fine powder by mortar and pestle.

*Lipid Extractions*

Three 1-g (for lake trout >150mm) or 0.5-g (for lake trout <150mm) samples 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 weight) 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 pipetted off to avoid disturbing the pellet, and the process was repeated a second time. The resulting pellets were then dried for 24 hr at 65°C to evaporate any remaining chloroform:methanol solution. Samples were weighed again in the centrifuge tubes to estimate the final lipid-free dry mass measurement.

*Data Analysis*

Mean percent total lipid concentration (MPTLC) of the dry fish weight was determined by dividing the lipid weight (i.e., the pre-extraction weight minus the post-extraction weight) of each sample by the pre-extraction weight and converting to a percent. The three subsamples for each fish were used to calculate average MPTLC; the average coefficient of variation among all fish was 0.09

MPTLC was transformed using the logit function (Warton and Hui, 2011) and compared across sites (north, south, and central) and seasons (spring, summer, autumn). We used a three-way Analysis of Covariance (ANCOVA) with length as a covariate to test our hypothesis that total lipid content of juvenile lake trout varied between sources (i.e., stocked versus wild), and among seasons and locations. The data did not conform to the parametric assumption of homoscedasticity and sample sizes were low for some locations and seasons. Therefore, we used a non-parametric bootstrapping approach to conduct our analyses. We generated a bootstrap sample by randomly assigning, with replacement, a lipid content, length, source, season, and location to a bootstrapped fish, for each of 182 fish (i.e., the number of observations in the original sample). The F statistic of the covariate (length), independent variables (source, season, and location), and all 11 possible interactions of these variables, were extracted from the bootstrap sample ANCOVA. The resampling procedure was repeated 10,000 times to create a distribution of bootstrapped F statistics for each variable and interaction. We calculated 95th percentile F statistics from each bootstrap distribution. The observed F statistic from the ANCOVA of the original data was deemed statistically significant if it fell above the 95th percentile of the bootstrap distribution of F statistics. All analyses were conducted using the R statistical environment v3.6.1. (R Core Team, 2019).

**Results**

One-hundred and ninety-seven juvenile lake trout (86 wild and 96 stocked, plus 15 hatchery-sampled fish) were analyzed for MPTLC (Table 1). The overall average (± SD) MPTLC was 15.2 ± 7.1% of dry mass for stocked fish in the lake and 17.0 ± 6.8% for wild fish. MPTLC of lake trout from the hatchery, just prior to stocking into Lake Champlain, was 35.1 ± 2.9% of dry mass.

All main effects were confounded with interaction effects and do not allow for interpretation. We found significant interaction effects between MPTLC in length and season (p < 0.01), length and source (p < 0.0001), and season and location (p < 0.01; Figures 2 & 3). Seasonal variation in MPTLC increased with length in stocked and wild juvenile lake trout, with spring MPTLC higher than summer and autumn as length increases. Stocked juvenile lake trout showed a continuous drop in MPTLC from pre-winter levels at stocking in November to the following autumn. Wild juvenile lake trout displayed higher MPTLC than stocked juvenile lake trout but a slower increase in MPTLC by length (Figure 2).

Spatial variation in stocked and wild juvenile lake trout was confounded with seasonal variation.

Wild juvenile lake trout from the south and central Main Lake had lower MPTLC in spring (June) and higher MPTLC in summer (July – August; Figure 3). MPTLC of wild juvenile lake trout in the central Main Lake decreased in autumn to similar levels found in spring (September; Figure 3). Wild juvenile lake trout in the north Main Lake showed high MPTLC in summer but was based on low sample size (n = 3; Figure 3 & Table 1). Stocked juvenile lake trout from the south and central Main Lake had higher MPTLC in spring (June) and lower MPTLC in summer (July – August). MPTLC of stocked juvenile lake trout in the central Main Lake continued to decrease in autumn (September). MPTLC of stocked juvenile lake trout in summer showed a continuous decrease from the south to north Main Lake (Figure 3).

**Discussion**

Our results were unexpected, and each of our hypotheses was refuted. First, we did not find any differences in MPTLC in lake trout sampled from the three different areas of the Main Lake despite higher CPUE and higher proportions of wild lake trout in the Main Lake relative to the northern and southern areas (Wilkins and Marsden in revision). Second, wild lake trout had higher MPTLC than stocked lake trout, despite a two-fold higher MPTLC in stocked lake trout just prior to release into the lake. Further, the high lipid concentration when hatchery fish were stocked was rapidly lost over their first winter in the lake, and the decline in lipid concentration continued over summer and into autumn.

We hypothesized that the spatial heterogeneity in abundance of wild juvenile lake trout in Lake Champlain was due to differences in prey quantity or quality across the different regions of the Main Lake that draw juveniles from the north and south to the central lake. Alternatively, lake trout hatched in the north and south could have lower survival than in the central region if prey resources were higher in the central lake. However, the lack of variation in lipid concentration among the three regions suggests that lake trout do not experience differences in prey availability across the Main Lake. The differential mortality hypothesis remains to be tested.

Hatchery-reared fish are typically fed a high-ration diet rich in lipids that is reflected in their body composition (Reinitz, 1983). Thus, we expected stocked juvenile lake trout would possess a higher MPTLC than their wild counterparts, similar to other stocked species (e.g., Atlantic salmon *Salmo salar*; Bergstrom, 1989). Analysis of lake trout collected from the Ed Weed Fish Culture Station just prior to stocking in November showed that hatchery-reared lake trout had a MPTLC approximately two times higher than wild lake trout of the same size in Lake Champlain. However, lipid content of newly stocked lake trout dropped markedly over their first winter to the level of age-1 wild fish in spring, and continued to drop throughout summer until by autumn the stocked juvenile lake trout were lower in MPTLC than wild juvenile lake trout of the same age class, although the stocked fish were longer than wild lake trout.

The high lipid content of wild juvenile lake trout compared to stocked juvenile lake trout suggests that wild lake trout may be more efficient foragers than stocked fish at the same size range. The artificial environment in which stocked fish are raised may not select for traits such as boldness and aggressiveness that are adaptive in natural settings (Brown and Laland, 2002; Brown et al., 2003; Saikkonen et al. 2011). In general, hatchery-raised fish post-stocking tend to consume less food and fewer prey types than wild fish, and exhibit reduced ability to switch to new prey types in the wild (e.g., Saikkonen et al., 2011). Age-0 stocked fish in Lake Champlain were much less likely to be feeding in November (85% empty stomachs) than wild fish at the same age (18% empty stomachs) or same size (13% empty stomachs, although growth rates of wild and stocked juvenile lake trout were similar; unpublished data). 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 are less efficient foragers than wild fish in a natural lake environment, potentially resulting in lower lipid levels compared to wild fish, as we found in our study.

We also found seasonal differences in MPTLC of juvenile lake trout in the central Main Lake. Stocked and wild fish showed different trends in seasonal lipid levels; the pattern in lipid content in the stocked fish appeared to influence the overall trend when all fish were analyzed together. Lipid content of wild fish was consistent with other piscivorous fishes, in which lipids are greatest in the summer and lower in spring and autumn (e.g. Madenjian et al., 2000; Metcalfe et al., 2002). In summer, age-1 to 3 lake trout have access to young-of-year smelt and alewife that hatch in June and July, respectively (Simonin et al 2016), and this prey base appears to be sufficient to allow accumulation of lipid storage in addition to growth. Stocked fish, in contrast, showed significant declines in lipid content from spring to summer to autumn. Lipid levels of the hatchery fish also declined substantially after stocking in November, as lipid levels in fish sampled from the hatchery just prior to stocking were substantially higher than in stocked fish caught in the lake in spring. Although this comparison was made between two cohorts (i.e., lake trout sampled prior to stocking in November, and the previous cohort sampled in spring and summer of the same year), hatchery conditions and diet are consistent from year to year, and we can assume reasonable consistency in lake conditions in two consecutive years. The consistent seasonal decline in lipid content of stocked juvenile lake trout suggests that these fish will have less energy reserves than wild juveniles to survive through their second winter in the lake. The high-nutrient diet that stocked lake trout were fed in the hatchery does not appear to give them a lasting advantage over wild lake trout, as wild fish surpass stocked fish in lipid content by the summer following their first winter in the lake. However, the high lipid content of stocked fish may be advantageous for survival through the first winter post-stocking, as they learn to feed on active prey and cope with stresses associated with predators.

Our results do not help to explain the greater abundance of wild recruits in the central Main Lake relative to other regions of Lake Champlain because we did not find spatial variation in lipid content in juvenile lake trout. Larger sample sizes and additional years of data would be useful to confirm this result. The increase in lipid levels of wild recruits during the summer is predictable and encouraging, as the data suggest that wild juvenile lake trout are feeding well; higher lipid content is associated with high survival potential. However, we only examined juveniles from June to September. Analysis of juvenile lake trout throughout the year would provide a more complete picture of lipid acquisition and depletion over the winter. The dramatic loss of the lipid advantage of the hatchery lake trout have at stocking is interesting; hatchery fish may be at a substantial disadvantage during their first winter as they acclimate to wild conditions and therefore need the higher lipid content provided by the hatchery. However, we do not know the survival rate of stocked lake trout during the first winter after stocking. The population of lake trout in Lake Champlain has been maintained by fish stocked with high lipid content, but we do not know whether post-stocking survival is dependent on this high lipid content. That is, could the same size lake trout population be supported by stocking fish with half the lipid content at stocking? We propose two competing hypotheses: high lipid content either 1) provides the necessary energy reserves for stocked fish to acclimate to life in the wild and learn to forage, or 2) imposes an energetic penalty that cannot be sustained in the wild. To test these hypotheses, hatcheries could evaluate post-stocking performance and survival of lake trout raised with normal and reduced hatchery diets. If the second hypothesis is supported and the first refuted, hatcheries may be able to achieve the same level of survival by stocking smaller lake trout earlier in the year (e.g., May), when seasonal prey production is increasing and transition to a wild diet may be easier than in November.

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Table 1. Size range (mm total length) and sample sizes (in parentheses) of stocked and wild juvenile lake trout collected for lipid analysis from three areas of the Main Lake of Lake Champlain in three seasons, 2018. Samples were also obtained from the Ed Weed Fish Culture Station in early November, 2018.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Pre-winter | Spring | | | Summer | | | Autumn | | |
| Stocked | North | -- | -- | | | 159 – 306 (15) | | -- | | |
|  | Central | -- | 181 – 285 (13) | | | 192 – 269 (16) | | 192 – 292 (15) | | |
|  | South | -- | 152 – 310 (31) | | | 206 – 243 (6) | | -- | | |
|  | Hatchery | 149 – 211 (15) | -- | | | -- | | -- | | |
| Wild | North | -- | | -- | 236 – 280 (3) | | -- | | |
|  | Central | -- | | 81 – 245 (15) | 106 – 332 (27) | | 121 – 275 (15) | | |
|  | South | -- | | 95 – 237 (10) | 104 – 287 (15) | | -- | | |

**Figure headings**

Figure 1: Lake Champlain, showing north, central, and south sampling areas in the Main Lake and two major known lake trout spawning sites at Gordon Landing and Burlington Bay where lake trout are also stocked annually.

Figure 2: Seasonal comparison of mean percent total lipid content of the dry mass of wild and stocked juvenile lake trout ages 0-3 in Lake Champlain captured between 8 June and 29 September 2019. The colors denote seasons in which lake trout were captured: spring (June), summer (July – August), and autumn (September); the black line is the regression for all fish combined by season. Numbers on the graph indicate age of each fish; age-0 stocked fish were collected in November 2018 from the Ed Weed Fish Culture Station just prior to stocking (pre-winter).

Figure 3: Seasonal and spatial comparison of mean percent total lipid content of the dry mass of wild and stocked juvenile lake trout ages 1-3 in Lake Champlain captured between 8 June and 29 September 2019. Error bars show standard error. North, central, and south refer to the sampling regions in the Main Lake basin. The seasons refer to the month in which lake trout were captured: June (spring), July – August (summer), and September (autumn).