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Comparison of Lake Trout Diets Between Day and Night Sampling

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Abstract

Lake trout (*Salvelinus namaycush)* stocking in Lake Champlain began in 1973. Wild recruitment was not observed in the lake until 2015. The reasons for the recent wild recruitment suddenly starting are currently unknown. Diet analysis has been used to understand lake trout energetics as a potential clue to determine why wild recruitment started. Sampling for diet analysis is commonly done during the day for logistical reasons. However, lake trout feed during the night as well as during the day, and the availability of prey species changes at night. The purpose of this study was to test the assumption that diet data from lake trout collected during the day represents what lake trout eat throughout the 24-hour period. Sampling for juvenile lake trout was conducted using bottom trawling during the day and the night in Burlington Bay, Lake Champlain, in 2018 and 2019. Dissections of the stomachs of lake trout caught during the day and night resulted in comparable percentages of lake trout with food in their stomachs, comparable numbers of total diet items and significant diet overlap. However, the diet of lake trout caught at night had higher biomass and contained larger rainbow smelt (*Osmerus mordax*), fewer young-of-year fish, and smaller *Mysis* (*Mysis diluviana)* than lake trout caught during the day. Overall, daytime sampling provides accurate information on the composition of the diets of lake trout, but not the size of their prey.

Introduction

Importance of Lake Trout

Lake trout (*Salvelinus namaycush)* is an apex predator native to Lake Champlain (Langdon et al. 2006). They play an essential role in maintaining ecosystem health, and are a key indicator species (Lange and Smith 1995). Lake trout also provide substantial economic and social importance throughout their range, and have historically been a major resource for aboriginal peoples in northern North America (Muir et al. 2012). They support commercial and recreational fisheries in the Great Lakes and Vermont. They have a life span of over 25 years (Langdon et al. 2006) and reach large sizes, greater than 20 kg (Johnson and Martinez 2000). However, the collapse of the lake trout fisheries in the Great Lakes and Lake Champlain resulted in a need to stock lake trout to restore populations. The stocking programs for all hatcheries and all species in Vermont costs a total of about $3.4 million annually (Vermont Department of Fish and Wildlife 2018). However, over $205 million is generated each year by fishing-related activities in Lake Champlain, including money spent on bait and tackle, fishing rods, and fishing vessels, among other expenses (Decerega et al. 2016). Therefore, restoring a lake trout fishery in Lake Champlain is economically beneficial for the state of Vermont.

Management of Lake Trout

Lake trout were extirpated from Lake Champlain by 1900, but the cause is still unknown (Plosila and Anderson 1985). The four lower Great Lakes have also experienced local extinctions of lake trout (Hansen et al. 1996, Madenjian and Desorcie 2010, Muir et al. 2012). The two most likely causes of extirpation in the Great Lakes were commercial fishing and predation by non-native sea lamprey (*Petromyzon marinus*). However, the commercial fishery in Lake Champlain in the nineteenth century was limited to shoreline seining, a method that is unlikely to deplete the lake trout population (Marsden and Langdon 2012). A lack of documentation of sea lamprey in the late 19th and early 20th centuries raises question as to whether sea lamprey are native to Lake Champlain, and suggests that the sea lamprey population was not as abundant in Lake Champlain as it is now and did not contribute to the extirpation of lake trout (Marsden and Langdon 2012).

The states of Vermont and New York began stocking lake trout in Lake Champlain in 1973 (Marsden et al. 2018). The goal of stocking was initially to establish a population of lake trout to provide harvest of 18,000 lake trout annually (Plosila and Anderson 1985). However, in 2010 that goal changed to establishing a self-sustaining lake trout population (Marsden et al. 2010). Recruitment of wild lake trout into the population was not observed until 2015 when young-of-year (YOY), age-1, and age-2 wild lake trout were found throughout the Main Lake basin (Marsden et al. 2018).

Lake Champlain fishery agencies primarily rely on stocking to restore lake trout populations. However, understanding what is causing the sudden recruitment of wild lake trout is important to help the population recover. One necessary aspect for lake trout recruitment to occur is lake trout must avoid predation and starvation at the critical phase in their development, when they switch from absorbing nutrients from their yolk to exogenous feeding (Ladago et al. 2016). Lake trout that forage successfully increase their chance of survival by consuming energy that they can store as lipids to survive through their first winter, when prey is limited. Successful feeders also grow faster than unsuccessful feeders. Fast growth increases the probability of survival because the larger the lake trout, the more gape-limited predators that can be avoided, and the better swimmers they are, making it easier for the lake trout to escape predators and catch prey. Therefore, analyzing the diets of lake trout is important to fully understand lake trout energetics and growth.

Lake Trout Diet

Lake trout is a cold-water, piscivorous species (Scott and Crossman 1973). However, when lake trout first hatch, they are not capable of eating other fish because their mouths are too small, and they are not strong enough swimmers to catch other fish. Therefore, newly hatched lake trout consume zooplankton, primarily *Bosmina*, copepods, and *Daphnia* (Ladago et al. 2016). As YOY lake trout grow, they transition to consuming *Mysis diluviana* (Roseman et al. 2009). However, as lake trout get bigger, they reduce their *Mysis* consumption, and start feeding on small fish, including rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and slimy sculpin (*Cottus cognatus)* (Elrod 1983, Ray et al. 2007). By age-2, lake trout are primarily eating fish (Schumacher and Marsden 2019). Adult lake trout primarily prey on rainbow smelt, alewife, and slimy sculpin in the benthopelagic zone (Miller and Holey 1992, Ray et al. 2007).

Lake Trout Feeding Behavior

Lake trout are able to hunt both in the benthic zone and pelagic zone. They have high fat content and are almost neutrally buoyant when their swim bladders are empty, which allows them to engage in rapid vertical migration (Muir et al. 2012). Moonlight provides enough light for lake trout to see their prey in the water column (Rogers et al. 2016). Therefore, lake trout eat at dusk and into the night as well as during the day (Gorman et al. 2012).

Mysis are an important component of juvenile lake trout diets. *Mysis* exhibit partial diel vertical migrations (DVM), in which they move vertically through the water column in a 24-hour cycle (Beeton 1960). *Mysis* are near the bottom of the lake during the day, and migrate to shallower depths at night throughout the year (Ahrenstorff et al. 2011). *Mysis* conduct these migrations to hunt for their prey, zooplankton, with a reduced risk of predation (Ahrenstorff et al. 2011, Euclide et al. 2017). However, large *Mysis* and gravid female *Mysis* do not migrate frequently, possibly because large *Mysis* may already have sufficient energy reserves and both large and gravid female *Mysis* want to avoid predation (Euclide et al. 2017). Planktivorous fish such as rainbow smelt and alewife also engage in DVM because they follow *Mysis* and other species of prey throughout the water column (Janssen and Brandt 1980, Gorman et al. 2012). Lake trout of all year classes hunt for *Mysis* and prey fish at night (Gorman et al. 2012); however, the specifics of quantity and size of their prey at night are understudied.

While the diel migrations of important prey species are a factor in lake trout feeding behavior, several other factors influence lake trout feeding. Exposure to live prey before the yolk sac is absorbed is a major factor in determining how effective juvenile lake trout are at foraging (Savino et al. 1993, Ladago et al. 2016). Wild lake trout are more successful at capturing live prey than lake trout that have been stocked (Savino et al. 1993). Predator avoidance also impacts energy intake in juvenile lake trout (McDonald et al. 1992). YOY lake trout lose weight when predators are present, but gain weight in the absence of predators (McDonald et al. 1992). When YOY lake trout are in the presence of predators, they spend more time hiding, and expend energy faster due to stress, whereas in the absence of predators YOY lake trout are more free to forage (McDonald et al. 1992).

Lake Trout Sampling Methods

Several sampling methods are used to obtain fish for diet analysis. Gillnetting can be used to target particular species and sizes, usually larger size classes. Gillnets can be set overnight; however, fish caught in gillnets continue digesting their prey while the net is set, decreasing the reliability of the data. Fish in gillnets are also vulnerable to predators while the net is set. Trawling is commonly used for catching a lot of fish in a short amount of time, decreasing the amount of time fish digest their food before being put on ice. Bottom trawling is useful for sampling for benthic species including small fish such as juvenile lake trout.

Regardless of the method used, sampling for lake trout specifically to analyze their diets has rarely been conducted at night. Yule et al. (2008) conducted a bottom trawl survey in Lake Superior to evaluate how factors including diel period affect the catch of bottom-oriented species, including lake trout (Yule et al. 2008). The study found no significant difference in catch-per-unit-effort (CPUE) for lake trout caught during the day and at night in Lake Superior (Yule et al. 2008).

A literature search conducted in April 2020 in the Web of Science database using the search terms “lake trout” and “diet” and “night” yielded two results. Neither of the results were about the diets of lake trout. However, the diets of other species have been analyzed during different diel periods. Arctic char (*Salvelinus alpinus*) consumed a greater biomass at night compared to the day, however the composition of the diet of Arctic char did not change (Björnsson 2001). The feeding patterns of Arctic char differ during different diel periods, however whether or not lake trout follow similar behavior is unknown.

Refining the search to include just “lake trout” and “night” yielded 17 results, but the results focused on lake trout diel distributions, not lake trout diet. When “lake trout” and “diet” were searched together, only 26 papers analyzed the diets of the morphotype of lake trout found in Lake Champlain. Many of the papers that used bottom trawling as the sampling method did not specify whether sampling was conducted during the day or night, however some studies also used gillnets for sampling. The data used in several papers were collected from seasonal government surveys. The Lake Ontario spring bottom trawl survey, cited by two papers (Elrod 1983, Roseman et al. 2009), has been collaboratively conducted by NYSDEC and USGS since 1978, and bottom trawling is done during the day (U.S. Geological Survey 2018).

Sampling conducted during the day is logistically easier than during the night. Lack of lake trout sampling during different diel periods could be problematic if lake trout feed differently during the day and night. Many studies done on the diets of lake trout exclusively sampled during the day, thus ignoring the potential that important aspects of the lake trout diet could be consumed at night. Therefore, sampling during both the day and night is important to test the assumption that sampling at night is unnecessary, and determine whether there are components of lake trout diets that are missed by only sampling during the day.

I tested the hypothesis that lake trout feed on more prey items during the day than at night. The objectives of this paper were (1) to examine differences between the diets of juvenile lake trout caught during the day and the diets of lake trout caught during the night and (2) to examine the rationale for conducting day sampling and night sampling for research on lake trout diets.

Methods

Study Site

Lake Champlain is located between New York to the west, Vermont to the east, and Quebec to the north, has a length of 193 km, and is 20 km at its widest point (Marsden and Langdon 2012). The average depth of the lake is 19.5 m and maximum depth is 122 m (Marsden and Langdon 2012). Islands, narrows, and causeways divide Lake Champlain into five basins. The Main Lake is the deepest and largest basin (Marsden and Langdon 2012). All sampling was conducted in Burlington Bay, the part of the Main Lake basin nearest the city of Burlington, Vermont, where previous sampling yielded a high catch per effort of lake trout compared to other areas of the lake.

Sampling

Samples were collected in July and October, 2018, and monthly from May through November, 2019. Daytime sampling periods were paired with nighttime sampling periods and conducted within 48 hours of each other. Nighttime sampling was defined between sunset and sunrise.

Sampling was done using a three-in-one bottom trawl (DeAlteris et al. 1989), consisting of an 8-m headrope, 9.3-m footrope, and 1.25-mm stretch cod end liner (Marsden et al. 2018). Trawling was done at depths between 28 and 63 m, focusing on depths of 35 to 45 m. The trawl was towed at about 5 km/hr. Most tows were 10 to 20 min each, with one occurring for 40 minutes, and one for 27 minutes. CPUE was measured as the catch per 10-minute trawl.

All lake trout caught in the trawls were kept; however, juveniles were targeted because juvenile lake trout are easier to sample using bottom trawling than adults. The total length (TL) of all lake trout was measured on board the trawling vessel, and the lake trout were assessed for fin clips that identified whether they were stocked or wild fish. The juvenile lake trout were put on dry ice on board to stop digestion. All lake trout were transferred to a -20°C freezer where they were stored until they were processed and dissected.

Diet Analysis

Fish were thawed completely in lukewarm water. The weight of the fish was measured to the nearest 0.01 gram, and total length was measured to the nearest millimeter. Whether the fish was caught during the day or night was unknown to the person doing the dissections, and all dissections were done by the same person. Stomach contents were identified to the lowest taxonomic level, and quantified. Amphipods and insects were identified to order, chironomids and sphaeriids were identified to family, and fish were identified to species. All *Mysis* found in the diets are *Mysis diluviana* because that is the only species in Lake Champlain. The lengths of *Mysis* found in the stomachs were measured from the tip of the rostrum to the base of the telson (Environmental Protection Agency 2015), and the total length of any intact fish was measured. Lengths were also measured from any fish missing exclusively either the head or caudal fin, and the absence was noted. Fish in the diet that were determined to be YOY based on their size were counted separately from non-YOY of the same species. The wet weight of identifiable (i.e., undigested) contents of the stomachs was measured.

Data Analysis

Only diets of lake trout between 100 mm and 400 mm in total length were used for most comparisons, as sample sizes of lake trout smaller than 100 mm and greater than 400 mm were small (N = 25; 7 smaller than 100 mm, 18 greater than 400 mm). Wild and stocked juvenile lake trout diets had significant overlap (Schumacher and Marsden 2019), therefore the origin of the lake trout should not be a factor in their diet composition for this study. Thus, stocked and wild lake trout were combined for all analyses.

Diet diversity was quantified using Shannon's H index:

$$H = -\sum_{i=1}^{n} p_i \ln p_i$$

where n is the number of taxa found in the stomachs, and p_i is the proportion of diet items belonging to the ith taxon (Shannon 1948).

Diet similarity between lake trout caught during the day and night was determined using Schoener's index:

$$C_{xy} = 1 - 0.5\left(\sum |p_{xi} - p_{yi}|\right)$$

where p_{xi} is the proportion of diet item i eaten by lake trout caught during the day, and p_{yi} is the proportion of diet item i eaten by lake trout caught at night (Schoener 1971). Diet overlap was considered biologically significant if C_{xy} was greater than 60%.

Comparative analysis was performed using RStudio (RStudio team 2019). Welch two-sample independent t-tests with a significance threshold of 0.05 were used to compare lengths of prey items between fish caught during the day and the night, as well as stomach weight, and diet diversity.

Results

A total of 61 trawls was conducted between 2018 and 2019; 41 trawls during the day and 20 trawls during the night. Every trawl, expect for two night trawls, caught at least one lake trout. However, six night trawls only caught one lake trout whereas only two day trawls caught one lake trout. The diets of a total of 326 fish were analyzed, of which 301 were within the target range of 100 mm to 400 mm total length (Table 1). Of the lake trout within the target range, 263 were captured during the day and 38 were captured during the night (Table 1). A significantly larger CPUE was collected during the day (9.0 lake trout per 10 min trawl) than night (2.8 lake trout per 10 min trawl; $p < 0.0001$; Table 2).

The percent of stomachs that contained food from daytime samples (78.8) and nighttime samples (76.9) was not significantly different ($p = 0.77$; Table 1). Of the fish with food in their stomachs, the average count of diet items in the stomachs did not differ between fish caught during the day (3.0) versus night (2.9) ($p = 0.76$; Table 3). The average wet weight of the stomach contents of the fish caught during the day (1.53 g) was significantly less than the wet weight of the stomach contents of the fish caught during the night (3.56 g; p = 0.006; Table 3).

By number, *Mysis* composed the majority of the diet of daytime samples (44%) and were the second largest component of the diet of nighttime samples (26%; Figure 1). Rainbow smelt were the second largest component of the diet of daytime samples (30%) and composed the majority of the diet of nighttime samples (43%; Figure 1). YOY fishes composed a significantly larger part of the diet of daytime samples (11%) than nighttime samples (3%; p = 0.005; Table 3). Rainbow smelt YOY composed a significantly larger amount of the diets of daytime samples (6%) than nighttime samples (1%; p = 0.002). Alewife YOY composed similar percentages of the diets of daytime samples (3%) and nighttime samples (2%; p = 0.7). YOY of other species including slimy sculpin and yellow perch (*Perca flavescens*) were only found in daytime samples (2%). Other species found in the diets of daytime and nighttime samples included slimy sculpin, *Bosmina*, and macroinvertebrates. Yellow perch and tessellated darters (*Etheostoma olmstedi*) were also found in the stomachs of daytime samples, and *Daphnia* and trout-perch (*Percopsis omiscomaycus*) were also found in the stomachs of nighttime samples.

The average length of intact rainbow smelt found in the stomachs of lake trout caught during the night (93.3 mm) was significantly larger than those in lake trout caught during the day (78.3 mm; p = 0.02; Table 4). The sample size of intact rainbow smelt found in the stomachs of lake trout caught at night was limited (N = 55; 11 from nighttime samples, 44 from daytime samples; Table 5). Partial rainbow smelt found in stomachs were excluded from length analyses, but are reported in Table 5. Analysis could not be conducted on the lengths of other prey fish species due to insufficient sample sizes between daytime and nighttime samples. The average length of *Mysis* found in the stomachs of lake trout caught during the day (14.2 mm, N=55) was significantly greater than the average length of *Mysis* found in the lake trout collected at night (12.9 mm, N = 7; p = 0.041; Tables 4 and 6).

Schoener's index was 80.9%, indicating that fish caught during the day and those caught during the night had significant dietary overlap. The average Shannon's Index for daytime and nighttime samples was 0.175 and 0.197, with no significant difference between the values (p = 0.72; Table 3), indicating that the diversity of the diets of daytime lake trout and nighttime lake trout was similar.

The diets of lake trout YOY smaller than 100 mm were analyzed separately from the main size group due to the small sample size (N = 7; 4 daytime samples, 3 nighttime samples; Table 1). All lake trout YOY except one caught during the night had food in their stomachs (Table 7). YOY caught during the day had an average of 1.8 prey items in their stomachs, while the three YOY caught during the night had an average of 3.7 prey items in their stomachs ($p = 0.61$; Table 7). YOY caught during the day and YOY caught during the night had similar stomach weights ($p = 0.4$) and Shannon Indices ($p = 0.4$; Table 7). Analysis of prey length could not be conducted because no prey length data could be collected due to digestion of diet items.

Lake trout greater than 400 mm were also analyzed separately from the target size range due to a small sample size (N = 18; 7 daytime samples, 11 nighttime samples; Table 1). A greater percentage of the large lake trout caught during the night had food in their stomachs (55%) than caught during the day (29%) although this difference was not significant ($p = 0.3$; Table 7). Large lake trout caught during the night also had more total items in their stomachs, greater stomach weight, and a greater Shannon Index than adult lake trout caught during the day, however none of these differences were significant (Table 7). Statistical analysis of prey length in lake trout greater than 400 mm could not be conducted because insufficient prey length data could be collected due to low prey item counts and digestion of prey items.

Discussion

The total number of items found in the stomachs of lake trout and their diversity did not differ between daytime and nighttime samples. Schoener's Index indicated significant overlap between the proportion of each species composing the diets of lake trout caught during the day and during the night. However, the stomachs of fish caught during the night weighed significantly more than the stomachs of fish caught during the day.

Lake trout fed on different sizes of fish and *Mysis* during the two diel periods, which explains the difference in stomach weight between lake trout caught during the day and night. At night, lake trout fed on larger rainbow smelt than during the day. Juvenile and adult rainbow smelt engage in DVM (Gorman et al. 2012, Simonin et al. 2012). Rainbow smelt may aggregate near the thermocline while they adjust to warmer water. Therefore, at night lake trout could have greater opportunity to select larger rainbow smelt. Although I was unable to determine if this pattern holds true for other prey fishes, alewife have been seen engaging in DVM (Janssen and Brandt 1980). Lake trout caught during the day have also been found to select for small alewife

(Elrod 1983). Elrod (1983) found that the length-frequency distribution of alewife found in the stomachs of juvenile lake trout caught in bottom trawls during the day was shifted towards smaller alewife compared to the length-frequency distribution of alewife caught in the same bottom trawls, indicating lake trout likely chose prey that were captured more easily, rather than targeting larger prey (Elrod 1983). The larger lake trout analyzed in the study should have been capable of catching and swallowing larger alewife than were found in their stomachs.

During the day, a larger portion of the lake trout diet comprised YOY fishes than at night. At night, lake trout that fed on YOY fish were more likely to also feed on larger fish. During the day, lake trout may not be able to easily select larger prey compared to nighttime, so they prey on YOY because YOY are easier to catch than larger prey.

Lake trout also fed on different sizes of *Mysis* during the day (average = 14.2 mm) and night (12.9 mm). The difference in the size of *Mysis* found in the stomachs of lake trout caught during the day compared to nighttime could be due to *Mysis* DVM (Ahrenstorff et al. 2011, Euclide et al. 2017). Lake trout feed on what is available, and at night fewer size classes of *Mysis* expose themselves by entering the water column (Euclide et al. 2017). Large *Mysis* and gravid females engage in DVM less frequently than smaller *Mysis* (Euclide et al. 2017). The difference in CPUE between day sampling (9.00) and night sampling (2.78) from this study indicates that juvenile lake trout are not on the bottom during the night as much as they are during the day. If they are not on the bottom, they are in the water column. Therefore, when lake trout are preying on *Mysis* at night in the water column, the size selection of Mysis for lake trout to prey on is smaller than during the day. While the significant difference in size of *Mysis* found in the stomachs of lake trout caught during the day and night is interesting, the small number of lake trout caught during the night (7) is not sufficient to have confidence in these results.

YOY lake trout are too small to feed on other fish, and exhibit different feeding behavior than larger juvenile lake trout, which is why they were analyzed separately (Ladago et al. 2016). Diets of YOY lake trout caught during the day and night were different than lake trout between 100 mm and 400 mm caught during the same periods. More items were found in the stomachs of YOY lake trout caught during the night than during the day, but these data are likely skewed because there were only three lake trout from the night, and one lake trout had ten prey items, one had one prey item, and the other lake trout was empty. The trends found by comparing the lake trout YOY are interesting, however the sample sizes are too small to draw conclusions.

The small sample of adult lake trout caught also limits the conclusions that can confidently be drawn from diet trends. Interestingly, a larger percentage of lake trout caught during the night had food in their stomachs compared to those caught during the day, as well as more items, greater stomach weight, and greater diet diversity.

The CPUE was different between diel sampling periods for both years of this study. The CPUE for day sampling (9.0) was significantly greater than the CPUE for night sampling (2.8), in contrast to Yule et al. (2008) who found the same lake trout CPUE during the day and night (Yule et al. 2008). However, Yule et al. (2008) did not differentiate between juvenile and adult lake trout when sampling, and they conducted midwater trawls in addition to bottom trawls, which were factored into the CPUE. Lake trout have been found leaving the benthic zone at night, where bottom trawls sample (Gorman et al. 2012). The low CPUE of bottom trawling at night compared to during the day indicates that juvenile lake trout change their distribution between day and night. Either fewer juvenile lake trout are in the benthic zone during the night than during the day, or lake trout move to shallower or deeper depths along the bottom at night. Therefore, bottom trawls are unlikely the most effective method for catching lake trout at night, or the location of trawling needs to change between day sampling and night sampling.

The diets of the juvenile lake trout reflect where they are feeding in the water column. During the day, the lake trout feed on a large size variety of *Mysis*, and *Mysis* compose the largest proportion of their diet, likely because lake trout and *Mysis* are both primarily in the benthic zone during the day (Janssen and Brandt 1980, Gorman et al. 2012). During the night, the largest component of lake trout diet is rainbow smelt, which are in the pelagic zone at night (Simonin et al. 2012).

The similarities in the total items, percentage of lake trout with food in stomachs, and diversity between lake trout caught during the day and lake trout caught during the night indicates that exclusively sampling during the day can be effective for understanding what lake trout are eating, and how much. However, daytime sampling does not provide an accurate representation of the size of prey eaten by lake trout. The size of smelt would be underestimated with exclusively daytime sampling.

The small sample sizes of lake trout caught during the night in this study and small number of diet items limit the conclusions that can be drawn from this study. My hypothesis that lake trout feed on more prey items during the day than at night was unsupported by the findings in this study. Future work consisting of night sampling using a different sampling method with a larger CPUE would be helpful for determining if there are length differences of other prey species in lake trout caught at different times. A larger sample size would also provide more confidence in the results found in this study.

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References

Ahrenstorff, T. D., T. R. Hrabik, J. D. Stockwell, D. L. Yule, and G. G. Sass. 2011. Seasonally dynamic diel vertical migrations of *Mysis diluviana*, coregonine fishes, and siscowet lake trout in the pelagia of Western Lake Superior. Transactions of the American Fisheries Society 140:1504.

Beeton, A. M. 1960. The vertical migration of *Mysis relicta* in Lake Michigan. Journal of the Fisheries Research Board of Canada 17:517-539.

Björnsson, B. 2001. Diel changes in the feeding behaviour of Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Ellidavatn, a small lake in southwest Iceland. Limnologica 31:281-288.

DeAlteris, J. T., C. W. Recksiek, A. Fahfouhi, and X. Liuxiong. 1989. Comparison of the performance of two bottom-sampling trawls. Transactions of the American Fisheries Society 118:119-130.

Decerega, J., O. Guerra, and D. Tramonte. 2016. The value of Lake Champlain. Dartmouth College, PRS Policy Brief 1516-01.

Elrod, J. H. 1983. Seasonal food of juvenile lake trout in U.S. waters of Lake Ontario. Journal of Great Lakes Research 9:396-402.

Environmental Protection Agency. 2015. Standard operating procedure for mysid analysis. https://www.epa.gov/sites/production/files/2017-01/documents/sop-for-mysis-sample-collection-and-preservation-201504-8pp.pdf.

Euclide, P. T., S. Hansson, and J. D. Stockwell. 2017. Partial diel vertical migration in an omnivorous macroinvertebrate, *Mysis diluviana*. Hydrobiologia 787:387-396.

Gorman, O., D. Yule, and J. Stockwell. 2012. Habitat use by fishes of Lake Superior. I. Diel patterns of habitat use in nearshore and offshore waters of the Apostle Islands region. Aquatic Ecosystem Health & Management 15:333-354.

Hansen, M. J., M. P. Ebener, R. G. Schorfhaar, S. T. Schram, D. R. Schreiner, J. H. Selgeby, and W. W. Taylor. 1996. Causes of declining survival of lake trout stocked in US waters of Lake Superior in 1963-1986. Transactions of the American Fisheries Society 125:831-843.

Janssen, J., and S. B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 37:177-184.

Johnson, B. M., and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:127-143.

Ladago, B. J., J. E. Marsden, and A. N. Evans. 2016. Early feeding by lake trout fry. Transactions of the American Fisheries Society 145:1-6.

Langdon, R. W., M. T. Ferguson, and K. M. Cox. 2006. Fishes of Vermont. Vermont Agency of Natural Resources, Waterbury, VT.

Lange, R. E., and P. A. Smith. 1995. Lake Ontario fishery management: The lake trout restoration issue. Journal of Great Lakes Research 21:470-476.

Madenjian, C. P., and T. J. Desorcie. 2010. Lake trout population dynamics in the Northern Refuge of Lake Michigan: Implications for future rehabilitation. North American Journal of Fisheries Management 30:629-641.

Marsden, J. E., B. D. Chipman, B. Pientka, W. F. Schoch, and B. A. Young. 2010. Strategic plan for Lake Champlain fisheries. Great Lakes Fishery Commission Misc. Publ. :2010-2003.

Marsden , J. E., C. L. Kozel, and B. D. Chipman. 2018. Recruitment of lake trout in Lake Champlain. Journal of Great Lakes Research 44:166-173.

Marsden , J. E., and R. W. Langdon. 2012. The history and future of Lake Champlain's fishes and fisheries. Journal of Great Lakes Research 38:19-34.

McDonald, M. E., A. E. Hershey, and W. J. Obrien. 1992. Cost of predation avoidance in young-of-year lake trout (*Salvelinus namaycush*) - growth differential in suboptimal habitats. Hydrobiologia 240:213-218.

Miller, M. A., and M. E. Holey. 1992. Diets of lake trout inhabiting nearshore and offshore Lake Michigan environments. Journal of Great Lakes Research 18:51-60.

Muir, A. M., M. J. Hansen, and C. C. Krueger. 2012. Re-establishing lake trout in the Laurentian Great Lakes: past, present, and future. Pages 533-588 *in* W. W. Taylor, A. J. Lynch, andN. J. Leonard, editors. Great Lakes Fisheries Policy and Management: A Binational Perspective. Michigan State University Press, East Lansing MI.

Plosila, D. S., and J. K. Anderson. 1985. Lake Champlain salmonid assessment report. Lake Champlain Fish and Wildlife Management Cooperative.

Ray, B. A., T. R. Hrabik, M. P. Ebener, O. T. Gorman, D. R. Schreiner, S. T. Schram, S. P. Sitar, W. P. Mattes, and C. R. Bronte. 2007. Diet and prey selection by Lake Superior lake trout during spring, 1986-2001. Journal of Great Lakes Research 33:104-113.

Rogers, L. S., T. D. Keyler, and A. F. Mensinger. Scotopic Visual Sensitivity of Lean Lake Trout (Salvelinus namaycush) and Siscowet Lake Trout (Salvelinus namaycush siscowet): A Morphotype Comparison. , *in* Conference Scotopic Visual Sensitivity of Lean Lake

Trout (Salvelinus namaycush) and Siscowet Lake Trout (Salvelinus namaycush siscowet): A Morphotype Comparison. . August 21-25, 2016.

Roseman, E. F., W. Stott, T. P. O'Brien, S. C. Riley, and J. S. Schaeffer. 2009. Heritage strain and diet of wild young of year and yearling lake trout in the main basin of Lake Huron. Journal of Great Lakes Research 35:620-626.

RStudio team. 2019. Version 1.2.5001. Boston, MA.

Savino, J. F., M. G. Henry, and H. L. Kincaid. 1993. Factors affecting feeding-behavior and survival of juvenile lake trout in the Great Lakes. Transactions of the American Fisheries Society 122:366-377.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369-404.

Schumacher, M. N., and J. E. Marsden. 2019. A diet analysis of juvenile lake trout in Lake Champlain. Honors Thesis, University of Vermont, Rubenstein School of the Environment and Natural Resources.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada Ottawa : Fisheries Research Board of Canada, Ottawa.

Shannon, C. E. 1948. A mathematical theory of communication. The Bell System Technical Journal 27:379-423.

Simonin, P. W., D. L. Parrish, L. G. Rudstam, P. J. Sullivan, and B. Pientka. 2012. Native rainbow smelt and nonnative alewife distribution related to temperature and light gradients in Lake Champlain. Journal of Great Lakes Research 38:115-122.

U.S. Geological Survey. 2018. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2017. http://www.glfc.org/pubs/lake_committees/common_docs/CompiledReportsfromUSGS2017.pdf.

Vermont Department of Fish and Wildlife. 2018. Fish & wildlife FY2017 budget documents. Vermont Legislative Joint Fiscal Office, , https://ljfo.vermont.gov/assets/docs/appropriations/fy_2017/Department-Budgets/44226ac6d3/Fish-and-Wildlife-FY2017-Budget.pdf.

Yule, D. L., J. V. Adams, J. D. Stockwell, and O. T. Gorman. 2008. Factors affecting bottom trawl catches: Implications for monitoring the fishes of Lake Superior. North American Journal of Fisheries Management 28:109.

Tables

Table 1. Number of lake trout caught during the day and night, and percent without stomach contents, in 2018 and 2019 in Lake Champlain, grouped by 100 mm size intervals.

Sampling Period	TL (mm)	Stomach contents: No	Stomach contents: Yes	% Stomachs Empty	Total
Day	0-99	0	4	0.0	4
	100-199	10	34	22.7	44
	200-299	35	151	18.8	186
	300-399	8	25	24.2	33
	400-499	2	2	50.0	4
	600-699	1	0	100.0	1
	700-799	2	0	100.0	2
	All fish	58	216	21.2	274
Night	0-99	1	2	33.3	3
	100-199	1	2	33.3	3
	200-299	4	27	12.9	31
	300-399	2	2	50.0	4
	400-499	3	4	42.9	7
	500-599	1	0	100.0	1
	600-699	0	1	0.0	1
	700-799	1	0	100.0	1
	800-899	0	1	0.0	1
	All fish	12	40	23.1	52
	Total	70	256	21.5	326

Table 2. Average catch of lake trout per 10-min trawl for trawls during the day and the night in 2018 and 2019 in Lake Champlain.

	Catch per 10-min Trawl		
Sampling Period	2018	2019	Total
Day	9.24	8.93	9.00
Night	4.28	1.27	2.78
Total	6.63	7.11	

Table 3. Average number of diet items, stomach weights, percent of diet consisting of YOY fish, and Shannon H Index of juvenile lake trout caught during the day and night in Lake Champlain in 2018 and 2019.

Sampling Period	Total Diet Items	Stomach Weight(g)	Percent of diet consisting of YOY	Shannon H Index
Day	3.00	1.53	10.6	0.175
Night	2.87	3.56	2.7	0.197
p – value	0.76	0.006	0.005	0.72

Table 4. Average length of measurable smelt and *Mysis* found in stomachs of juvenile lake trout caught during the day and night in 2018 and 2019 in Lake Champlain.

	Average Length (mm)		
Species	Day	Night	p-value
Smelt	74.7	83.6	0.015
Mysis	14.2	12.9	0.041

Table 5. Number of rainbow smelt in 10-mm size intervals found in the stomachs of juvenile lake trout caught during the day (N = 51) and night (N = 17) in 2018 and 2019 in Lake Champlain.

Sampling Period	Size Interval (mm)	Count Intact	Count Partial
Day	20-29	0	1
	30-39	0	8
	40-49	0	2
	50-59	9	3
	60-69	14	5
	70-79	7	3
	80-89	1	2
	90-99	3	1
	100-109	5	3
	110-119	4	3
	120-130	3	2
	Total	46	33
Night	50-59	1	0
	60-69	0	3
	70-79	2	10
	80-89	1	6
	90-99	4	0
	100-109	1	2
	110-119	2	0
	120-130	1	0
	Total	12	21

Table 6. Number of *Mysis* in each size interval found in the stomachs of juvenile lake trout caught during the day (N = 31) and night (N = 3) in 2018 and 2019 in Lake Champlain.

Sampling Period	Length interval (mm)	Count
Day	7-9	7
	10-12	10
	13-15	18
	16-18	14
	19-22	6
	Total	55
Night	10-12	2
	13-15	5
	Total	7

Table 7. Percent of lake trout less than 100 mm TL (N = 7) and greater than 400 mm TL (N = 18) without stomach contents, and average total diet items, stomach weight, and Shannon H Index of lake trout caught during the day and night in Lake Champlain in 2018 and 2019.

Sampling Period	% Stomachs Empty	Total Items	Stomach Weight	Shannon Index
<100 mm				
Day	0	1.8	0.008	0
Night	33.3	3.7	0.001	0.1
p-value	0.4	0.6	0.4	0.4
> 400 mm				
Day	71.4	0.3	0.283	0
Night	45.5	1.2	2.010	0.07
p-value	0.3	0.2	0.1	0.3

Figures

Figure 1. Percent abundance of prey items by number in lake trout between 100 mm and 400 mm TL caught during the day (N = 210) and night (N = 31) in Lake Champlain in 2018 and 2019. YOY fishes consisted of rainbow smelt, alewife, slimy sculpin, and yellow perch. Other fishes consisted of yellow perch, tessellated dater, and trout-perch.